ESCUELA TÉCNICA SUPERIOR DE INGENIEROS DE MONTES
UNIVERSIDAD POLITÉCNICA DE MADRID

AN INTEGRAL MODEL FOR NATURAL REGENERATION OF *Pinus pinea* L. IN THE NORTHERN PLATEAU (SPAIN)

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Contents

Resumen

La regeneración natural es un proceso ecológico clave que posibilita la persistencia de las especies vegetales y, por tanto, representa un elemento de gran relevancia para la gestión forestal sostenible. Sin embargo, la regeneración natural en rodales regulares de *Pinus pinea* L. de la Meseta Norte (España) no siempre se consigue de forma satisfactoria, a pesar de más de un siglo de gestión centrada en la producción de piñón. Como consecuencia, la regeneración natural es en la actualidad una cuestión de gran interés para los gestores, en un momento de racionalización de los recursos destinados a la gestión forestal. Mediante la presente tesis se pretende ofrecer respuestas en este sentido al gestor mediante el desarrollo de un modelo integral multietápico de regeneración para rodales del *P. pinea* de la Meseta Norte. A partir de este modelo se pueden derivar recomendaciones para una selvicultura basada en la regeneración natural bajo el clima actual y también considerando escenarios climáticos futuros. Además, la estructura del modelo permite la detección de los cuellos de botella que pudieran afectar al proceso. El modelo integral consta de cinco submodelos correspondientes a cada uno de los subprocesos que ligan las diferentes fases de la regeneración natural (producción de semillas, dispersión, germinación, predación y supervivencia del regenerado). Las salidas de los submodelos representan las probabilidades de transición entre estas fases en función de variables climáticas y de masa que, a su vez, recogen el efecto de los factores ecológicos que gobiernan el proceso de regeneración. A nivel de subproceso, los resultados de esta tesis deben interpretarse como sigue. La programación de las cortas del aclareo sucesivo uniforme que se viene aplicando en rodales altamente aclarados induce a una limitación por dispersión desde las primeras fases del periodo de regeneración. En lo relativo a la predación, la actividad de los predadores aparentemente sólo queda condicionada por las intensas sequías estivales y los eventos veceros, de donde se deduce que el verano es un periodo seguro para las semillas. Fuera de este periodo, la práctica totalidad de las semillas son consumidas. Dado que la diseminación en *P. pinea* se produce en verano (el periodo seguro para las semillas), la probabilidad de que una semilla no sea destruida depende de que la germinación tenga lugar con anterioridad a la reactivación de la actividad predadora. Sin embargo, las condiciones óptimas para la germinación no se dan de forma habitual, limitando la emergencia a unos pocos días durante el otoño. En suma, existe una ventana muy estrecha para

alcanzar la fase de plántula. Además, el submodelo de supervivencia del regenerado predice tasas de mortalidad de plántulas extremadamente altas y por tanto sólo algunos individuos de cohortes numerosas podrán instalarse definitivamente. Estas circunstancias, junto con el fuerte carácter vecero de *P. pinea*, controlado por factores climáticos, indican que la probabilidad final de establecimiento es baja. Partiendo de estas circunstancias, la gestión actual –bajas densidades como consecuencia de claras intensas y un esquema de regeneración estricto– condiciona la ocurrencia de un número suficiente de eventos favorables para la consecución de la regeneración natural durante el periodo de regeneración actual. Las simulaciones y optimización estocástica que se han llevado a cabo por medio del modelo integral confirman este extremo, sugiriendo que los tratamientos de regeneración deberían ejecutarse de forma más flexible y progresiva. Desde un punto de vista ecológico, estos resultados son informativos de una estrategia reproductiva que implica una estructura irregular de masa, en la línea de lo que podría deducirse del temperamento medianamente tolerante de la especie. Como observación final, las simulaciones estocásticas realizadas bajo un escenario de cambio climático muestran que la regeneración en la especie no se verá fuertemente afectada en el futuro. Este comportamiento resiliente refuerza el fundamental papel ecológico que juega *P. pinea* en áreas donde la severas condiciones ambientales impiden la persistencia de otras especies arbóreas.

Abstract

Natural regeneration is an ecological key-process that makes plant persistence possible and, consequently, it constitutes an essential element of sustainable forest management. In this respect, natural regeneration in even-aged stands of *Pinus pinea* L. located in the Spanish Northern Plateau has not always been successfully achieved despite over a century of pine nut-based management. As a result, natural regeneration has recently become a major concern for forest managers when we are living a moment of rationalization of investment in silviculture. The present dissertation is addressed to provide answers to forest managers on this topic through the development of an integral regeneration multistage model for *P. pinea* stands in the region. From this model, recommendations for natural regeneration-based silviculture can be derived under present and future climate scenarios. Also, the model structure makes it possible to detect the likely bottlenecks affecting the process. The integral model consists of five submodels corresponding to each of the subprocesses linking the stages involved in natural regeneration (seed production, seed dispersal, seed germination, seed predation and seedling survival). The outputs of the submodels represent the transitional probabilities between these stages as a function of climatic and stand variables, which in turn are representative of the ecological factors driving regeneration. At subprocess level, the findings of this dissertation should be interpreted as follows. The scheduling of the shelterwood system currently conducted over low density stands leads to situations of dispersal limitation since the initial stages of the regeneration period. Concerning predation, predator activity appears to be only limited by the occurrence of severe summer droughts and masting events, the summer resulting in a favourable period for seed survival. Out of this time interval, predators were found to almost totally deplete seed crops. Given that *P. pinea* dissemination occurs in summer (i.e. the safe period against predation), the likelihood of a seed to not be destroyed is conditional to germination occurrence prior to the intensification of predator activity. However, the optimal conditions for germination seldom take place, restraining emergence to few days during the fall. Thus, the window to reach the seedling stage is narrow. In addition, the seedling survival submodel predicts extremely high seedling mortality rates and therefore only some individuals from large cohorts will be able to persist. These facts, along with the strong climate-mediated masting habit exhibited by *P. pinea*, reveal that

the overall probability of establishment is low. Given this background, current management –low final stand densities resulting from intense thinning and strict felling schedules– conditions the occurrence of enough favourable events to achieve natural regeneration during the current rotation time. Stochastic simulation and optimisation computed through the integral model confirm this circumstance, suggesting that more flexible and progressive regeneration fellings should be conducted. From an ecological standpoint, these results inform a reproductive strategy leading to uneven-aged stand structures, in full accordance with the medium shade-tolerant behaviour of the species. As a final remark, stochastic simulations performed under a climate-change scenario show that regeneration in the species will not be strongly hampered in the future. This resilient behaviour highlights the fundamental ecological role played by *P. pinea* in demanding areas where other tree species fail to persist.

“Mais les destins se forment lentement et nul ne sait, parmi tous nos actes semés au hasard, lesquels germeront pour s’épanouir, comme des arbres”

Maurice Druon

Les rois maudits

Chapter 1

Introduction

1. Introduction

1.1. *Pinus pinea* ethnobotany

Pinus pinea L., the Mediterranean stone pine, is one of the most emblematic Mediterranean plant species. Its current distribution in the Mediterranean area comprises forests that, although sparse, are widely spread all over the northern shore of the Mediterranean basin, from Lebanon to Portugal. Easily recognizable at first glance for its distinctive umbrella-like crown, *P. pinea* is acknowledged as a structural element of the Mediterranean landscape. The species is remarkably plastic in the Mediterranean context, able to bear severe and persistent droughts, relatively extreme temperatures as well as poor and sandy soils. These features inform a valuable ecological role of *P. pinea*, which can occur in limiting sites, even where other tree species fail to persist. In this respect, *P. pinea* has been reported to provide shelter and food to wild and endangered fauna (SEO/BirdLife, 1999), to protect watershed and soil and to efficiently stabilize dunes (Montero *et al.*, 2008). However, it is the edible and highly nutritious seed born by its cones (pine nuts, pinyons, piñons, pignons) what renders *P. pinea* an inseparable companion of Mediterranean inhabitants from ancient times. Indeed, pine nuts from *P. pinea* have been exploited by human communities since the Palaeolithic era, as demonstrated by the findings from various archaeological sites (Carrión *et al.*, 2008).

Because *P. pinea* has been so intimately present in human ecohistory, it is difficult –not to say impossible– to precisely determine its original distribution area. Both accidental and intentional installation due to human transit and trade, taking place since Neolithic times 6,000 years BP (Earle, 2011), may have favoured the occurrence of the species in the northern Mediterranean. In addition, modern protective and productive plantations have extended the presence of *P. pinea* within the boundaries of the Mediterranean basin (up to 0.7 million hectares) but also beyond them as far as Chile, Argentina, South Africa or Australia (Mutke *et al.*, 2012) .

Nevertheless, there is overwhelming abundance of macrofossil and palynological records that confirm the presence of *P. pinea* as a native species or a protohistoric archeophyte throughout all the current Mediterranean distribution area during the Holocene (Feinbrun, 1959; Franco-Múgica *et al.*, 2005; García-Amorena *et al.*, 2007; Henri *et al.*, 2010, among many others) and even before and during the Last

Glacial Maximum (50,000–18,000 years BP; Bazile-Robert (1981); Carrión *et al.* (2008)). The recent finding of a practically null genetic variation between and within populations suggests that the species experienced a rigorous and prolonged demographic bottleneck before its quaternary expansion (Vendramin *et al.*, 2008). This fact gives rise to the hypothesis that the species already occupied southern European areas in the upper Tertiary, as confirmed by the studies by Menéndez-Amor (1951) and Klaus (1989) in the Iberian Peninsula and Austria, respectively.

A detailed review on *P. pinea* natural and cultural history can be found in Mutke *et al.* (2012).

1.2. *Pinus pinea* in the Northern Plateau of Spain

The Northern Plateau of Spain is located in north central Iberian Peninsula. It consists of an inland tableland of about 50,000 km^2 at a mean altitude of 700 m above sea level surrounded by mountain ranges. The latitude of the plateau determines its Mediterranean-dominant climate, mainly evidenced by the occurrence of severe, four-month summer droughts. In this context, its sheltered physiographic situation, which prevents the ocean humid influence, leads to low mean precipitation values (ranging from 300 to 500 mm), only higher in the Iberian Peninsula than those recorded in the semi-desert southeasternmost areas (AEMET-IM, 2011). In addition, its relatively high elevation conditions the winter period, colder than in most of the peninsular territory (AEMET-IM, 2011), with occasional minimum temperatures below – 10 ºC (Fig. 1.1).

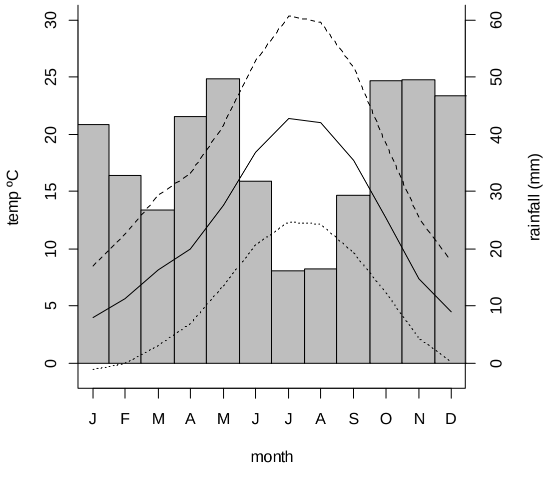


Figure 1.1. Climograph for the central area of the Northern Plateau. Data corresponds to seven climatic series from stations scattered over the study area. Dashed, solid and dotted lines represent maximum, mean and minimum temperatures, respectively. Bars stand for mean monthly total precipitation.

Northern Plateau's origin dates from the late Mesozoic and early Cenozoic, when the Alpine orogeny (65–100 Ma BP) produced the depression of the territories corresponding to central Iberian Peninsula nowadays. During the Miocene (23–5 Ma BP), the sediments of an inland lake gave rise to a calcareous plain, origin, in turn, of the Duero River basin. Later, during the Pleistocene (2,588–11.7 ka BP), Duero tributaries flowing northwards through the plateau from the Central Range deposited an important amount of eroded siliceous materials, which were ultimately spread by aeolian erosion. As a result of these processes, the areas located between the Duero River and the Central Range are presently dominated by two main units: limestone flat uplands and sandy plains. It is in these areas where one of the more extensive Iberian *P. pinea* woodlands currently lies (over 50,000 ha; Gordo *et al.* (2012)) and consequently named after as *Tierra de Pinares* (Pinewoods Land; Fig. 1.2).

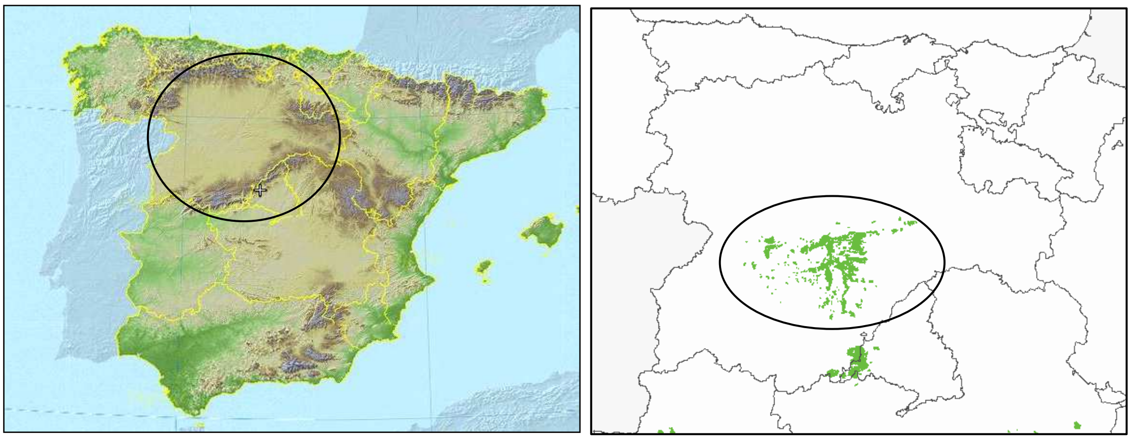


Figure 1.2. Location of the Northern Plateau in the Iberian context (left) and natural distribution of *Pinus pinea* in the Northern Plateau (right). Source: INIA

Although the occurrence of *P. pinea* in the Iberian Peninsula during the Pleistocene is widely accepted, there is not a general agreement on the naturalness of the species in the Northern Plateau, probably as a result of a divergence on the approaches to interpret the past landscape (see Navarro and Valle (1987) and Rivas-Martínez (2007) for a geographical and phytosociological approach, respectively). However, the persistence of the species both in the limestone and sandy environments of the region, at least throughout the Holocene, can no longer be ignored, as supported by the palynological analyses by Franco-Múgica *et al.* (2001; 2005). Moreover, the findings by Rubiales *et al.* (2011) and Hernández *et al.* (2011) based on macro-remains indubitably indicate the intense use of *P. pinea* resources by pre-Roman populations about 2500 years BP.

Natural occurrence of pure stands of *P. pinea* is unlikely in the Northern Plateau, except when very specific soil and climate conditions take place (Gordo *et al.*, 2012). Ideally, the species would grow intimately associated to *Pinus pinaster* Ait. when highly sandy soils are present and to *Quercus ilex*, *Quercus faginea*, *Juniperus thuriphera* and *Juniperus communis* on limestone uplands (Clément, 1993; Franco-Múgica *et al.*, 2001; Franco-Múgica *et al.*, 2005). This landscape must be what Roman invaders found in the area in the 2nd century BC. According to Apiano's chronicles (151 BC), pinewoods located southwards Duero River were not severely altered by Celtiberian Vaccaean indigenous tribes, in contrast to the total deforestation accomplished over the northern shore as a result of its superior quality as agricultural land and grassland (Hopfner, 1954). Human pressure on these forests during the Roman domination (2nd century BC to 5th century AC) and the Visigoth period (5th–7th century AC) was most probably neither drastic nor irreversible, given the persistence of dense woodlands used as a "convenient unpopulated border" (the so called "Duero desert") between Arabians and Christians until the 11th century (Clément, 1993). After the taking of Toledo by Christians in 1085, the first permanent settlements were established in the area and a period of increasing transformation of woodlands, normally communal, into agrarian exploitations took place. This deforestation process was augmented as a result of the privileges bestowed by the Castilian Crown to grazing activities after the 13th century. Contemporary to this change in land uses, the density of *P. pinea* within pinewoods notably decreased due to the uncontrolled timber extraction from this species, given its higher adequacy as lumber over the wood from *P. pinaster* (Gordo *et al.*, 2000). As a consequence of the higher power concentration on the Monarchy after the 15th century (and especially during the 18th century), different laws and rules were passed as an attempt to protect these forests and particularly *P. pinea* individuals, reaching different degrees of success (Guerra, 2001). However, the liberal thought arising by the half of the 19th century in Spain along with the complicated situation of the Public Treasure, led the State to confiscate, among many other goods, an important fraction of communal forests for immediate selling, which in many cases also implied immediate logging. Had not been for the new conservationist concerns that simultaneously appeared in opposition to the confiscation law of 1855, *P. pinea* forests would have been seriously endangered. Efforts were not spared by forest managers in order to survey all relevant forests throughout Spain and to select those to be excluded from selling. As a result, the Catalogue of Forests of Public Utility of 1866 indicated that about 65,000 ha of public forests with presence of *P. pinea* had been preserved in the Northern Plateau. Contrastingly, a more realistic value of 27,263 ha is found in the Catalogue of 1901, the difference being probably due to errors in the first inventories but also to illegal selling and logging during the period (Gordo, 1999). Despite the enormous task undertaken to conserve the integrity of these forests, the degree of conservation of *P. pinea* stands was poor. Grazing, which prevented recruitment, and abusive pruning and debarking, leading to high mortality of adult trees, promoted extremely low stand densities all over the region. Therefore, modern managers at the end of the 19th century faced a sad heritage of sparse, scattered and extremely clear pinewoods in the Northern Plateau (Gordo, 1999).

Although *P. pinea* played an important economic role linked to pine nut production and it was still retained as the main species in a number of stands, forest management was at the moment resin-oriented. This fact led to promote pure stands of *P. pinaster* from 1894 onwards over the region, favouring this species where present or through extensive afforestations (Gordo, 1999). As a proof of the higher interest of management in *P. pinaster*, resin-extraction strategies were rapidly developed whereas pine nut harvesting was only tentatively planned in the 1960s (i.e. Ximénez de Embún, 1959).

Only the resin crisis arising in the 1970s made it possible a recovery of *P. pinea* throughout the region. Nowadays, the species is more appreciated from an economic point of view than *P. pinaster,* providing very important benefits to local population mainly from pine nuts, but also from timber. *P. pinea* is also preferred when afforestation is required, since it would be better adapted to summer droughts (Gandía *et al.*, 2009). Consequently, there is a clear tendency towards a landscape of *P. pinea*-dominated forests throughout the *Tierra de Pinares*.

1.3. Regeneration of *Pinus pinea* in managed forests of the Northern Plateau

Despite over a century of management, natural regeneration of *P. pinea* is not always successful in the sandy flats of the Northern Plateau under the formerly and currently applied regeneration methods. In the first monographic work on *P. pinea* in the region, dating back to the 19th century (Romero, 1886), the transformation of the stand structure into even-aged stands was recommended. For this purposes, the shelterwood system was proposed. However, the very low stand density at rotation-length age suggested that seeding cuttings should be avoided, which results, in practice, in the seed-tree system. The same author also recognised that the poor state of conservation of the overstory may prove unsuitable for achieving natural regeneration and then clearcuttings followed by direct seeding could be an adequate alternative. This last option was considered in the first management plans but budget limitations soon led to the application of the seed-tree system. The seed-tree system produced good results concerning seedling occurrence although saplings were not always viable. According to the management plans carried out until the 1960s, the conservative criterion adopted when conducting the single removal cutting would be behind the aforementioned viability loss, as a result of an irradiation deficit on the saplings over 4–5 years old. Consequently, the system was modified and strip clearcuttings were applied, assisted by artificial regeneration (direct seeding). The positive results were observed already during the 1980s, when only very limiting sites conditioned by poorly qualified, highly sandy soils presented serious problems of regeneration.

Contrastingly, pure natural regeneration has become a major concern for forest managers nowadays and it is preferred within a context of rationalization and optimisation of silvicultural resources (Gordo *et al.*, 2012). Therefore, the shelterwood system is again the main regeneration method utilised, after 100–120-year rotations, complemented with seeding only when necessary (Fig. 1.3). The reader is referred to Gordo (1999), where further information on the evolution of management of *P. pinea* stands in the Northern Plateau over the last 150 years can be found.

Figure 1.3. Regeneration block in a *Pinus pinea* stand managed through the shelterwood system where complementary seeding was conducted

Silviculture in pine nut-oriented (even-aged) stands usually leads to final low stand densities (75–125 stems·ha^{-1}), attained at ages of 50–60 years. Thinnings are carried out less intensively when the stand is managed for timber production, with final densities of 200–250 stems·ha^{-1}, although this alternative is seldom considered. In both cases, once an age of 100–120 years is reached, the regeneration treatments commence and restrictions to cone harvesting are imposed. The regeneration period ranges from 20 to 25 years (Montero *et al.*, 2008). According to Gordo *et al.* (2012), the current felling scheme would consist of preparatory cuttings to be conducted during the first three to four years of the regeneration period to reduce the stand density up to 100–150 stems·ha^{-1}, when the stocking exceeded this value. Subsequently, harvesting through seeding cuttings is carried out until the half of the period, leading to densities of 50–60 stems·ha^{-1}. Providing natural regeneration is attained, removal cuttings are performed and only 25–30 stems·ha^{-1} are retained until the final felling, when about 6–10 stems·ha^{-1} are reserved for the next rotation. However, most stands reach the end of the rotation with densities lower than 100 stems·ha^{-1} and then the method actually applied is the seed-tree method (Gordo *et al.*, 2012): stand density is reduced in the very beginning of the regeneration period to 37 to 50 stems·ha^{-1} and afterwards only two harvesting operations are conducted (Montero *et al.*, 2008). The first of them is carried out around the 10th year (intensity 50% of the trees; remaining density 18 to 25 stems·ha^{-1}) and the second one corresponds to the final felling.

The inventories carried out in regeneration blocks in the province of Valladolid by the Regional Forest Service between 2001 and 2010 reveal that the aforementioned felling schedule has only partially achieved its purposes (Gordo *et al.*, 2012). Taking as a reference the Forest Service’s thresholds for successful regeneration of (i) sapling density of at least 200 seedlings·ha^{-1}; and (ii) regeneration covered fraction of at least 75%, only the 33% of the surveyed area could be considered adequately regenerated. Moreover, the percentage of zero counts between 2006 and 2010 was as high as 30%, probably indicative of a strongly clustered distribution of seedlings.

In the light of these data, it is clear that there exists a gap in the knowledge related to the regeneration ecology of *P. pinea*. To date, various factors have been noted as determinants of *P. pinea* natural regeneration failure but they have not been conveniently tested: (i) intense, long summer droughts and extreme maximum temperatures may negatively impact on seedling survival; (ii) masting habit, which constricts potential establishment to few cohorts, may additionally reduce the overall probability of recruitment if lacking a synchrony with regeneration fellings; (iii) cone harvesting operations during the rotation result in depauperate seed banks prior to the regeneration period; (iv) too long rotations could lead to tree vigour decline and therefore poor seed crops can be expected during the regeneration period; (v) the species' gravity-based seed dispersal would probably determine a clumped seedling distribution; and (vi) the influence of post-dispersal seed predation, which would be responsible of a non-negligible reduction of the amount of seed available for germination (Calama and Montero, 2007; Barbeito *et al.*, 2008; Manso *et al.*, 2010).

Furthermore, there is high uncertainty concerning the effect of climate change on Mediterranean ecosystems and it is specifically unknown how predictions from climate global models will impact on natural regeneration in the Mediterranean (Valladares *et al.*, 2005). Together with the current difficulties in this respect, future perspectives urge managers and scientists to unify efforts and aims to understand the underlying ecological processes involved, to quantify the influence on regeneration of different silviculture alternatives under varying climatic scenarios and to take the adequate decisions in consequence.

1.4. Reproductive ecology of *Pinus pinea*

A first step to take before analysing the aforementioned issues is to gather all the available information concerning *P. pinea* regeneration ecology. Presently, there are very scarce and partial studies on the topic, offering only a fragmented view of the overall process. In the subsequent paragraphs I shall summarize the state of knowledge of the different phases involved in natural regeneration in the species, including the aspects that need further research as well as the main hypotheses arising from the traits exhibited by *P. pinea*.

The first stage in all regenerative process is seed production. At present, it is well known that *P. pinea* is a masting species whose masting habit is climate-mediated (Mutke *et al.*, 2005a; Calama *et al.*, 2011). The occurrence of favourable climatic conditions during key-phenological stages of cone formation determines mast events. Over the three-year cycle of reproductive development of cones, (i) bud formation and bud differentiation are positively affected by spring and fall precipitation of the first year; (ii) extreme drought or frost occurring during the summer and winter, respectively, of the second year (cone setting) could lead to the destruction of the whole crop; and (iii) precipitation during the maturation year enhances cone growth and ripening.

P. pinea is referred as to a gravity-dispersed species (Montero *et al.*, 2008) but dispersal of pine nuts is often assumed to be also animal-mediated (e.g. Mutke *et al.*, 2012), even though it has been rarely described as so (but see Richardson *et al.* (1990)).

The first statement can be considered beyond any doubt, as it is a physical fact resulting from the morphology of the large and wingless seeds produced by *P. pinea*. Masetti and Mencussini (1991) found empirical evidence of this circumstance in their study in a *P. pinea* forest in Toscana (Italy), where only 3% of dispersed seeds dropt beyond crown influence. Moreover, the observed clustered distribution of seedlings beneath the crown of parent trees in sample plots in the study area has been attributed to this dispersal syndrome (Barbeito *et al.*, 2008). Nevertheless, the specific dispersal kernel still needs to be quantified to determine the optimal stand densities that prevent the occurrence of dispersal and seed limitation processes. Concerning the second issue, the same rationale may theoretically apply: large, highly nutritious seeds would represent an adaptation to benefit from frugivorous acting as mutualists (dispersers). Dispersers would harvest and then cache the seeds from large-seeded species relatively far from parent trees, but they would not ultimately retrieve all of them, leading to establishment of new seedlings (see Gómez (2003) and Gómez *et al.* (2008), for studies on genus *Quercus*; and Chambers *et al.* (1999), Johnson *et al.* (2003) and Vander Wall (2008), for research on genus *Pinus*). However, this theoretical framework does not rely on solid empirical work when referring to *P. pinea*. The extent at which animal-mediated dispersal plays a relevant role in *P. pinea* needs further research.

One aspect that cannot be neglected when studying regeneration is seed predation. Frugivorous can also behave as intense antagonists (predators), exploiting and depleting seed crops. Pre-dispersal seed predation has not been described as a serious thread for seed production in the species, although pests are present (e.g. *Pissodes validirostris*, *Dioryctria mendacella*) and damages due to squirrels are sometimes observed (Montero *et al.*, 2008). This fact could be linked to the development of massive scales in *P. pinea* cones, which has been described as a probable adaptation to prevent pre-dispersal foraging in similar large-seeded pine species of subsection *Sabinaniae* growing in the Mediterranean areas of North America (Johnson *et al.*, 2003). Contrastingly, the size and nutritional value of *P. pinea* seeds may not go unnoticed by post-dispersal seed predators. Regardless the stage at which seed exploitation takes place, a preeminent role of predators over dispersers would diminish the theoretical importance of the latter in the species' regeneration strategy. In this sense, several Mediterranean species have proved very sensitive to seed predation by rodents, specifically *Apodemus sylvaticus* L. (Hulme, 1997; Castro *et al.*, 1999;

Gómez *et al.*, 2003; Gómez *et al.*, 2008), becoming a major concern in respect to natural regeneration. As in seed dispersal, I am not aware of any previous study addressed to quantify the impact of predation in *P. pinea*. Therefore, the challenge remains to determine this impact and, specifically, to identify the species foraging on *P. pinea* seeds, the climatic factors driving the temporal pattern of seed predation, the possible distance dependence accounting for its spatial pattern or the functional response of predators.

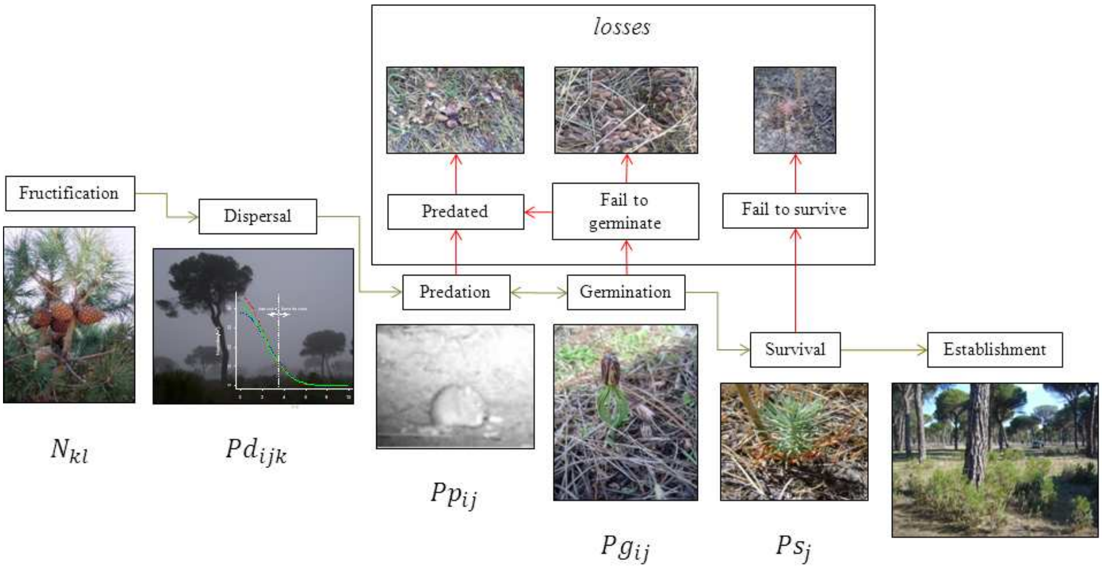
Concerning seed germination in *P. pinea*, the sole available reference appears to be that of Magini (1955). From this study, we roughly know the cardinal temperatures (base, ~10 ºC; ceiling, ~25–28 ºC; and optimal, ~17.5 ºC) for germination in the species and the influence of three different levels of substrate humidity. However, this information is of little interest for forest managers out of the scope of experimental nurseries. On the one hand the thermal ranges for germination need to be provided at daily or monthly basis, as this is the work scale in management. On the other hand, humidity conditions must be related to easily available variables. In addition, the effect of many other essential factors typically associated to germination remains unknown, such as the influence of frosts, light or microhabitat conditions.

Establishment and seedling survival is the last stage in the regeneration process. As in the other subprocesses, we currently lack much information on the importance of seedling mortality in *P. pinea*, its spatio-temporal incidence and the factors involved. An interesting remark in this matter is that *P. pinea* has been classically assumed to be a strongly shade-intolerant species (e.g. Montero *et al.*, 2008). However, the study by Awada *et al.* (2003) reveals that this species can tolerate some degree of shading. The relevance of these findings should not be overlooked, as they could motivate deep changes in the species' silviculture paradigm.

1.5. A model for natural regeneration of *Pinus pinea*

A powerful approach to study regeneration is the modelling of the process. In addition to shed new light on the ecological factors involved in natural regeneration, models provide predictions that can be used as a decision-making tool for forest managers, particularly if model formulation is silviculture-oriented through convenient variables and, additionally, it is flexible enough to make simulations of different social and environmental scenarios possible.

Regeneration modelling has been carried out from two different perspectives. Recruitment models represent the first and far more used approach, probably due to their simplicity: the response variable is the abundance and/or occurrence of recruits, which is directly modelled through environmental, climatic or silvicultural explanatory variables (e.g. Eerikäinen *et al.*, 2007; Fortin and DeBlois, 2007; Barbeito *et al.*, 2011). An alternative approach are multistage regeneration models (e.g.: Leak, 1968; Ferguson *et al.*, 1986; Pukkala and Kolström, 1992; Ordóñez *et al.*, 2006). In this case, regeneration is synthesized as a multistage process consisting of underlying consecutive subprocesses (i.e. seed production, dispersal, predation, germination and seedling survival) that usually can be identified as a series of successive survival thresholds for potential seedlings (Fig. 1.4). These thresholds are independently modelled as corresponding transition probabilities, whose product yields the probability of regeneration occurrence in space and time. Consequently, the response variable in multistage models does not aggregate all the information from the previous processes relevant for establishment. Rather, multistage models can actually be described as process-based models, presenting mechanistic basis at subprocess level.



$$S_{ij} = \left[S_{ij-1} + \sum_{k} \left(N_{kl} \cdot Pd_{ijk} + N_{ij-1} \right) \cdot Pg_{ij} \cdot \left(1 - Pp_{ij} \right) \right] \cdot Ps_j$$

Figure 1.4. Diagram of the regeneration process through all the considered stages. S_{ij} is the number of established recruits, N_{kl} represents seed production, whereas Pd_{ijk}, Pp_{ij}, Pg_{ij} and Ps_j stand for the dispersal, predation, germination and survival transition probabilities, respectively. *i*, *j*, *k* and *l* are the indices for the location, the time, the tree and the year

These characteristics, inherent to multistage models, are supportive for the development of this approach in the case of *P. pinea*, as the mechanisms involved in regeneration at subprocess level could require special attention. Specifically, multistage models can detect bottlenecks, defined as the collapse of the entire regeneration process due to one or several transition probabilities equalling or approaching zero. This phenomenon is expected in *P. pinea* given the highly limiting conditions present in its locations in the Northern Plateau.

Finally, the applicability of a multistage regeneration model to *P. pinea* real management strongly depends on the kind of explanatory variables used. Transition probabilities need to be modelled taking into account the ecological processes briefly described in section 1.4 but also through covariates that are easily modifiable and/or easily accessible to managers. These two latest features can be considered by means of a model formulation based on silvicultural-related variables and climatic variables. In turn, silvicultural-based and climatic-based models offer the valuable possibility of (i) computing predictions under different silviculture alternatives and climatic scenarios; and (ii) implementing optimisation routines that lead to optimal management schedules.

Throughout the present thesis these essential developments are assessed to meet the requirements of forest managers concerning natural regeneration in the Northern Plateau of Spain.

1.6. Study site

When developing a multistage model, independent data relative to each of the considered subprocesses are required. For these purposes, independent experiments specifically designed to study seed dispersal, seed germination, seed predation and seedling survival were set up. The study site was chosen, on the one hand, to be representative of the average conditions of the pinewoods of the Northern Plateau –the *Tierra de Pinares*– and, on the other hand, to comprise stands at the end the rotation. Hence, the trials were based in the *Corbejón y Quemados* public forest, located in the municipality of La Pedraja de Portillo, province of Valladolid. Additionally, the study site was extended to the *Común y Escobares* public forest, belonging to the municipality of Nava del Rey, also in Valladolid (Fig. 1.5). In the main site, six plots of 0.48 ha (60 m × 80 m) were installed, where the fellings of two different regeneration methods were in process (seed-tree system and shelterwood system; three replications each; Fig. 1.6).

Moreover, a control plot (no fellings) of similar dimensions was also deployed. In Nava del Rey, two similar plots were established, the shelterwood system being the regeneration method used (Fig. 1.7).

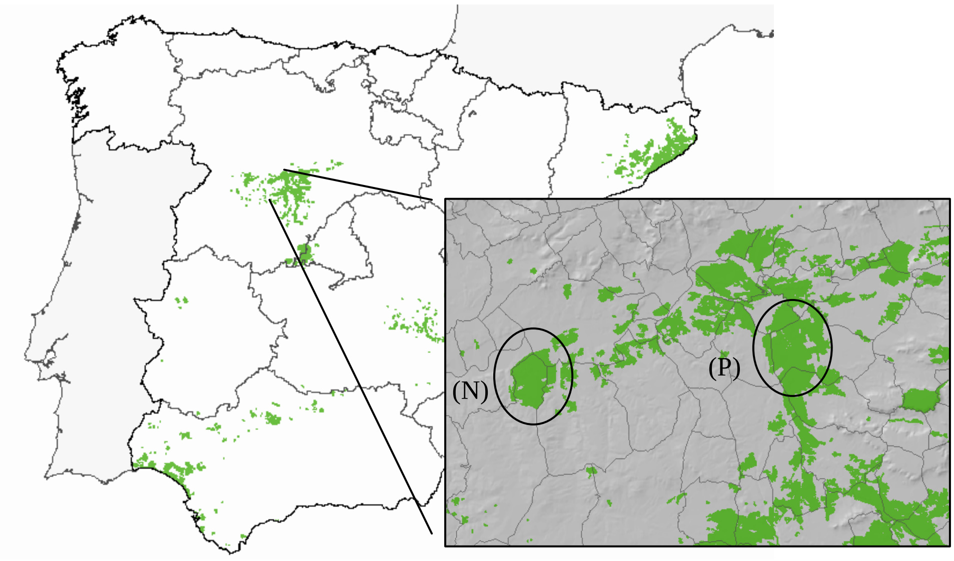


Figure 1.5. Location of the study area. (P) stands for the site in La Pedraja de Portillo, whereas (N) represents the site in Nava del Rey. Source: INIA

Figure 1.6. Sample plots of La Pedraja de Portillo site. The seed-tree felling system was applied in plots P1–P3. Shelterwood system corresponds to P4–P5. P7 stands for the control. Orthoimages source: Google Maps visor

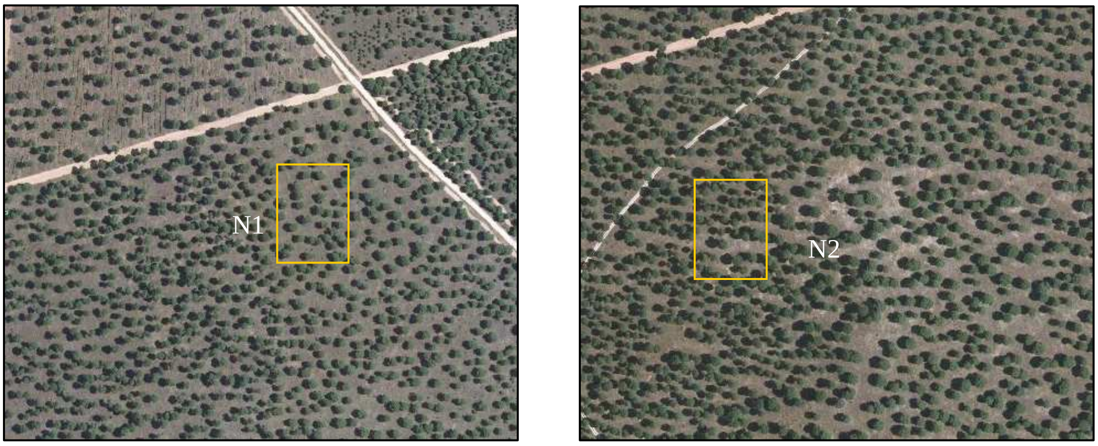


Figure 1.7. Sample plots of Nava del Rey site. Orthoimages source: Sigpac visor

1.7. Objectives and organization

The objective of this thesis is to develop and apply an integral multistage model for natural regeneration of *P. pinea* from where recommendations for natural regeneration-based silviculture can be derived under present and future climate scenarios. This main aim is attained by means of the following specific objectives:

1. Selecting variables to include in the different submodels that are easily-accessible or controllable by forest managers so that the final model can truly constitute a decision-making tool.

2. Modelling the spatio-temporal transition probability of seeds to be dispersed, considering the physical features governing seed release and dispersal.

3. Modelling the spatio-temporal transition probability of the dispersed seeds to germinate, through the ecological factors involved in the germination subprocess.

4. Modelling the spatio-temporal transition probability of non-germinated seeds to be predated, taking into account the ecological factors driving seed predation.

5. Modelling the temporal transition probability of seedlings to survive.

6. Identifying the potential bottlenecks that could affect natural regeneration at subprocess level, taking into consideration the silvicultural practices and the ecological processes involved.

7. Formulating the multistage model, from where (i) different silviculture alternatives can be evaluated under varying climatic scenarios; and (ii) the optimal schedule for regeneration fellings can be found out.

The present thesis is structured into seven chapters, preceded by a bilingual Abstract (Spanish and English). The current Introduction (Chapter 1) is followed by Chapter 2 (dealing with the specific objective 2), Chapter 3 (corresponding to specific objective 3), Chapter 4 (developing the specific objective 4), Chapter 5 (coping with the specific objective 5) and Chapter 6 (addressing the specific objective 7). Specific objectives 1 and 6 are common for Chapters 2 to 5. Each of these central chapters is self-consistent, including a brief introduction to the topic, a material and methods section and an exposition and discussion of the main results achieved. Given the inherent unifying essence of Chapter 6, which summarizes and, in turn, accomplishes the fundamental target of this study, contrasting the research with the available literature, the current dissertation does not include a general discussion. Finally, thesis Conclusions are listed in Chapter 7.

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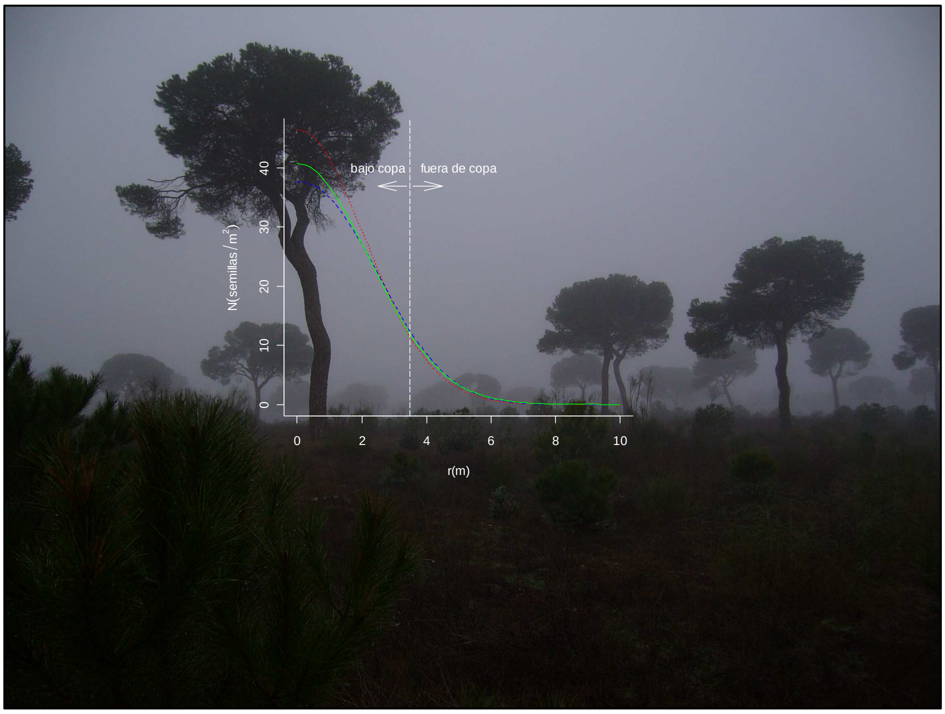
Chapter 2

Primary dispersal



Based on:

Manso, R., Pardos, M., Keyes, C.R. & Calama, R. (2012) Modelling the spatio-temporal pattern of primary dispersal in stone pine (*Pinus pinea* L.) stands in the Northern Plateau (Spain). *Ecological Modelling*, **226**, 11-21.

Specific objectives:

1. Selecting variables to include in the different submodels that are easily-accessible or controllable by forest managers so that the final model can truly constitute a decision-making tool

2. Modelling the spatio-temporal transition probability of seeds to be dispersed, considering the physical features governing seed release and dispersal

6. Identifying the potential bottlenecks that could affect natural regeneration at subprocess level, taking into consideration the silvicultural practices and the ecological processes involved

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Data:

- Seed trap data series (2005-2011) from plots P1 to P6 from the natural regeneration INIA site in La Pedraja de Portillo (Valladolid)

Methodology:

- Maximum likelihood estimation of parameters of established non-linear dispersal models

- Simple regression analysis including correction for temporal correlation

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Main findings:

- The resulting seed shadow is highly aggregated, the vast majority of the seeds being dispersed up to 2 crown radii

- Seed release starting is controlled by a thermal threshold, whereas release rate is related to the occurrence of rainfall events

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Management implications:

- Under currently-applied regeneration systems, dispersal limitation can be considered as a serious concern, and therefore the dispersal pattern of the species may result in a bottleneck for natural regeneration

- Higher densities are to be maintained until successful regeneration events occurs

2. Primary dispersal

2.1. Abstract

Natural regeneration in stone pine (*Pinus pinea* L.) managed forests in the Northern Plateau of Spain is not achieved successfully under current silviculture practices, constituting a main concern for forest managers. We modelled spatio-temporal features of primary dispersal to test whether (i) present low stand densities constrain natural regeneration success; and (ii) seed release is a climate-controlled process. The present study is based on data collected from a 6-years seed trap experiment considering different regeneration felling intensities. From a spatial perspective, we attempted alternate established kernels under different data distribution assumptions to fit a spatial model able to predict *P. pinea* seed rain. Due to *P. pinea* umbrella-like crown, models were adapted to account for crown effect through correction of distances between potential seed arrival locations and seed sources. In addition, individual tree fecundity was assessed independently from existing models, improving parameter estimation stability. Seed rain simulation enabled to calculate seed dispersal indexes for diverse silvicultural regeneration treatments. The selected spatial model of best fit (Weibull, Poisson assumption) predicted a highly clumped dispersal pattern that resulted in a proportion of gaps where no seed arrival is expected (dispersal limitation) between 0.25 and 0.30 for intermediate intensity regeneration fellings and over 0.50 for intense fellings. To describe the temporal pattern, the proportion of seeds released during monthly intervals was modelled as a function of climate variables –rainfall events– through a linear model that considered temporal autocorrelation, whereas cone opening took place over a temperature threshold. Our findings suggest the application of less intensive regeneration fellings, to be carried out after years of successful seedling establishment and, seasonally, subsequent to the main rainfall period (late fall). This schedule would avoid dispersal limitation and would allow for a complete seed release. These modifications in present silviculture practices would optimise seed arrival in managed stands.

Keywords: inverse modelling, fecundity, crown effect, seed limitation indexes, climate control, regeneration fellings

2.2. Introduction

Pinus pinea L. is an essential species of Mediterranean ecosystems that provides important economic benefits to local populations from its edible seed production and timber production. In addition, the species plays a valuable ecological role as its natural distribution occupies challenging sites that exhibit general Mediterranean weather conditions, continental winters and highly sandy soils, where few arboreal species persist. Such an environment can be often found throughout the Northern Plateau of Spain (Prada *et al.*, 1997), where there are more than 50,000 ha of indigenous *P. pinea* forests. These stands have been managed for over a century through modern silviculture techniques.

P. pinea natural regeneration in the species has become a primary concern for forest management. Like other Mediterranean species (e.g. species of genus *Quercus*), natural regeneration is commonly unsuccessful under currently-applied silvicultural methods, which lead to low densities to optimise cone production per tree. Regeneration fellings derived from these treatments (seed-tree system, and, increasingly, shelterwood system) produce even-aged non-coetaneous stands as they intend to imitate natural forest decay leading generally to these structures (Schütz, 2002). Several factors have been noted as determinants of this regeneration failure, including: climate, and specifically severe summer droughts and high summer temperatures that lead to establishment failure; masting habit and lack of synchrony with regeneration fellings and adequate years for seedling establishment; intensive cone harvesting, resulting in depauperate seed banks prior to regeneration fellings; long rotations, inducing poor seed crops during the regeneration period due to tree vigour decline; the species's gravity-based seed dispersal strategy, resulting in patchy seed distribution; and post-dispersal seed predation (Calama and Montero, 2007; Barbeito *et al.*, 2008; Manso *et al.*, 2010).

The study of primary seed dispersal spatial patterns has focused on understanding the general mechanisms that control fundamental population dynamics (Clark *et al.*, 1998; Clark *et al.*, 1999b; Nathan *et al.*, 2002; Levin *et al.*, 2003; Muller-Landau *et al.*, 2008; Martínez and González-Taboada, 2009), or their ecological consequences in local circumstances (Ordóñez *et al.*, 2006; Santos *et al.*, 2006; Debain *et al.*, 2007; Gómez-Aparicio *et al.*, 2007; Sagnard *et al.*, 2007). Similarly, most studies about cone opening processes have mainly aimed to test the relative importance of pyriscence and xeriscence strategies from an ecological perspective (Nathan *et al.*, 1999; Nathan *et al.*, 2000), evolutionary perspective (Tapias *et al.*, 2001) and structural perspective (Nathan and Ne'eman, 2004). With few exceptions (such as Tsakaldimi *et al.* (2004) or Ganatsas and Thanasis (2010)), little effort has been undertaken to apply the valuable information generated from ecological studies to inform practices of promoting natural regeneration.

The density of seeds deposited in a particular location within a stand is a function of stand stocking and the spatial arrangement of trees (source), and of seed production and the capacity for seed dispersal over long distances (Clark *et al.*, 1998). Provided that the latter is a serious constraint for colonization in *P. pinea*, due to the species' large wingless seed (Magini, 1955), a deeper knowledge of seed dispersal spatial traits can offer essential information with reference to the suitability of current densities in stands after seed fellings for natural regeneration. Low stockings promote a higher cone production per tree (Calama *et al.*, 2008b) but may result in a seed arrival limitation (dispersal limitation). On the other hand, dense stands largely favour an even distribution of seeds but may contribute to insufficient seed production (seed limitation). Optimal densities would lead to a compromise between both situations, with acceptable trade-offs in both seed production and seed dispersal. Because cone opening is related to physical variables (Dawson *et al.*, 1997), accurate predictions of seed release rates based on climate variables would allow for optimised temporal regeneration felling schedules.

In the present study, an established methodology to analyze the spatial pattern of seed dispersal was used. The methodology, introduced by Ribbens *et al.* (1994) to study the spatial distribution of seedlings from seed source locations, utilizes "inverse modelling" procedures in order to estimate the summed seed shadow from data collected in a seed trap experiment. Although broadly applied (Clark *et al.*, 1998; Clark *et al.*, 1999b; Uriarte *et al.*, 2005; Debain *et al.*, 2007; Sagnard *et al.*, 2007; Nanos *et al.*, 2010), the approach is not without controversy, especially with regard to the experimental design (Clark *et al.*, 1999a). Recently, comparisons carried out with seed dispersal kernels attained from genetic analysis demonstrated that trap location can dramatically bias parameter estimation (Robledo-Arnuncio and García, 2007). Furthermore, a more stable and reliable estimation is achieved if the fitting process is independent of the fecundity parameter. It has also been argued that other considerations, such as the bias introduced by immigrant seeds (i.e. from no mapped sources), should be taken into account (Jones and Muller-Landau, 2008). For *P. pinea*, however, the relatively short dispersal distance (Rodrigo *et al.*, 2007) and the availability of existing models to independently estimate seed production (Calama *et al.*, 2008b) severely reduce parameterization stability problems, and immigrant seeds occurrence can be safely considered negligible. In addition, potential bias derived from trap location can be minimized with a sensible trap deployment in order to obtain a larger representation of critical (and more relevant) dispersal distances.

Alternative kernels estimated by inverse modelling have been recently proposed based on different assumptions that deal better with species specific dispersal features. Mechanistic approaches (Greene and Johnson, 1989; Stoyan and Wagner, 2001; Wright *et al.*, 2008) were specifically developed to model wind dispersed species kernels. From a non-mechanistic perspective, different variants of the Weibull distribution have been assessed (Ribbens *et al.*, 1994; Clark *et al.*, 1998), while improvements on those methods were attained to manage its specific rigid behaviour (Clark *et al.*, 1999b; Bullock and Clarke, 2000). Eventually, other empirical approaches comprising genetics procedures have been developed to obtain more accurate predictions (González-Martínez *et al.*, 2006; Robledo-Arnuncio and García, 2007). For our study, we tested and compared the performance of alternative models, *sensu* Debain *et al.* (2007), selected according to *P. pinea* specific dispersal syndrome, as a useful protocol to achieve the best fit and, consequently, a correct interpretation of the phenomenon. Additionally, from simulations assessed through the model of best fit, we calculated and compared source abundance and dispersal limitation index values (Clark *et al.*, 1998; Muller-Landau *et al.*, 2002) under *P. pinea*'s two most common regeneration felling systems and a control stand (i.e. no prior fellings).

The main aims of the present work were to understand, model and predict the spatio-temporal patterns of the primary dispersal in *P. pinea* managed stands in the Northern Plateau of Spain. The purpose was to identify the likely bottlenecks occurring during the first step of the natural regeneration process. Our hypotheses were (i) that current stand densities at rotation age in managed *P. pinea* forests condition natural regeneration success; and (ii) there exists a climate control on the temporal pattern of primary dispersal, similar to the phenomenon driving cone production (Mutke *et al.*, 2005a; Calama *et al.*, 2011). Our findings will serve as an essential tool for forest managers attempting to achieve satisfactory natural regeneration of *P. pinea*.

2.3. Material and methods

2.3.1. Study site

The study site is located at 700 m above sea level in a representative *P. pinea* stand on the flat sandy soils of the Northern Plateau, Spain. The study was performed in a 120-year-old even-aged pure stand in the *Corbejón y Quemados* public forest (41º28’N, 4º43’W; municipality of La Pedraja de Portillo). Site location was selected and regeneration felling treatments designed to represent typical conditions in a mature managed forest, when restrictions on cone collection for commercial purposes are commonly imposed to allow for seed rain and regeneration. Regeneration fellings commenced during 2002–2003 following the highly intensive seed-tree method (ST) and the more progressive shelterwood method (SW). Both systems have been broadly applied as regeneration treatments for the species. Pre-felling and post-felling stand densities are shown in Table 2.1. Climate is continental-Mediterranean. Mean monthly temperatures range from 4.0 ºC in January to 21.7 ºC in July. Mean annual precipitation is 435 mm, with a period of summer drought (July–September mean precipitation of 66 mm). Site index is 15–16 m at 100 years, characteristic of a II class quality (Calama *et al.*, 2003). This index defines the quality of a stand as a function of its dominant height at a particular age. The considered dominant height criterion was the height of those trees whose diameter at breast height (1.3 m; *dbh*) was included amongst the 20% of the thickest trees of the stand (Weise, 1880).

Table 2.1. Summary of stand densities

Plot	Treatment	Nb/f [c](ha^{-1})	N[d] (ha^{-1})	BA[e] (m^2/ha^{-1})	Dg[f] (cm)	H[g] (m)	FCC[h] (%)
P1	ST[a]	144	46	8.17	47.6	13.6	19
P2	ST	115	48	9.37	49.9	15.5	22
P3	ST	156	46	6.99	44.1	12.6	14
P4	SW[b]	192	73	10.82	43.4	14.1	31
P5	SW	233	75	9.70	40.6	12.9	30
P6	SW	169	75	12.26	45.6	15.8	34
P7	Control	149	149	18.42	40.1	13.8	70

[a]ST-Seed tree method; [b]SW-Shelterwood method. [c]Nb/f-Density prior fellings. After fellings:[d]N-remaining density; [e]BA-basal area; [f]Dg-quadratic mean diameter; [g]H-average height; [h]FCC-Forest canopy cover

Our study is part of a broader project focused on the overall process of *P. pinea* natural regeneration in the Northern Plateau.

2.3.2. Experimental design

The primary dispersal trial was installed in 2005, to allow for a stand response to fellings in cone production. It consisted of six 60 m × 80 m (0.48 ha) sample plots that were established under different stand densities produced by regeneration fellings. Densities in plots P1–P3 were representative of the ST method, whereas those in plots P4–P6 were distinctive of the SW method. On the one hand, these treatments provided a convenient range of stand densities, essential for modelling purposes. On the other hand, they offer an excellent framework for further model simulation. A 7.5 m buffer area was included around each plot, increasing the overall plot surface up to 0.7 ha. An available control plot (P7; no fellings) of identical dimensions was used exclusively for simulation purposes. All trees within plots were stem-mapped and measured. Tree measurements included *dbh*, total height, and 4 perpendicular crown radii in cardinal directions.

In May 2005, a systematic grid (17.7 m × 17.7 m) of ten circular seed traps of 0.25 m^2 was established within each of the six plots (control excluded). Two traps in plot P1 were destroyed at the beginning of the experiment and were discarded from the analysis. The shortest distance from a trap to plot boundary was 12 m. The trap design was a bag made of textile fine mesh stapled on three wooden sticks at 1 m above the ground (to prevent rodent predation). Trapped seeds were collected on 60 occasions from trap deployment to January 2011 at intervals averaging 34.6 days (range from 19 to 70, standard error 1.26), with longest intervals corresponding to low intensity seed rain months or difficult access to plots (winter).

2.3.3. Modelling the spatial pattern

The inverse modelling approach

In order to determine the spatial pattern of dispersal, an approach based on non-mechanistic models involving inverse modelling procedures was attempted (*sensu* Ribbens *et al.*, 1994). With this type of model, the seed shadow is calculated as the product of two factors: the kernel and source fertility. The first factor, the kernel (k_{ij}), represents the probability that a seed is primary dispersed to location i, given a source j

and travelling, isotropically, a distance r_{ij} (m). The kernel includes parameters to be estimated that control the shape of the curve as a function of distance. The second factor is the fertility of the source. In our approach, the model developed by Calama *et al.* (2008b) is used to estimate average cone weight (wc_j) during the studied period (2005–2010) for each individual tree *j*. Rather than estimate a parameter to obtain the number of seeds from the response variable of the aforementioned model, we used the model developed by Morales (2009) to predict the number of seeds per kg of cones (*P*). *P* was calculated considering a constant fraction of cone weight attributable to seeds (0.259) and assuming an average seed weight of 0.615 g. Consequently, the value N_{ij} (seeds·m^{-2}) of the generic seed shadow for a single tree *j* at a location *i* is defined as:

$$N_{ij} = P \cdot wc_j \cdot k(r_{ij}) \qquad [2.1]$$

In the case of non-discrete sources (e.g. a stand), the number of seeds reaching a location *i* is computed as the sum of the expected number of seeds dispersed to this location from the *T* trees considered. In that case, the summed seed shadow can be expressed as:

$$N_i = P \cdot \sum_{j=1}^{T} wc_j \cdot k(r_{ij}) \qquad [2.2]$$

Note that definition of the summed seed shadow leads to individual tree kernel parameterization.

Source determination

For modelling purposes, we optimised the number of sources *T* to contribute to the summed seed shadow at a specific location. Therefore, we initially plotted the inverse cumulative rate of seed arrival to each trap along normalized distances (total distance between a trap *i* and a tree *j* (*dc*) / crown radius dimension (*db*)) to the nearest tree. Crown radii were calculated as the distance from the crown centroid *j* to dripline in the direction of the trap *i* (Fig. 2.1)). Such simplification

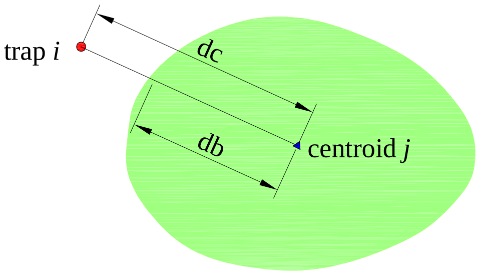

Figure 2.1. Crown radii definition. *db* is the crown radius of tree *j* and *dc* the distance between centroid *j* and trap *i*

indicates both the degree of clumping of data and the relative distance of traps no receiving seeds to the closest tree. The latter defines the maximum relative dispersal distance found from the data available (2 crown radii). Thus, the procedure to optimise the *T* contributor seed sources was to exclude from analysis trees located over a distance of 2 crown radii from traps. To do it, we calculated the empirical distribution of distances in crown radii from each trap to the stem of the nearest 1st to *T*th tree. Then, *T* was considered optimum when the distribution of distances between traps and the *T*th+1 nearest tree only included figures over 2 crown radii, resulting in *T* = 3 (Fig. 2.2).

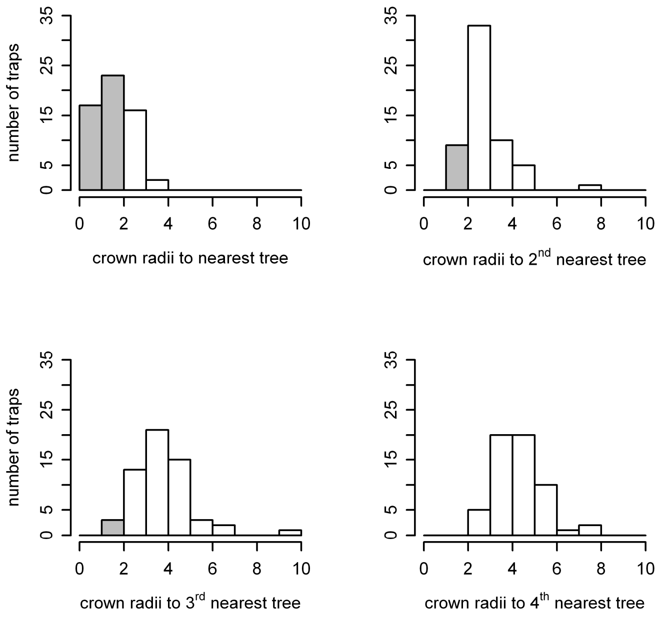

Figure 2.2. Histograms of frequency for relative distances from trap *i* to the closest 1st, 2nd, 3rd and 4th tree *j*. Distances below 2 crown radii are grey coloured for clarity. Note that the 4th nearest tree was always further than 2 crown radii. Mean crown radius was 3.5 m

Distance definition

In order to consider crown effect in the kernel value assignment, we computed standardized distances between traps and sources, normalizing the beneath-crown segment *db* to an average crown radius ($\overline{R}$), leaving the rest (beyond crown) unaltered. When a trap was located beneath a crown shadow, its distance to source was assessed as the corresponding proportion of $\overline{R}$. In turn, beneath-crown distances are slightly rescaled, whereas two points located at the same distance to dripline of equally productive trees of different crown sizes are considered to be reached by the same number of seeds. Corrected distance r'_{ij} (m) analytic definition is then:

$$\begin{array}{ll} (dc - db) + \overline{R} & \text{if the trap is beyond crown} \\ (dc / db) \cdot \overline{R} & \text{if the trap is beneath crown} \end{array} \qquad [2.3]$$

where *db* is the real crown radius length and *dc* is the distance between the centroid of tree *j* and the trap *i*.

Kernel formulation

In order to estimate the seed shadow that best fit the data, two kernels were tested: the Weibull (Clark *et al.*, 1998), and the 2Dt model (Clark *et al.*, 1999b). Parameter estimation was performed through the optimisation of the log-likelihood function for the assumed theoretical distribution of data, through a variant of the simulated annealing algorithm (Belisle, 1992).

The Weibull kernel can be re-formulated as:

$$k_{ij} = \frac{1}{n} \exp\left[-\left(\frac{r'_{ij}}{\alpha} \right)^{c} \right] \qquad [2.4]$$

where α is the dispersal parameter, c is the shape parameter and n is the normalizer:

$$n = \frac{2 \cdot \pi \cdot \alpha^{2} \cdot \Gamma(2/c)}{c}$$

with $\Gamma(\cdot)$, the gamma distribution

Shape parameter c is assessed together with α in the log-likelihood maximization. Nevertheless, whenever optimisation becomes unstable we assumed, like Clark *et al.* (1998), a Gaussian curve ($c = 2$).

On the other hand, the 2Dt kernel consists of a reformulation of the Weibull curve with $c = 2$, allowing α to vary along r_{ij}:

$$k_{ij} = \frac{u}{\pi \cdot p \cdot \left(1 + {r'^{2}_{ij}} \big/ {p} \right)^{(u+1)}} \qquad [2.5]$$

where u is the scale parameter and p is the shape parameter.

Likelihood functions

Parameters involved in both k_{ij} formulations were achieved through log-likelihood maximization, under two alternative hypotheses (Poisson and negative binomial) with respect to the stochastic process of seed arrival. In the case of the 2Dt model, only the Poisson hypothesis was used. Poisson and negative binomial log-likelihoods adapted by Ribbens *et al.* (1994) and Clark *et al.* (1998), respectively, are expressed as:

$$\log \ell = \sum_i \left(y_i \cdot \log N_i - N_i - \log y_i! \right) \tag{2.6}$$

$$\log \ell = \sum_i \left(\log \Gamma(y_i + \theta) - \log \Gamma(y_i + 1) - \log \Gamma(\theta) + y_i \cdot \log N_i + \theta \cdot \log \theta - (y_i - \theta) \cdot \log(N_i + \theta) \right) \tag{2.7}$$

where ℓ is the likelihood function to maximize, y_i is the observed number of seeds collected from the trap i, N_i is the expected number of seeds in trap i, θ is the clumping parameter and $\Gamma(\cdot)$ is the gamma distribution. Maximization of the log-likelihood functions was assessed using the data from all traps simultaneously.

Model evaluation

Comparisons between models were performed through the Akaike Information Criterion (AIC) to test model accuracy and select that one which best fitted the data. We also computed a regression between observed and expected seed density values, testing whether the intercept and slope differed significantly from 0 and 1, respectively (H_0: $a = 0$, $b = 1$), as a measure of the level of concordance between data and model. In addition, the coefficient of determination for this regression was calculated, as suggested by Clark *et al.* (1998).

Seed limitation

For the two proposed regeneration felling treatments and control, we tested whether changes in density (post-harvesting basal area) could lead to severe variations in seed availability (in regard to both abundance and occurrence). This was accomplished by computing the source limitation index, or *SL*, and the dispersal limitation index, or *DL* (Clark *et al.*, 1998; Muller-Landau *et al.*, 2002). *SL* is expressed as the proportion of sites where no seeds arrive assuming that the total amount of seeds is distributed uniformly:

$$SL = 1 - \Pr\left\{ \hat{N}_i > 0 \mid Poisson\left(\sum \hat{N}_i \big/ l \right) \right\} = e^{-\left(\sum \hat{N}_i / l \right)} \qquad [2.8]$$

with $\hat{N}_i$, the expected number of seeds reaching the location *i*, and *l* the number of locations taken into consideration. *DL* can be defined as the comparison between the proportion of sites actually reached by dispersed seeds and the proportion of locations where seeds would arrive if dispersal were uniform, where *a* is the number of points reached by at least one seed:

$$DL = 1 - \left\{ \frac{a/l}{1 - SL} \right\} \qquad [2.9]$$

Using the best model, we assessed a simulated seed rain at 1 m^2 scale throughout 2501 points (*l*) located in a regular grid in the central 41 m × 61 m rectangle of each plot. Regarding model consistence, distances between simulation points and trees must be modified similarly to equation [2.3]. These simulations allowed for *SL* and *DL* calculation throughout all plots, including the control.

2.3.4. Modelling the temporal pattern

In order to model seed dispersal from a temporal perspective, the total seed collected in traps during each data collection interval was graphically compared with that period’s mean climate variables, including mean temperature, maximum temperature, mean relative humidity and total precipitation. Based on this analysis, the most suitable variables were selected to control the process of cone opening. All climate data were achieved from a nearby meteorological station (coordinates 40º17′N, 4º40′W; data available in www.inforiego.org).

Concerning seed release, we constructed a response variable (*sr*) related to the total amount of collected seed that also considered the seasonally decreasing aerial seed bank over time, as the percentage of seeds released in a particular period with respect to the total amount of seeds remaining in the cone. The nature of the response variable (a percentage) renders it insensitive to extremely low cone crops, thus we only considered years of appreciable crops in the analysis (i.e. 2006–2007, 2007–2008, 2008–2009 and 2010–2011). Significant differences among yields were determined via the non-parametric Kruskal-Wallis test for non-normal data ($\alpha = 0.05$).

A graphical analysis was also undertaken to indentify prior relationships between climate variables and *sr* as a basis to model *sr* through a simple linear regression. In order to prevent unrealistic confidence intervals for the parameters, an auto-regressive error structure was applied within dispersal periods, due to the fact that the observations of the response variable are intrinsically autocorrelated from a temporal perspective. In addition, those cases where *sr* = 100 were not used in the regression as it is a constant throughout all terminal values of every dispersal period with no ecological meaning. Eventually, potential transformations in explanatory variables were carried out when necessary to linearize the relationship. Model evaluation was performed comparing the AIC of alternative models.

All statistical analyses and calculations in this study were performed in R 2.12.0 (R Core Team, 2009).

2.4. Results

2.4.1. Seed rain

During the dispersal periods from 2005 to 2010, 753 seeds were collected in the seed traps. The spatial distribution of trapped seeds was not uniform. Twenty-four traps (41%) were not reached by any seed during all periods. The Kruskal-Wallis test indicated significant differences among years in number of seeds collected (χ^2 = 48.6924, *p*-value < 0.0001). Dispersal was especially scarce (non-appreciable) during 2005–2006 (6 seeds) and 2009–2010 (7 seeds); higher yields occurred during 2008–2009 (29 seeds) and 2010–2011 (73 seeds). In contrast, 2006–2007 (237 seeds) and 2007–2008 (401 seeds) were strong masting years. Statistics per trap are summarized in Table 2.2.

Table 2.2. Main annual seed dispersal statistics per trap and seed rain density (seeds·ha^{-1})

Period	2005-2006	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011
mean	0.10	4.09	6.91	0.50	0.12	1.26
sd[a]	0.36	9.24	11.65	1.23	0.46	2.57
CI[b] (95%)	±0.09	±2.38	±3.00	±0.32	±0.12	±0.66
seeds·ha^{-1}	4,137.93	163,448.28	276,551.72	20,000.00	4,827.59	50,344.83

[a]*sd: standard deviation;* [b]*CI: Confident Intervals*

Cone opening took place during June and July all years, when seeds reaching traps increased considerably. Concerning the progressive seed release after opening, although a strong dispersal peak occurred at the beginning of each dispersal period, a relative maximum at advanced stages of the process arose as a common feature for all years holding appreciable yields (Fig. 2.3). Notably, in 2006 a large portion of the year's dispersed seeds fell during November. The same trend occurred in 2007, when a high percentage of the year's seedfall was collected during September. In 2008, the peak occurred in October, while in 2010 two late maxima were recorded in September and November. During the years of appreciable cone crop, those data collection intervals of lesser seed rain intensity showed a residual (non-null) dispersal rate, with only four lags where no trapped seeds were found.

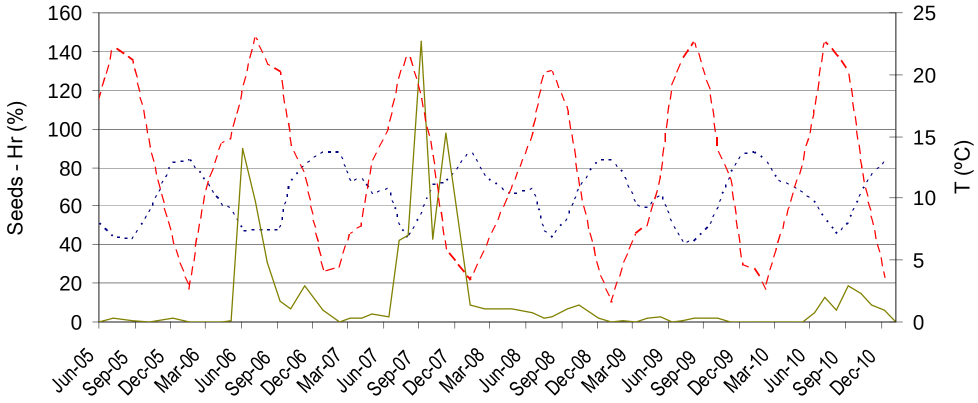

Figure 2.3. Number of seeds trapped (solid line), monthly mean relative humidity (Hr; dotted line) and monthly mean temperature (T; dashed line) during 2005-2010

2.4.2. Spatial pattern

The Weibull model considering a Poisson distribution of data (henceforth W.P) proved the most accurate, with the lowest AIC value, together with the 2Dt model (Table 2.3). The maximization of the negative binomial log-likelihood function for the Weibull curve (hereafter W.NB) presented high instability in parameter estimation even fixing *c*. The clumping parameter in the negative binomial had a trend to large values (θ>100), meaning lack of overdispersion in the data.

Table 2.3. Estimated parameters. In bold, the lowest AIC. for each model is also shown

	α	c	u	p	AIC[b]	$\log\ell$[c]	r^{2}[d]
W.P	3.308	2.065	-	-	**2358.300**	– 1,177.150	0.428
2Dt	-	2[a]	24.837	253.6	2358.758	– 1,117.379	0.424

[a]fixed parameter; [b]AIC:Akaike Information Criterium; [c]logℓ: loglikelihood; [d]r^2: coefficient of determination among observed and predicted values

Consistently, few differences in regard to prediction were found among all tested models. Even for the W.NB, which showed unstable parameter estimation, the range of attained parameters commonly tended to produce similar curves to those from the other proposed approaches. Basically, the models differed in seed dispersal estimation at short distances (beneath crown) with expected density at source ranging from 39.89 (2Dt) to 37.71 seeds·m^{-2} (W.P), as illustrated in Fig. 2.4 for an average tree with a 3.5 m crown radius. The probability that a seed is dispersed beyond crown varied from 0.312 (W.P) to 0.310 (2Dt). Beyond 3.5 m from the dripline (2 mean crown radii), the probability was less than 0.01 for all models, indicating a highly aggregated spatial pattern (Fig. 2.5).

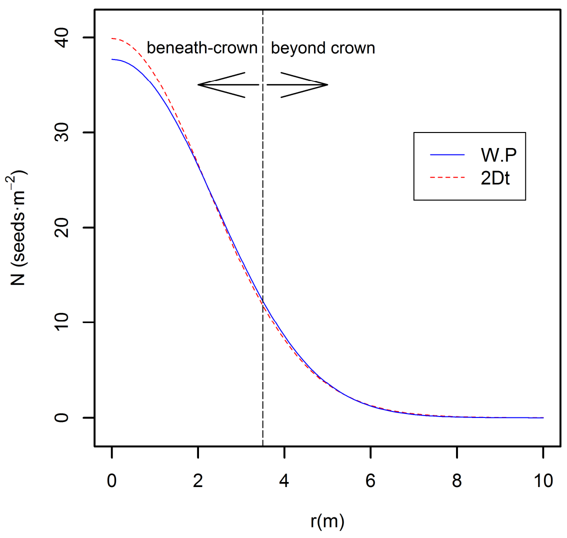

Figure 2.4. Comparison of seed density curves produced by the fitted models for an average tree with crown radius $\overline{R}$

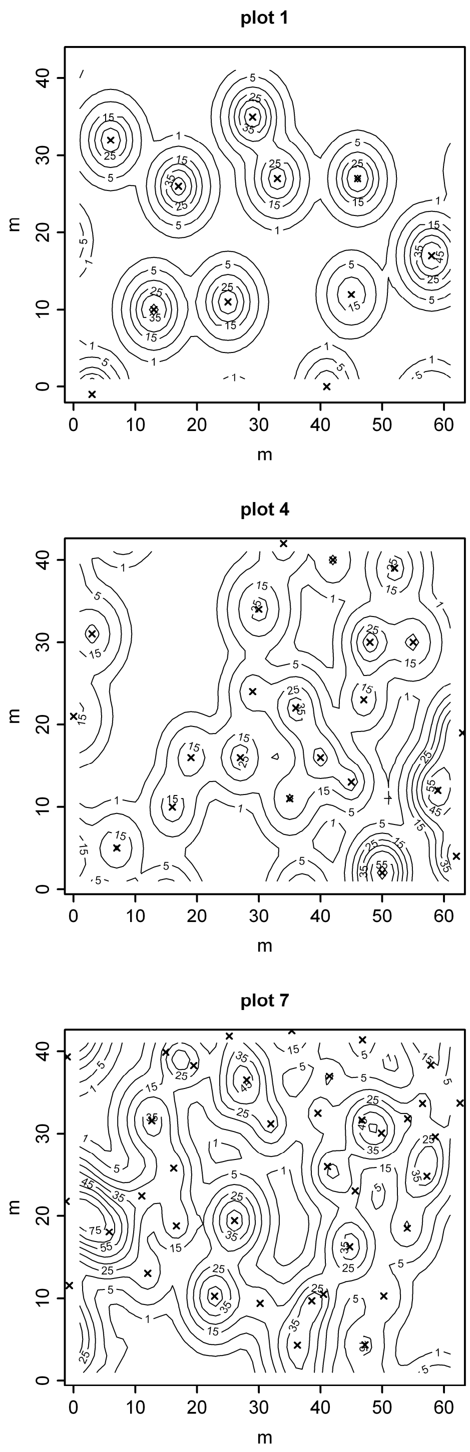

Figure 2.5. Examples of seed shadow maps for plot P1 (ST treatment), plot P4 (SW treatment) and plot P7 (control). Crosses correspond to stems locations. Lines represent levels of equal predicted seed density (value indicated by the figure within lines)

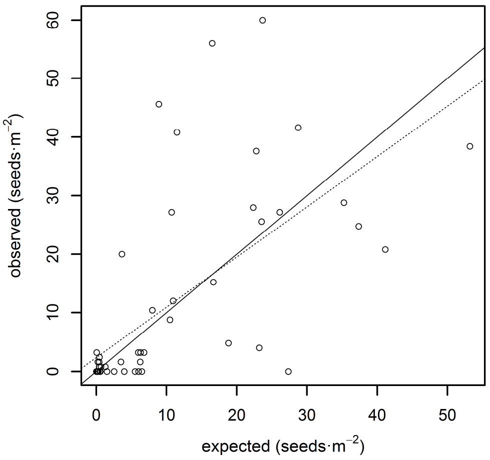

Figure 2.6. Observed *vs* expected seed shadow in traps *i*. Solid line indicates a theoretical perfect agreement between model and data (slope=1, intercept=0). Dotted line shows the real degree of accordance (slope=0.858; a=2.361)

A high level of agreement between model and data was found in the case of the W.P model. As shown in Fig. 2.6 and Table 2.3, there were no evidences for rejecting the null hypothesis of a linear relationship with slope = 1 (p-value > 0.05) and intercept = 0 (p-value = 0.24) among observed and expected values. Coefficients of determination between them in the W.P and 2Dt models were similar (Table 2.3), exhibiting relatively low values.

Simulations to calculate limitation indexes were performed with the W.P model (Fig. 2.4). Source limitation index (Fig. 2.7) indicated that limitation due to seed availability was negligible for all plots (SL<0.005), implying that under a uniform seed rain, most of the space would be reached. Dispersal limitation showed a tendency for lower values as basal area increased (Fig. 2.7). At low densities (basal area < 9 m^2·ha^{-1}; plots P3 and P1), *DL* was 0.58 and 0.49, respectively; *DL* was 0.32 (plot P5), 0.29 (plot P2), 0.28 (plot P4) and 0.25 (plot P6), where basal area was between 9 and 13 m^2·ha^{-1}. *DL* in plot P7 was 0.13 (basal area = 18.4 m^2·ha^{-1}).

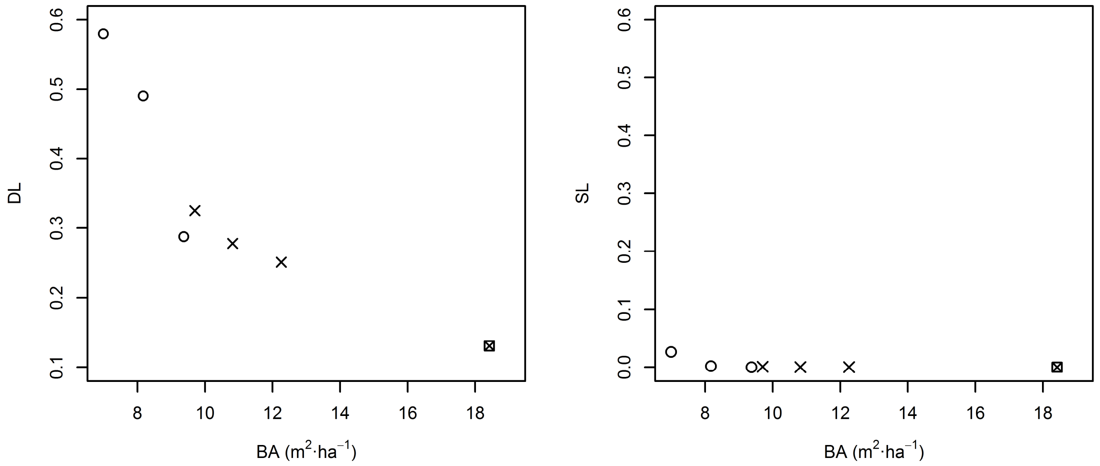

Figure 2.7. Source limitation (*SL*) and dispersal limitation (*DL*) indexes *vs BA* (m^2·ha^{-1}) for the seven plots. Circles indicate seed tree treatment; crosses, shelter wood treatment; and the squared symbol corresponds to the control

2.4.3. Temporal pattern

An exploratory analysis of different climate variables showed that cones opened when mean temperature of data collection intervals (mostly monthly) reached 16 ºC (Fig. 2.3). However, when considering the subsequent seed release, there was no apparent relationship of the number of harvested seeds to temperature variables or mean relative humidity.

On the contrary, when taking into account the percentage of seeds fallen during the collecting interval related to the overall amount of seeds to be released at the end of the dispersal period (*sr*), a synchronic pattern with total precipitation was found (Fig. 2.8; anomalous values in this trend were those corresponding to February and March of 2007).

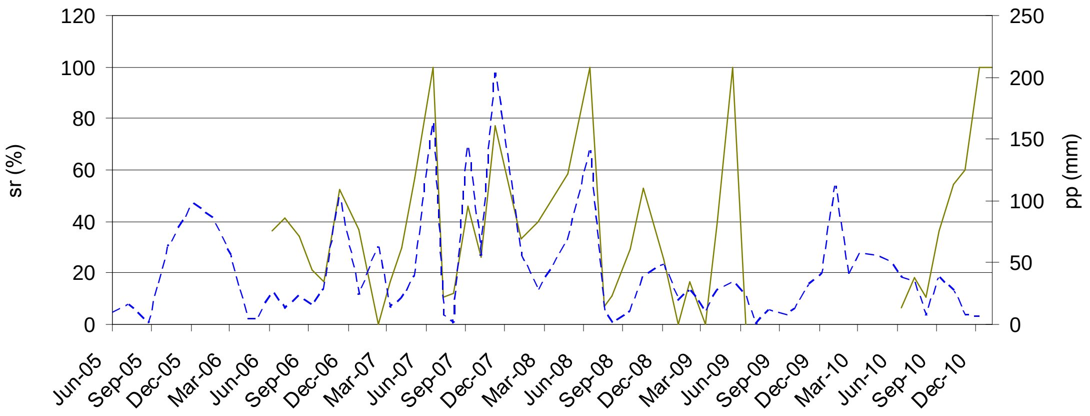

Figure 2.8. Variable *sr* (solid line) and total precipitation per dispersal period (pp; dashed line) in time. For clarity, we do not show *sr* data from 2005-2006 and 2009-2010 dispersal periods (negligible). Note that *sr*=100 corresponds to the last value of each dispersal period

The best fit at modelling *sr* was achieved using the cubic root of total precipitation ($pp^{1/3}$) during the collection interval as the explanatory variable (see Table 2.4, Fig. 2.9). A slight

Table 2.4. Summary of the estimated coefficients for the temporal model

	coefficient	standard error	t	*p*-value
Intercept	– 0.0989	9.2157	– 0.0107	0.9915
$pp^{1/3a}$	10.1624	2.7346	3.7162	0.0008
φ^{b}	0.3727	-	-	-

[a] $pp^{1/3}$: cubic root of precipitation. [b] φ: auto-regressive parameter of order 1

improvement in the AIC value was obtained when an autoregressive structure (AR-1) was applied within each dispersal period (ranging from 285.939 without structure to 284.538 with structure).

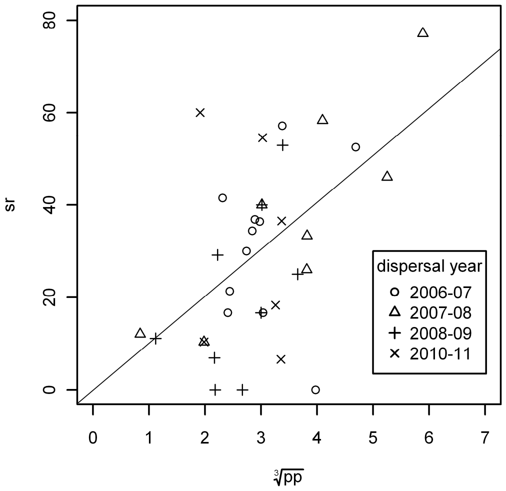

Figure 2.9. Regression model for the temporal pattern of seed release (solid line) between *sr* and the cubic root of total precipitation (*pp*). Data from the dispersal years used to fit the model are displayed separately

2.5. Discussion

2.5.1. The inverse modelling approach

We attempted to fit empirical models using inverse modelling procedures to describe and predict seed shadow and, by implication, the spatial pattern of primary seed dispersal and its consequences in natural regeneration of *P. pinea*. Our main concern was short dispersal distance, particularly, the scope of the crown. Therefore, we used two competing models (Weibull and 2Dt) that work properly at this scale. Even though the flexibility of the 2Dt kernel was developed to account for long distance events (Clark *et al.*, 1999b), those models have been reported to underestimate long dispersal distances (Debain *et al.*, 2007), in comparison with the mixture model proposed by Bullock and Clarke (2000). Similarly, mechanistic approaches were not taken into consideration, as they have been developed using physical variables specifically related to wind dispersal mechanisms (e.g. Greene and Johnson, 1989; Bullock and Clarke, 2000; Stoyan and Wagner, 2001; but see also Martínez and González-Taboada, 2009) or even to model secondary dispersal by animals (Greene *et al.*, 2004).

A serious constraint of inverse modelling is that plot size and spatial distribution of seed traps may lead to underestimation of mean dispersal distance when leptokurtic dispersal takes place (Robledo-Arnuncio and García, 2007). However, this problem does not severely apply to this study, as an extremely high kurtosis is not expected in *P. pinea*, provided the gravity primary dispersal strategy in the species. In addition, our regular grid maximizes the number of traps between one and 2 crown radii, where dropped seeds in traps commence to be uncommon (deficient sampling in those circumstances could result in an unreliable parameter estimation). An indirect consequence of this dispersal feature is that the arrival of immigrant seeds is expected to be a highly unlikely event in this case, considering also the spatial disposition of the grid in regard to the plot boundaries.

On the other hand, although genetic analysis deals with these difficulties, dispersal kernel estimation through parentage analysis requires the use of highly variable molecular markers, which provide an exact identification of all potential seed sources (Robledo-Arnuncio and García, 2007; Jones and Muller-Landau, 2008). This interesting and powerful technique is unfeasible to be applied in the case of *P. pinea*, due to the extremely low genetic diversity in the species (Vendramin *et al.*, 2008).

Depending on the nature of the data, several authors have proposed different theoretical distributions to fit the dispersal models. The obvious approach is the Poisson distribution, as the response variable is obtained from counts (Ribbens *et al.*, 1994; Sagnard *et al.*, 2007). However, Clark *et al.* (1998) first appreciated the unsuitability of the Poisson process when clumping of data was present, suggesting the use of the negative binomial distribution instead. This interesting finding and the subsequent proposal may deal with clumping, at cost of an extra parameter (θ), being, in practice, a generalization of the Poisson approach. Indeed, θ tends to be large when data accommodates a Poisson process.

The 2Dt model involves the Poisson assumption by definition. This very flexible Gaussian model deals reasonably well with a clumped data distribution, not being essential to construct complex likelihood functions (Clark *et al.*, 1999b). However, we attempted the negative binomial for the Weibull model. Parameter estimation became unstable and the clumping parameter frequently produced high figures (θ>100; in contrast to Clark *et al.*, 1998). Consequently, we used the Poisson likelihood as a particular case of the negative binomial to achieve accurate estimates. Difficulties in fitting and lack of stability are not uncommon for poorly primary dispersed species (zoochorous and barochorus dispersal syndromes) as reported by Clark *et al.* (1998) and Martínez and González-Taboada (2009).

Eventually, given the specific features of *P. pinea* spatial primary dispersal, all models showed a similar behaviour in terms of prediction (comparable r^2), with slight differences nearby the stem. In addition, the coefficient of determination was relatively low, as a result of increasing variance along with the value of the mean (Poisson assumption), especially at short distances (below crown).

2.5.2. Model improvements

In accordance with the findings of Rodrigo *et al.* (2007), through our preliminary analysis to estimate the maximum relative dispersal distance (crown radii), it was observed that seed traps located further than 2 crown radii from the nearest tree seldom received any seed, dropping 80% of seeds under the crown. This circumstance, due to the aforementioned gravity dispersal pattern and to the low stand densities, allowed us to assume a limited number of sources associated with each trap. Consequently, it was possible to improve computing efficiency to assess high resolution distances and, in turn, to supply more accurate inputs for model fit. In addition, our systematic trap design, deployed throughout a variety of stand densities, provided a high range of distances under this assumption, which constitutes a desirable circumstance (Clark *et al.*, 1998).

Commonly, inverse modelling procedures reduce seed sources to points. To our knowledge, there is no study where crown size has been taken into account in kernel parameterization, but Sagnard *et al.* (2007) in a different case study. Nevertheless, due to the umbrella-like shape of *P. pinea* crowns and cone occurrence throughout the upper fraction of the crown (Mutke *et al.*, 2005b), the whole crown must be considered as a seed source. Besides, as its size may strongly influence primary seed arrival (Barbeito *et al.*, 2008), it is of great interest to predict the proportion of seeds dropped beneath crowns. We propose a method that successfully accomplishes this objective. Providing that a summed seed shadow model impedes using relative distances (crown radii) between trees and traps, due to dimensional inconsistence, distances from trap to source are corrected, implying a double scale: beyond crown, distance to the dripline is known and unaltered, whereas beneath crown, relative distances are assessed in terms of crown radii (1 crown radius = 3.5 m, mean crown radius at our experimental plots). Beyond its application in *P. pinea* stands, the approach provides an interesting tool to accurately study primary dispersal in large-seeded species with broad crowns (e.g. genus *Quercus*), with modest changes to customize the model (mean crown radius).

One of the main drawbacks in classic seed shadow estimation using inverse modelling is that it requires source fecundity figures. Frequently, these values are difficult to achieve and are defined as the product of some known variable related to seed productivity. For example, *dbh* (Ribbens *et al.*, 1994; Clark *et al.*, 1998; Uriarte *et al.*, 2005) or number of cones (Sagnard *et al.*, 2007) plus a parameter to estimate number of seeds per *dbh* unit or cone. A different approach was proposed by Nanos *et al.* (2010), where fecundity was allowed to vary among trees without restrictions. The simultaneous estimation of fecundity and dispersal parameters may comprise high instability in the process (Clark *et al.*, 2004; Nanos *et al.*, 2010). In our approach, we reduced model complexity derived from this issue by estimating fecundity via the existing model developed by Calama *et al.* (2008b) and the dimensional corrections assessed by Morales (2009), which enable accurate prediction of seed production in *P. pinea* as a function of *dbh* and site index.

2.5.3. Spatial pattern of seed dispersal

The seed shadow estimated from the selected model (W.P) showed a highly aggregated spatial pattern of primary seed dispersal for *P. pinea*. Therefore, the presence of dropped seeds is bounded beneath crowns or in nearby areas (up to 2 crown radii for an average tree), in full accordance with the findings of Rodrigo *et al.* (2007). Simulations produced by the selected model allowed to attain source and dispersal limitation indexes. Comparisons of these indexes with the corresponding basal area values within each plot showed that source limitation was negligible for all plots considering the whole period, although due to the species' masting habit, limitation would occur frequently in no mast years (Calama *et al.*, Unpublished data). Nevertheless, the results supported our hypothesis that current management densities are inefficient in regard to dispersal limitation. For post-harvest basal area values under both regeneration fellings (especially the seed-tree method), the current seed shadows produced a notable percentage of gaps where dispersed seeds are not expected to arrive. These results are consistent with those from Dalling *et al.* (2002) when considering large seeded, non-zoochorus species with low densities within a stand. This issue could limit natural regeneration if stand density is reduced prior to seedling establishment, particularly when basal area is reduced below a critical value of 10 $m^2 \cdot ha^{-1}$ (seed-tree method). In that circumstance, the remaining trees are insufficient to successfully regenerate the stand, even if highly favourable dispersal events take place, and thus necessitating artificial regeneration (direct seeding). This scenario constitutes a common circumstance given current felling schedules, involving stand densities that range from 50 to 60 $stems \cdot ha^{-1}$ (or even less) during the first 10 years of the regeneration period (Montero *et al.*, 2008).

2.5.4. Temporal pattern of seed dispersal

From a temporal perspective, the results also support our hypothesis that climate controls cone opening and seed release in *P. pinea*. During our study, cones opened in response to a temperature threshold (16 ºC). Accordingly, Tapias *et al.* (2001), in a comparative study under controlled conditions, found that *P. pinea* cones opening took place at 28º C (the lowest temperature tested). On the other hand, the relationship between *sr* and total precipitation could be connected to passive physical processes involving scale tissues structure and changes in relative humidity (Dawson *et al.*, 1997). That would promote cone scales movements, alternatively opening and closing the cone, which would facilitate seed release. Contrastingly, Masetti and Mencuccini (1991) observed dispersal peaks for *P. pinea* during the driest month in two correlative years in Toscana (Italy), although that analysis was performed without taking into account the seasonally-declining of the canopy seed bank. In our case, such an effect was observed only during the dispersal peak that began in March 2007. A daily analysis of precipitation rates shows that most of the rainfall took place at the end of the previous interval (February) along correlative days. However, the dispersal peak was recorded next month (March, which was drier). This discrepancy might indicate that seed release can be controlled by alternate dry and humid events in climates characterized by a lower and more uneven precipitation than in Toscana, such as the Northern Plateau of Spain. Similarly, Nathan *et al.* (1999) claimed that *Pinus halepensis* seed release was strongly related to extremely dry and hot climate events. Although rainfall was not involved in the process, short changes in humidity with respect to prior daily values produced the release.

2.5.5. Management implications

Our findings suggest that under the current management of *P. pinea* stands in the Northern Plateau, primary dispersal could constitute a bottleneck for the species' natural regeneration, provided that secondary dispersal has not been documented in the area. Interestingly, Pardos *et al.* (2010) found out poor physiological performance of seedlings located beyond the crown influence, whereas Calama *et al.* (Unpublished data) observed higher mortality in seedlings located beyond 2 crown radii from trees. In addition, Awada *et al.* (2003) established that *P. pinea* response to late shade releasing did not condition further plant development. Therefore, the absence of long dispersal distance events could apparently beneficiate the species. The models developed in this study showed a highly clumped dispersal spatial pattern, where the occurrence of seed rain is intimately related to rainfall events. Seed limitation indexes obtained from selected model simulations suggest that natural regeneration failure is due to, at least in part, dispersal limitation. In addition, as seed release proved climate-controlled, current felling schedules following no ecological criteria can result in unsuitable stand density reduction before dispersal takes place. These spatial and temporal constrictions limit dispersal through space and time, and indicate that present silviculture practices in *P. pinea* stands can be modified in order to optimise seed arrival. A reduction in the intensity of regeneration fellings and their scheduling a few years after the occurrence of favourable recruitment events would reduce the probability of regeneration failure through a more evenly distributed dispersal. Because the control dispersal limitation index showed a negligible seed limitation with respect to basal area, the residual densities at the beginning of the regeneration period should exceed 16–18 $m^2 \cdot ha^{-1}$ of basal area. Regeneration fellings should be limited to post-dispersal periods, after the rainfalls that follow cone opening in this area (i.e. October–December) in order to guarantee the release of all the seeds. In conclusion, silvicultural recommendations based on the models developed in the present study would increase the available seed in the soil bank necessary for the next processes in natural regeneration.

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Chapter 3

Seed germination

Based on:

Manso, R., Fortin, M., Calama, R. & Pardos, M. (2012) Modelling seed germination in forest tree species through survival analysis. The *Pinus pinea* L. study case. *Forest Ecology and Management*, **in press**.

Specific objectives:

1. Selecting variables to include in the different submodels that are easily-accessible or controllable by forest managers so that the final model can truly constitute a decision-making tool

3.- Modelling the spatio-temporal transition probability of the dispersed seeds to germinate, through the ecological factors involved in the germination subprocess

6. Identifying the potential bottlenecks that could affect natural regeneration at subprocess level, taking into consideration the silvicultural practices and the ecological processes involved

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Data:

- Germination occurrence data series (2006-2010) from plots P3 and P4 from the natural regeneration INIA site in La Pedraja de Portillo (Valladolid)

Methodology:

- Proportional-hazards mixed model

Main findings:

- Seed germination is mainly a climate-mediated processes, strongly hampered by frost occurrence and temperatures out of a narrow optimal range

- The absence of overstory negatively affects germination. Also, a time-lag in the response was detected

- Proportional-hazards models with no assumptions in the definition of the baseline represent an interesting tool for modelling seed germination in forest tree species

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Management implications:

- Germination may constitute a bottleneck for regeneration, given the high incertitude of the process as a consequence of the narrow window of adequate conditions

- The strict scheduling of current regeneration systems neglect this aspect and, consequently, more flexible felling schemes should be applied

3. Seed germination

3.1. Abstract

The direct application of existing models for seed germination may often be inadequate in the context of ecology and forestry germination experiments. This is because basic model assumptions are violated and variables available to forest managers are rarely used. In this paper, we present a method which addresses the aforementioned shortcomings. The approach is illustrated through the case study of *Pinus pinea* L. Our findings will also shed light on the role of germination in the general failure of natural regeneration in managed forests of this species. The presented technique consists of a regression mixed model based on survival analysis. Climate and stand covariates were tested. Data for fitting the model were gathered from a 5-year germination experiment in a mature, managed *P. pinea* stand in the Northern Plateau of Spain in which two different stand densities can be found. The model predictions proved to be unbiased and highly accurate when compared with the training data. Germination in *P. pinea* was controlled through thermal variables at stand level. At microsite level, low densities negatively affected the probability of germination. A time-lag in the response was also detected. Overall, the proposed technique provides a reliable alternative to germination modelling in ecology/forestry studies by using accessible/suitable variables. The *P. pinea* case study highlights the importance of producing unbiased predictions. In this species, the occurrence and timing of germination suggest a very different regeneration strategy from that understood by forest managers until now, which may explain the high failure rate of natural regeneration in managed stands. In addition, these findings provide valuable information for the management of *P. pinea* under climate-change conditions.

Keywords: Survival analysis, hazard function, random effects, natural regeneration, climate change, dormancy

3.2. Introduction

Natural regeneration is a key process in plant population dynamics consisting of several well-defined stages such as dispersal, predation, germination and establishment (Gómez-Aparicio, 2008). Germination occurrence and germination timing play an essential role in subsequent seedling emergence (Baskin and Baskin, 2001) and therefore, in the overall success of natural regeneration. Hence, the development of tools to predict germination events will lead to an improvement in our understanding of regeneration dynamics, which is a major issue in sensitive ecosystems affected by global change or where natural disturbances have been substituted by management (Dullinger *et al.*, 2004; Castro *et al.*, 2005; Brudvig and Asbjiornsen, 2009).

Germination modelling has been developed extensively within an agronomic framework, mainly through the hydrothermal model (Gummerson, 1986; Bradford, 1990), which is a nonlinear regression approach based on the cumulative effect of water potential and temperature on the cumulative germination rate. However, these methods have been reported to be limited when the true germination time is unknown (Onofri *et al.*, 2010). This is the case in experiments that are revisited at specific intervals (Rees and Long, 1993) or where seeds do not germinate before the end of the experiment (Scott and Jones, 1990). Therefore, rather than the exact moment of germination, the observation data situates the time of germination either within a given interval (interval censoring) or at an undetermined moment after the last measurement (right censoring). Not considering the data as censored in these cases (e.g. hydrothermal model) leads to misspecifications of the likelihood function, which results in biased parameter estimates (Onofri *et al.*, 2010).

Another constraint of the hydrothermal model in studies concerned with predicting germination under natural conditions is the type of covariate used. In practice, water potential is difficult to obtain, hence it is not feasible to make predictions based on this data type at stand, forest or regional scale. However, there are a number of other variables closely associated with water availability which are more readily available and which can be used instead. Soil water content, in particular, can be expressed as a function of time since the last significant rainfall (Roman *et al.*, 2000), depending on the water-holding capacity of the soil. The relative humidity of the air influences water loss through evapotranspiration (Müller, 2000). Additionally, when attempting to identify the thermal requirements for germination under natural conditions, frost occurrence should be taken into account together with temperature. Although low temperatures can induce changes in a hypothetical dormancy state (Baskin and Baskin, 2001), little is known about the effect of frosts on the instantaneous capacity to germinate. In addition, stand structure and density can modify the general climatic conditions at microsite scale (Keyes *et al.*, 2009) as well as limit the possible influence of light as a germination enhancing factor (Seiwa *et al.*, 2009). However, stand-related variables are commonly overlooked in existing germination models.

Germination modelling based on survival time analyses was suggested as an option to cope with censoring in the 1980s (Scott *et al.*, 1984; Pyke and Thompson, 1986). The first applications arose about 10 years afterwards. Rees and Long (1993) developed a likelihood function for interval censoring in order to analyse cohorts of emerged plants at year level. Right censoring was, however, the main concern where data were collected at short enough intervals that made interval censoring negligible (Fox *et al.*, 1995; Evans *et al.*, 1996). Although there are some other subsequent examples of this approach for germination, new improvements have only recently been developed, for instance, to include corrections for seeds that acquire dormancy (Onofri *et al.*, 2011). However, all these models relied on the assumption that time to germination follows a specific distribution, which leads to a time-dependent underlying process for germination (also referred as to “baseline”). Additionally, as these experiments were not designed within a forestry framework, the correspondent models usually neglect to test stand and/or other easily measurable variables, just as in the case of the hydrothermal approach.

Two main families of regression models which include survival time analysis have been commonly used: Accelerated Failure Time (AFT) models and proportional hazard (PH) models (Lawless, 2003). These two types differ in the way that the covariates enter the model. Whereas in AFT models the covariates modify the survival response by altering the time scale, PH models include a fixed survival response (or “baseline”) as a function of time, which is affected by a function of covariates. In the present study, a PH model is developed in order to achieve a clearer understanding and more precise prediction of seed germination in forest tree species under natural conditions.

In order to illustrate (i) the way in which this methodology can be used avoiding strong assumptions on the distribution of time to event and (ii) to test the applicability of more accessible variables than those normally utilised, we present a case study of *Pinus pinea* L. in the Northern Plateau of Spain. *P. pinea* is an essential species in Mediterranean ecosystems, often occupying sites where few tree species are able to thrive due to the typical Mediterranean weather conditions, continental winters and sandy soils. In addition, the species provides important economic benefits to local populations from its timber and edible seed production. There are over 50,000 ha of managed *P. pinea* forest on the Northern Plateau. Natural regeneration in these forests is rarely successful using the existing regeneration methods and this situation may worsen under future climate scenarios in Spain according to predictions (De Castro *et al.*, 2005). Although several studies have been conducted to detect possible bottlenecks in the different stages of natural regeneration in *P. pinea* (cone production (Mutke *et al.*, 2005a; Calama *et al.*, 2008b; Calama *et al.*, 2011); seed dispersal (Manso *et al.*, 2012d); or seed predation (Manso *et al.*, 2012b), little attention has been paid to the importance of germination in the widespread failure of natural regeneration in this species.

The main aims of this study were (i) to test the performance of a proportional-hazards model applied to seed germination when no assumptions are made on the distribution of the time to event and when non-standard variables are included; and (ii) to quantify the influence of climatic and stand variables on germination in *P. pinea* in the Northern Plateau of Spain. Our key hypothesis is that germination is a climate-mediated process that can be modified by stand conditions.

3.3. Material and methods

3.3.1. Study area

The study area is located in the *Corbejón y Quemados* public forest (41º28’N, 4º43’W; municipality of La Pedraja de Portillo) at an altitude of 700 m above sea level. The terrain is flat with sandy soils, typical of the Northern Plateau. The climate is continental-Mediterranean with average monthly temperatures ranging from 4.0 ºC in January to 21.7 ºC in July. The mean annual precipitation is 435 mm, with a period of summer drought. The site index is 15–16 m at 100 years, typical II class quality (Calama *et al.*, 2003).

The experiment was conducted in a 120-year old even-aged *P. pinea* stand. In 2002–2003, regeneration fellings commenced. In order to reproduce the typical conditions found in mature managed *P. pinea* forests when the regeneration period has started, two different regeneration treatments were applied (the seed-tree method (ST) and the shelterwood method (SW)), the fellings in each case resulting in different final stand densities (Table 3.1).

Table 3.1. Summary of stand densities

Plot	Treatment	Nb/f[c] (ha^{-1})	N[d] (ha^{-1})	BA[e] ($m^2 \cdot ha^{-1}$)	Dg[f] (cm)	H[g] (m)	FCC[h] (%)
P3	ST[a]	156	46	6.99	44.1	12.6	14
P4	SW[b]	192	73	10.82	43.4	14.1	31

[a]ST-Seed tree method; [b]SW-Shelterwood method. [c]Nb/f-Density prior to fellings. After fellings: [d]N-remaining density; [e]BA-basal area; [f]Dg-quadratic mean diameter; [g]H-average height; [h]FCC-forest canopy cover

3.3.2. Experimental design

The germination trial began in 2006. The experimental design consisted of two 60 m × 80 m (0.48 ha) sample plots that were set up within each regeneration treatment. A 7.5-m buffer area was included around each plot, increasing the overall plot surface to 0.7 ha. All trees within the plots and buffer area were mapped and diameter at breast height (1.3 m; *dbh*) was measured.

In July 2006, 18 seed points were established in each plot. These seed points were distributed so as to include a wide range of light conditions. To minimize rodent predation, the seed points were protected with a 40 cm × 40 cm × 15 cm frame of hard wire mesh (span 0.7 cm × 0.7 cm), which was staked to the ground. The top of the frame could be opened to allow seed manipulation.

On 1 August each year between 2006 and 2010, 50 seeds were placed in each cage. This date was chosen since maximum dispersal rates usually occur at this time. Seeds were obtained from selected stands in the proximity of the study area and tested using the ISTA protocol (viability over 95%). No stratification treatment was applied. The seed points were revisited on a regular basis (average period 18 ± 1 days) either until the next sowing period or until all the seeds had germinated. The number of germinated seeds was recorded at each visit and these were then removed from the cage. Seeds were considered to have germinated when the radicle length exceeded 0.2 cm beyond the nutshell.

In addition to germination measurements, daily climatic variables, such as the mean, maximum and minimum temperatures, mean relative humidity (ratio of the partial pressure of water vapour in the air to the saturated vapour pressure of water), daily precipitation, days with precipitation and days with frost were gathered from a nearby meteorological station (41º17'N, 4º40'W; data available in www.inforiego.org). To estimate light availability at each seed point, Global Site Factor (*GSF*) was calculated from hemispheric photographs taken at each cage. *GSF* is the proportion of global solar radiation (direct plus diffuse) under a plant canopy relative to that in the open. The resulting index was corrected for the angle of incidence relative to a flat intercepting surface. The water-holding capacity of the surface layer of the soil was obtained for each point through texture analysis of two soil samples taken near to each seed point, following the method by Gandullo (1985). Each sample comprised the top 20 cm of the soil profile (soil cylinder of 1.57 dm^3).

Finally, in order to take into account the possible influence of trees on microclimate conditions at ground level, we calculated the influence potential (*IPOT*) of all trees located within a 15 m radius of each seed point. None of the seed points were located at distance below 15 m from the outside margin of the buffered area. *IPOT* is a competition index based on the concept of ecological field theory (Wu *et al.*, 1985) and empirically modified by Kuuluvainen and Pukkala (1989) and Barbeito *et al.* (2011):

$$IPOT_j = 1 - GPOT_j$$

where $GPOT_j = \prod_{h=1}^{n_j} \left(1 - I_{hj}\right)$ and $I_{hj} = I_{hj}(0) \times \exp(-b \cdot d_{hj})$

I_{hj} is the potential influence of tree h at seed point j, d_{hj} is the distance from tree h to seed point j, $I_{hj}(0)$ is dbh_{hj}/(max dbh_h at each plot), dbh_{hj} is the diameter at breast height of tree h in the influence area of seed point j, b is a parameter, and n_j is the number of trees in the influence area of seed point j. A value of 0.25 was heuristically assigned for b. *IPOT* ranges from zero (no competition) to one (maximum competition).

The range of all variables, along with observed seasonal cumulative germination rates are shown in Table 3.2.

3.3.3. Survival analysis

Germination modelling was approached through survival analysis. To illustrate the basis of this technique, let T be defined as a random variable that corresponds to the time until germination for a particular seed. The cumulative density probability of T at time t is actually the probability that germination occurred at or before time t, i.e. $F(t) = P(T \leq t)$. The survival function $S(t)$ is the probability that a particular seed remains latent after time t, i.e. $S(t) = 1 - F(t)$. The hazard function $h(t)$ represents the instantaneous germination rate, or hazard for a given seed at time t, providing it is still latent at time t. This hazard function is related to the survival function as follows:

$$S(t) = \exp\left(-\int_0^t h(x)\, dx\right) \tag*{[3.1]}$$

The survival function (equation [3.1]) implies that the probability of a seed remaining latent at time t is a decreasing function of the sum of all hazards prior to time t.

Table 3.2. Summary of variables of interest and observed values for seasonal cumulative germination for the 5 years of study

	mean	max	min	stand. error
spatial covariates				
WHC[a] (mm/cm depth of soil)	104.2267	141.7141	84.0367	2.2125
GSF[b]	0.6654	0.8629	0.4163	0.0169
IPOT[c]	0.4031	0.7174	0.1492	0.0272
time-varying covariates				
mean temperature (°C)	11.43	28.03	– 5.19	0.15
maximum temperature (°C)	18.36	38.5	– 1.71	0.19
minimum temperature (°C)	4.41	19.59	– 12.02	0.13
relative humidity (%)	67.14	100	17.83	0.37
freezing days year^{-1}	90.4	114	74	8.18
rainfall days year^{-1}	128.6	161	90	12.20
cumulative germination (%)				
	Fall	Winter	Spring	
2006-2007	89.74	90.92	-	
2007-2008	9.63	22.81	43.35	
2008-2009	4.31	7.04	8.3	
2009-2010	55.04	63.82	79.61	
2010-2011	60.94	65.12	71.13	

[a]WHC-water holding capacity; [b]GSF-Global Site Factor; [c]IPOT-overstory influence potential

3.3.4. Hazard function definition

The hazard function includes time-varying and time-independent explanatory variables as well as a number of unknown parameters. Covariates tested in this study were of three types: (i) thermal variables (days elapsed from the last frost event (*fr*) and, alternately, daily mean, maximum and minimum temperature (*temp*) in ºC); (ii) water availability-related variables (water-holding capacity (*WHC*), daily relative air humidity (*rh*), daily precipitation (*dp*) and days elapsed from the last precipitation event (*prec*)); and (iii) stand-related variables: Global Site Factor (*GSF*) and *IPOT*.

For the sake of clarity, let *i*, *j*, *k*, *l* and *m* be the indices of the plot, the seed point, the year, the seed and the day, respectively. In order to take into account the time-varying covariates, the hazard function can be expressed on a daily basis, i.e.

$$S_{ijkl}(t) = \exp\left(-\sum_{m=1}^{t} h(\mathbf{x}_{ijklm}, \boldsymbol{\beta}) \right) \qquad [3.2]$$

where t is the number of days since seed l at seed point j in plot i was sown on 1 August of year k; $\mathbf{x}_{ijklm}$ is a vector of explanatory variables, some of which are measured daily; and $\boldsymbol{\beta}$ is a vector of unknown but estimable parameters.

From a biological perspective, we can infer that the response of the germination to various explanatory variables is not linear, but rather, nonlinear with some optimal values. Consequently, it can be assumed that the hazard is the product of nonlinear functions of the explanatory variables such that

$$\begin{aligned} h(\mathbf{x}_{ijklm}, \boldsymbol{\beta}) = {} & \boldsymbol{\beta}_0 \cdot f_1(IPOT_{ij}, \boldsymbol{\beta}_1) \cdot f_2(GSF_{ij}, \boldsymbol{\beta}_2) \cdot f_3(WHC_{ij}, \boldsymbol{\beta}_3) \cdot f_4(rh_{km}, \boldsymbol{\beta}_4) \cdot \\ & f_5(dp_{km}, \boldsymbol{\beta}_5) \cdot f_6(prec_{km}, \boldsymbol{\beta}_6) \cdot f_7(fr_{km}, \boldsymbol{\beta}_7) \cdot f_8(temp_{km}, \boldsymbol{\beta}_8) + f_9(h(\mathbf{x}_{ijkl,m-1}, \boldsymbol{\beta}_9)) \end{aligned} \qquad [3.3]$$

where $\boldsymbol{\beta} = (\boldsymbol{\beta}_0^T, \boldsymbol{\beta}_1^T, \boldsymbol{\beta}_2^T, \boldsymbol{\beta}_3^T, \boldsymbol{\beta}_4^T, \boldsymbol{\beta}_5^T, \boldsymbol{\beta}_6^T, \boldsymbol{\beta}_7^T, \boldsymbol{\beta}_8^T, \boldsymbol{\beta}_9^T)^T$.

The functions f_1–f_8 define the effect of each explanatory variable on the daily probability of germination. The independent multiplicative parameter $\boldsymbol{\beta}_0$ is a sort of scaling factor that can be understood as a generic model baseline. The function $f_9(h(\mathbf{x}_{ijkl,m\text{-}1}, \boldsymbol{\beta}_9)) = \beta_9 h(\mathbf{x}_{ijkl,m\text{-}1})$ acts like a lag in the response. In other words, the current daily probability of germination is expected to depend also on the conditions of previous days. In statistical terminology, this lag function is similar to an autoregressive correlation structure (Pinheiro and Bates, 2000, ch. 5.3).

We defined the functions f_1–f_8 so that they range from 0 (maximum hazard reduction) to 1 (minimum hazard reduction). Negative values would be inconsistent as they would lead to a survival function $S_{ijkl}(t)$ that could exceed 1. In such a context, the product of the functions f_1–f_8 seemed to be a desirable feature because we expected the effect of the explanatory variables to be multiplicative. Also, from a biological standpoint, this form made more sense as unfavourable conditions from one explanatory variable are likely to reduce the hazard to zero for a particular day if we put aside the lag effect. Therefore, our hazard function can be seen as a product of ecological factors that can reduce the maximum daily germination hazard represented by $\boldsymbol{\beta}_0$. The challenge remained to find a functional form that made sense for each function.

Provided that the potential lowest value for $IPOT_{ij}$, GSF_{ij}, WHC_{ij}, rh_{km} and dp_{km} is zero and that it can be assumed that their influence on germination increases with the value of the explanatory variable, the corresponding functions can be parameterized as:

$f_1(IPOT_{ij},\boldsymbol{\beta}_1) = 1 - \exp(\beta_1 IPOT_{ij})$

$f_2(GSF_{ij},\boldsymbol{\beta}_2) = 1 - \exp(\beta_2 GSF_{ij})$

$f_3(WHC,\boldsymbol{\beta}_3) = 1 - \exp(\beta_3 WHC_{ij})$

$f_4(rh_{km},\boldsymbol{\beta}_4) = 1 - \exp(\beta_4 rh_{km})$

$f_5(dp_{km},\boldsymbol{\beta}_5) = 1 - \exp(\beta_5 dp_{km})$

where the parameters can only adopt negative values.

In the case of rainfall and frost events, we assumed that these have long lasting effects on the hazard. We hypothesised that germination hazard was intensified when a precipitation event takes place, the effect decreasing with the number of days since precipitation occurrence. As $prec_{km}$ equals zero on the day of precipitation occurrence, the corresponding function can be defined as $f_6(prec_{km},\boldsymbol{\beta}_6) = \exp(\beta_6 prec_{km})$, with $\beta_6<0$. Inversely, freezing was thought to reduce hazard as a function of the number of days elapsed since the last frost, with maximum reduction taking place on days when frost occurred $\left(fr_{km} = 0\right)$. Hence it can be parameterized as $f_7(fr_{km},\boldsymbol{\beta}_7) = 1 - \exp(\beta_7 fr_{km})$, where $\beta_7<0$.

Finally, the response to the temperature effect was defined as a non-negative function with a maximum in accordance with existing knowledge on seed ecology (Bewley and Black, 1994). Daily mean, maximum and minimum temperatures were tested under different parameterizations based on those summarized by Kamkar *et al.* (2012) plus an additional logistic option. We also considered a strictly non-skewed function through a scaled Normal probability density function that ranged from 0 to 1 (Table 3.3).

Table 3.3. Temperature functions tested

Function	Equation
Segmented	$\begin{cases} f_8(temp_{km}) = \dfrac{temp_{km} - \mu_b}{\mu_o - \mu_b} & if\ \mu_b < temp_{km} < \mu_o \\ f_8(temp_{km}) = 1 - \dfrac{temp_{km} - \mu_o}{\mu_{\max} - \mu_o} & if\ \mu_o \le temp_{km} < \mu_{\max} \\ f_8(temp_{km}) = 0 & if\ temp_{km} \le \mu_b \quad or \quad temp_{km} \ge \mu_{\max} \end{cases}$
Beta	$f_8(temp_{km}) = \left(\dfrac{temp_{km} - \mu_b}{\mu_o - \mu_b} \times \dfrac{\mu_{\max} - temp_{km}}{\mu_{\max} - \mu_o} \right)^{((\mu_m - \mu_o)/(\mu_o - \mu_b))^a}$
Logistic	$\begin{cases} \operatorname{logit}(f_8(temp_{km})) = \eta_1 + \lambda_1 temp_{km} & if\ temp_{km} \le \mu_o \\ \operatorname{logit}(f_8(temp_{km})) = \eta_2 + \lambda_2 temp_{km} & if\ temp_{km} > \mu_o \end{cases}$ where $\mu_o = (\eta_1 - \eta_2)/(\lambda_2 - \lambda_1)$
Scaled Normal	$f_8(temp_{km}) = \exp\left(\dfrac{-(temp_{km} - \mu_o)^2}{2\sigma^2} \right)$

The Segmented and Beta functions comprise the following parameters defining the appropriate thermal interval for germination: μ_o (optimum temperature), μ_b (base temperature) and μ_{max} (ceiling temperature). The logistic function includes intercept ($\eta_{1\text{-}2}$) and slope ($\lambda_{1\text{-}2}$) from where μ_o can be deduced. Parameters in the scaled Normal function are μ_o and σ, the latter accounting for the amplitude of the thermal interval. $temp_{km}$ stands for temperature at plot k in day m

3.3.5. Likelihood function formulation

The data presented in this study are actually interval censored seed lifetimes since observations were carried out periodically. As a consequence, the exact moment of germination is unknown. For each seed *l* in year *k* at seed point *j* in plot *i*, we only know that the germination time T_{ijkl} took place within an interval of time where the upper bound is the observation confirming seed germination and the lower bound is the previous observation when the seed had not yet germinated. In other words, we know that $t_{lower,ijkl} < T_{ijkl} < t_{upper,ijkl}$ where $t_{lower,ijkl}$ and $t_{upper,ijkl}$ represent the two limits of the time interval. If the seed fails to germinate during year *k*, then $t_{upper,ijkl} = \infty$ and T_{ijkl} is said to be right-censored.

Therefore, the marginal likelihood function for this experiment is

$$\ell = \prod_i \prod_j \prod_k \prod_l \left[S_{ijkl}\left(t_{upper,ijkl}\right) - S_{ijkl}\left(t_{lower,ijkl}\right)\right]^{q_{ijkl}} \cdot \left[S_{ijkl}\left(t_{lower,ijkl}\right)\right]^{1-q_{ijkl}} \qquad [3.4]$$

where $S_{ijkl}(t)$ is the survival function that sums the daily hazards $h(\mathbf{x}_{ijklm},\boldsymbol{\beta})$ (equation [3.3]) in the terms shown in equation [3.2] and q_{ijkl} is a dummy variable that equals one when the seed has germinated during a known interval $(t_{upper,ijkl}–t_{lower,ijkl}]$ and zero if it is right-censored in relation to this interval.

3.3.6. Model fitting and evaluation

In addition to the explanatory variables, we also tried to account for the data structure. In fact, the sampling scheme is likely to result in clustered data and the correlation between observations that belong to the same plot i, seed point j, and/or year k of study might be non-null. In order to prevent this violation of the independence assumption, a vector b of random effects u_i, v_j and w_k for the mentioned levels of variability was included through the expansion of parameter $\boldsymbol{\beta}_0$, the generic baseline. Random effects are assumed to be normally distributed so that b~N(0, D), where D is the random effects variance–covariance matrix. Although random effects are commonly included as a multiplicative parameter and they are assumed to follow a distribution adopting non-negative values only (i.e. Gamma; Lawless (2003, p. 497)), computing limitations to accommodate our customized hazard function with correction for data correlation forced us to use the present formulation. Also severe problems of convergence arise when different levels of variability are simultaneously considered, especially if it implies crossed effects. Therefore, random effects were tested separately and the resulting models were evaluated in terms of Akaike Information Criteria (AIC).

In order to illustrate the effect of each explanatory variable and optimal conditions for germination, the marginal hazard function was plotted against the covariate of interest whereas the rest was set to its theoretical maximum. Where possible, a comparison with average climatic conditions in the area was performed. *IPOT* influence on germination needs to be interpreted in terms of density. Therefore, *IPOT* was simulated in the central 70 m × 70 m subplot of a 100 m × 100 m plot at a scale of 1 m^2 for different stocking densities, considering regular spacing and identical diameters for all trees. The *IPOT* effect, where significant, was then computed based on the resulting model parameterization for each simulated plot.

The model accuracy was evaluated using graphical methods on the training data. Conditional predictions of cumulative germination proportion ($F(t) = 1 - S(t)$) were averaged for each interval across all seed points and compared with the corresponding observed values for those intervals. This approach provides evidence of the existence of bias (systematic error in the prediction of the mean) and shows in a simple manner the degree of agreement between model and data (overall agreement between the predicted and observed pattern of germination). Additionally, bias was quantified through the mean error (E) of $F(t)$ for all n individual observations:

$$E = \frac{\sum_{ijkl}\left(F(t)_{ijkl} - \hat{F}(t)_{ijkl}\right)}{n} \qquad [3.5]$$

All calculations were carried out using PROC NLMIXED in SAS 9.2.

3.4. Results

3.4.1. Hazard function

Optimisation of the likelihood function shown in equation [3.4] was not straightforwardly achieved under the proposed parameterization. In the selection process we found most of the combinations of parameters to result in severe problems of convergence. This is particularly true in all cases where dp_{km} and/or rh_{km} were included in the model. When the model was fitted without the aforementioned covariates, convergence was achieved either if GSF_{ij} and WHC_{ij} or, alternately, $prep_{km}$ were excluded from model formulation. When fitting the model considering the first possibility, $prep_{km}$ was the only non-significant covariate (p-value 0.2327). In regard to the second possibility, both GSF_{ij} and WHC_{ij} were also found to be non-significant (p-values 0.9315 and 0.9877, respectively) and consequently the model was alternately fitted with each of them at a time. In this process, WHC_{ij} was found to be non-significant, whereas convergence was not attained when the model included GSF_{ij}. As it can be seen, both possibilities led to the same set of parameters when non-significant covariates are dropped of the model. Therefore, germination hazard was finally defined by the overstory competition ($IPOT_{ij}$), number of days elapsed from last frost event (fr_{km}) and daily temperature ($temp_{km}$), all of them significant. These variables modulated the generic base germination through interaction with the baseline (parameter $\boldsymbol{\beta}_0$; p-value<0.0106). The autoregressive term was also found to be significant. Out of all the mentioned options for the temperature effect (Table 3.3), only the scaled Normal approach proved adequate, as the rest implied poorly-resolved estimates with large values in the gradient matrix. Maximum daily temperature produced the best fits and was therefore used in preference to mean and minimum temperature. Selected fixed effects were similar irrespective of the variance structure tested. As regards the random effects, year level of variability performed better (AIC 24,821) than seed point (AIC 24,861) or plot (AIC 25,218). The AIC value for the marginal model was 25,242, which indicates a better performance when random effects are included. Table 3.4 presents the parameter estimates of the preferred model.

In order to assure we did not have problems of collinearity among the spatial covariates that could yield an incorrect variable selection, the final model was additionally fitted excluding $IPOT_{ij}$ and alternately testing GSF_{ij} and WHC_{ij}. As a result, convergence problems identically arose when GSF_{ij} was considered in absence of WHC_{ij}, whereas the latter was non-significant (*p*-value 0.9820).

Table 3.4. Summary of parameter estimates for the selected model

parameter	estimate	std. error	df	t value	*p*-value
β_0[a]	0.0250	0.0057	4	4.53	0.0106
β_1[b]	– 8.4053	0.7211	4	– 11.66	0.0003
β_7[c]	– 0.0127	0.0016	4	– 7.94	0.0014
μ_o[d]	14.1700	0.0537	4	263.76	<0.0001
σ^2[e]	0.7486	0.0244	4	30.73	<0.0001
β_8[f]	0.9603	0.0023	4	421.8	<0.0001
σ^2_{wk}[g]	0.0001	-	-	-	-

[a]β_0: generic baseline; [b]β_1 and [c]β_7: parameters related to IPOT and frost occurrence, respectively; [d]μ_o: optimum daily maximum temperature; [e]σ^2: variance of the (scaled) normally distributed germination response to maximum temperature; [f]β_8: autoregressive parameter; [g]σ^2_{wk} : variance linked to year random effect

3.4.2. Optimum conditions for germination

The parameterized hazard function produces a hyperplane, depending on climatic and environmental variables, from which a set of the most favourable conditions can be deduced. Optimum daily maximum temperature was found to be 14.2 ºC, the value of parameter μ_0, and the symmetric thermal interval ranges from 12 to 16 ºC approximately (Fig. 3.1a). The hazard-reducing effect of frost occurrence only became negligible after 300 days from the frost event, whereas germination risk is set to zero on days when freezing occurs (Fig. 3.1b). As regards *IPOT*, only very low values for this variable notably reduced germination risk (when *IPOT* equals 0.3, hazard reduction with respect to the maximum is only 10.5%). Fig. 3.2 shows that densities over 25 stems·ha^{-1} resulted in a reduction in germination of up to 20% in simulated plots, which implies that only where the overstory is very sparse is there any notable conditioning of germination. Theoretically, germination hazard will be null when overstory competition completely disappears (Fig. 3.1c). Finally, the autoregressive term showed a notable influence, for example, considerably mitigating the effect of frost (Fig. 3.1d). In addition, the autoregressive factor causes the hazard value to increase beyond its theoretical maximum when suitable conditions for germination occur (Fig. 3.1e).

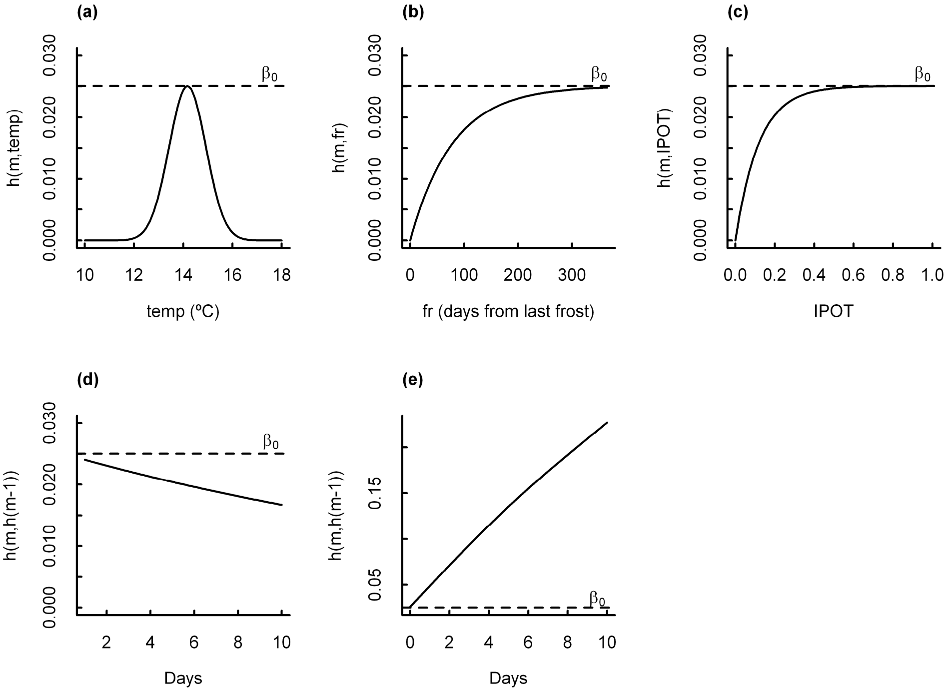

Figure 3.1. Marginal effects on hazard of the different covariates included in the model (solid line). (a-c) Daily maximum temperature (*temp*), frost occurrence (*fr*), *IPOT*. The rest of fixed effects were set to one and autoregressive term not consider. (d-e) Autoregressive parameter over time (maximum initial hazard) during 10 consecutive freezing days and during 10 consecutive days of optimum temperature

When considering historic climatic records, Fig. 3.3 shows how temperatures between June and September over the last 10 years were higher in general than those suitable for germination. In winter, the effect of frost cancels out the potential hazard increase, even if adequate thermal conditions are possible (December and January).

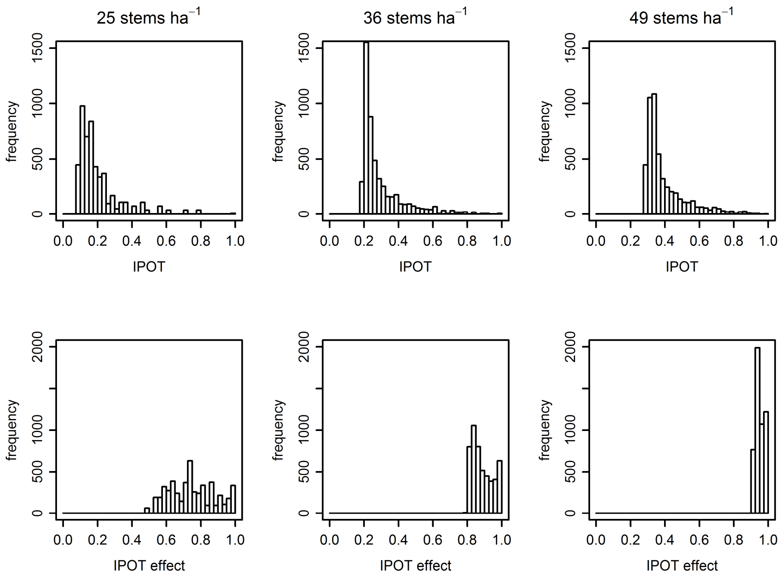

Figure 3.2. Histograms of *IPOT* values and corresponding reducing effects on hazard for three different densities. Evaluation was carried out in a simulated 70 m × 70 m plot at 1 m^2 scale

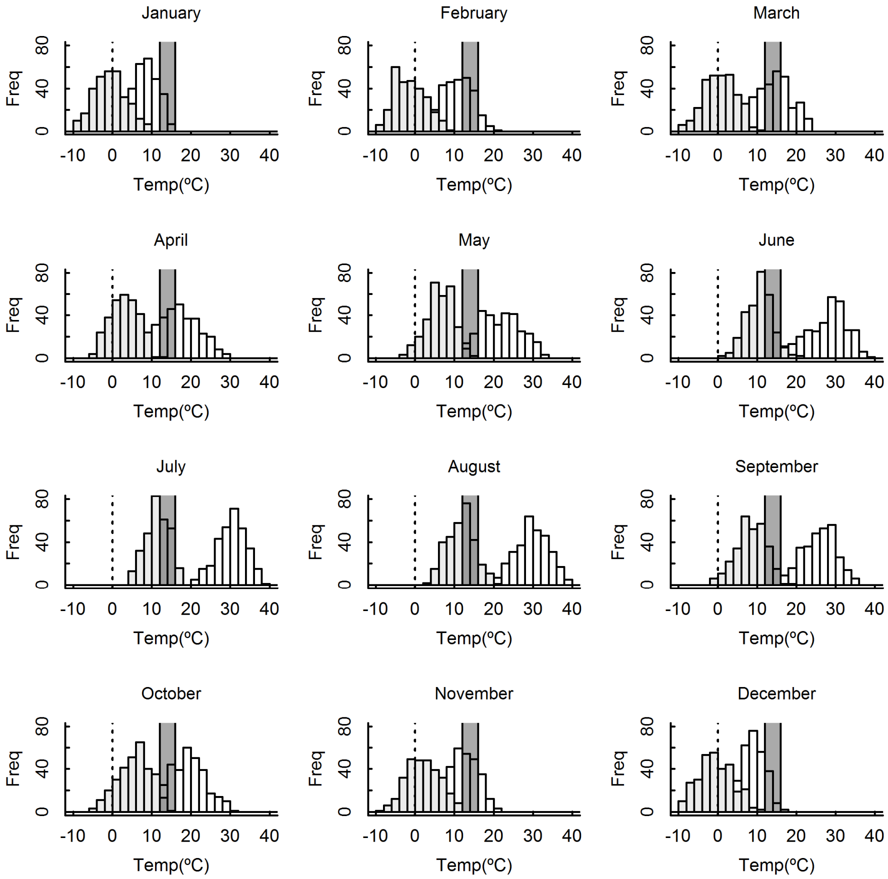

Figure 3.3. Histograms of maximum (white) and minimum (light grey) daily temperatures. Dark grey area represents theoretical suitable thermal interval for germination. Vertical dashed line highlights freezing value (0 ºC)

Given that frost presents a highly durable effect, spring germination is unlikely in the area and restricted to years with unusually warm winters, such as that of 2007–2008. It can be deduced, therefore, that the optimum germination period in the Northern Plateau are the months of October and November, when there is a greater probability of favourable conditions and the possible influence of frost is less likely.

3.4.3. Model evaluation

Predictions of the proportion of germinated seeds over time closely mimic the observed patterns in the two sample plots for all the years of the study (Fig. 3.4). The model proved to be highly accurate for all years, although displaying a slightly weaker performance in 2009–2010. Furthermore, no bias pattern was apparent, which is confirmed by the low absolute value of the mean error (*E* = – 0.0166).

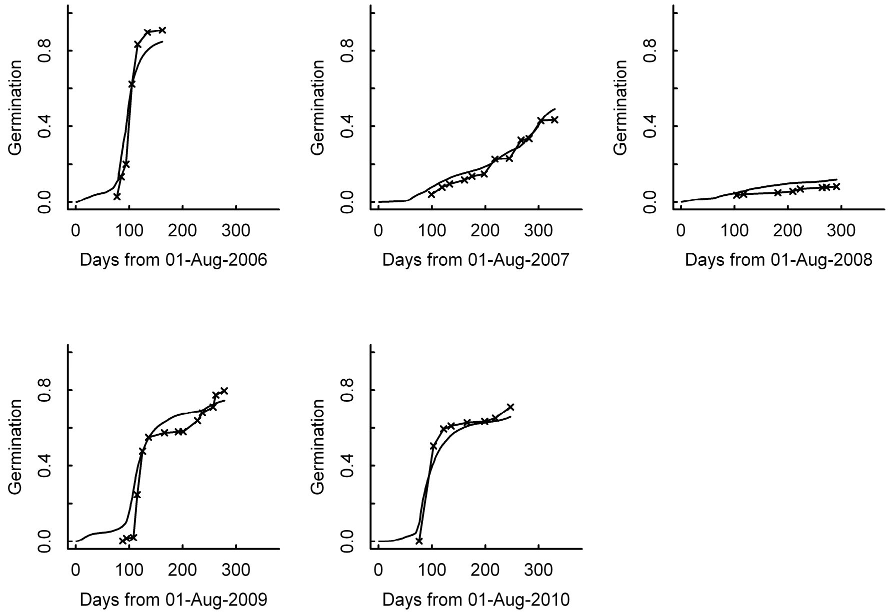

Figure 3.4. Predicted (solid line) and observed (crossed-solid line) cumulative proportion of germinated seeds. The abscissa is a one year temporal axis starting at the seed deployment date

3.5. Discussion

3.5.1. Modelling approach

Although survival analysis techniques have been scarcely used in the context of seed germination compared to other methodologies, the recent comparative studies carried out by Onofri *et al.* (2010) and Onofri *et al.* (2011) demostrate the superiority of those models developed through survival analysis. The present paper confirms the potential of survival analysis applied to germination when censored observations are present. We also demonstrate that conventional formulations can be successfully adapted to avoid strong assumptions on the baseline of the process and to include non-standard explanatory variables. Furthermore, the proposed model extends the existing methods to fulfil further model assumptions, such as independence of observations through random effects. Although the use of mixed effect modelling is unavoidable when the independence assumption is violated, it has been scarcely employed in the context of survival analysis (but see Rose *et al.*, 2006; Fortin *et al.*, 2008). In our case, we allowed our generic baseline to vary randomly among years, thus absorbing unnoticed aggregate climatic influences on germination.

A common procedure in survival analysis is to assume a prior behaviour of the process in question (baseline). This prior behaviour can be modified as a function of several covariates. For instance, Onofri *et al.* (2010) used an AFT model to predict seed germination based on a logistic baseline using water potential as an explanatory variable. However, under non-controlled field conditions, there is no evidence of an existing independent baseline for germination. In our model, we defined the germination hazard as a function of ecological factors with no prior assumptions as regards a baseline for seed germination, with the exception of a technically required scaling parameter.

In the present study we also show that germination can be accurately explained by climatic and stand covariates, at least in this particular case study. The proposed model gained applicability through the set of selected variables in two ways: firstly, they are readily available (as long as daily records are kept) and, secondly, they take into account the effects of forest structure and management on microclimatic conditions (stand variables). The inclusion of time-dependent variables allows predictions to be generated with varying field conditions. Although this paper focuses on the case of *P. pinea*, these possibilities can be explored for most tree species. As a shortcoming, it should be noted that the use of *IPOT* as a stand variable could produce non-comparable results if applied to stands with very different structures.

In contrast to the majority of germination studies, the covariates relating to water availability proved non-significant or convergence was not achieved when included. Concerning water-holding capacity, the notable homogeneity of the variable throughout the two sampled plots could be behind this lack of significance. In regard to precipitation, the low values for water-holding capacity would imply high drainage coefficients (Müller, 2000) and, consequently, little impact of the covariate on water potential reduction. With respect to relative air humidity, it is known to be highly collinear to temperature, which in turn already determines water loss through evapotranspiration (Müller, 2000). Given the high ecological homogeneity of this region, it is presumable that these results would have not notably differed should we have had a replicated design throughout the Northern Plateau. Nevertheless, it is important to note that the non-significance of our water ability-related variables does not necessarily mean that water potential is irrelevant: it only implies that these covariates, under these conditions, could not capture water potential variability and that the importance of water potential in this context is reduced in contrast to the influence of thermal variables.

Dormancy is a major concern in seed ecology research (Chambers *et al.*, 1999; Baskin and Baskin, 2001). In the case study presented here it was not possible to test dormancy processes, since the seed lots were exposed to natural conditions for a maximum of one year. Non-germinated *P. pinea* seeds are assumed to perish in the course of a year due to the high rodent predation rates occurring in the area (Manso *et al.*, 2012b). Under these conditions, distinction between non-germinated seeds and true dormant seeds (if any) is not feasible. However, the proposed methodology allows us to take into account the abovementioned phenomenon in dormancy related experiments. The variables currently included in the model are common for interval and right censored observations, meaning that non-germinated seeds result from an absence of suitable enhancing factors. In order to take into account potentially dormant seeds, the non-germinated fraction should be partitioned into those seeds that simply never abandoned latency and those that acquired dormancy. The latter can be related to a set of covariates z thought to induce the process through the function $\pi(z)$, representing the probability of not germinating due to dormancy. Therefore, the likelihood function in equation [3.4] can be extended as:

$$\ell = \prod_i \prod_j \prod_k \prod_l \left[\left(1-\pi_{ijkl}(z)\right) \cdot \left(S_{ijkl}\left(t_{upper,ijkl}\right) - S_{ijkl}\left(t_{lower,ijkl}\right) \right) \right]^{q_{ijkl}} \times \left[\pi_{ijkl}(z) + \left(1-\pi_{ijkl}(z)\right) \cdot S_{ijkl}\left(t_{lower,ijkl}\right) \right]^{1-q_{ijkl}} \qquad [3.5]$$

similar to those used in zero-inflated model fits (Affleck, 2006; Fortin and DeBlois, 2007; Calama *et al.*, 2011), in this case, a zero-inflated binomial distribution (Tyre *et al.*, 2003). A comparable approach accounting only for the dormant fraction as right censored observations can be found in Onofri *et al.* (2011), as an extension of an AFT model.

3.5.2. *Pinus pinea* case study

The proposed model succeeded in determining the importance of germination in *P. pinea* natural regeneration in our sample plots, providing some prior outcomes about regeneration dynamics in the species. The results of this study seem to confirm our key hypothesis of climatic control for seed germination and the importance of forest structure in the process.

The extrapolation of our findings to *P. pinea* stands in the Northern Plateau as a whole must be made prudently, as we did not have a randomized design over the region. However, the high homogeneity of conditions throughout the area leads us to suggest that the role of germination in the *P. pinea* regeneration strategy could be described as follows: *P. pinea* seed dispersal takes place from June to early November (Manso *et al.*, 2012d), whereas maximum rates of seed predation occur in winter months (Manso *et al.*, 2012b) due to higher rodent activity in Mediterranean areas outside the dry period (Díaz *et al.*, 2010). These circumstances lead to a seed-limiting scenario in spring, coinciding with the scarce likelihood of germination predicted for these months. In addition, Calama *et al.* (2012) found that seedlings established in the fall are more likely to survive the following summer drought period than those produced by spring germinated seeds. Therefore, rapid germination in fall, regardless of site characteristics, could be a key factor for natural regeneration in *P. pinea*, creating a perfectly synchronized post-fructification strategy.

However, this “window” of optimal conditions in fall is not guaranteed every year. Therefore, such a strategy only makes sense if there is a relatively long period for regeneration and a significant seed source density, which permits both dispersal and germination to occur simultaneously. Consequently, a light-independent germination pattern would be expected. Our findings suggest such a pattern (non-significant *GSF*), at least in the Northern Plateau. Accordingly, Seiwa *et al.* (2009) stated that large-seeded, non-pioneer species show little sensitivity to environmental signals which enhance germination potential. Non-detection of light as a gap signal along with germination reduction at very low densities leads to a seedling shadow which potentially mimics the seed shadow (Calama *et al.*, 2012). This fact would confirm the medium shade-tolerant behaviour of *P. pinea* reported by Awada *et al.* (2003) and therefore, the tendency to naturally produce uneven-aged stands (Calama *et al.*, 2008a). In turn, this stand structure ensures long periods for seedling emergence in the absence of large gaps.

In contrast with the strategy described above, the currently-applied regeneration methods in the study area assume a strong shade-intolerant behaviour in stone pine (Montero *et al.*, 2008). For this kind of species, intensive fellings are prescribed to achieve natural regeneration (Smith *et al.*, 1996). However, such practices rapidly lead to seed limitation in *P. pinea* forests (Manso *et al.*, 2012d). If efficient germination has not occurred prior to reducing tree density, natural regeneration will obviously be affected. Additionally, the presence of large gaps in the forest canopy is not favourable to germination.

The future climatic scenario in Spain is characterized by increasing mean and maximum temperatures, particularly during the warm period (De Castro *et al.*, 2005). Minimum temperatures in winter, however, are expected to be more stable. According to these predictions, suitable conditions for germination in terms of daily temperature may shift towards the colder months, but the only moderate reduction in frost occurrence during this period implies a high degree of uncertainty in regard to the likelihood of successful germination.

Under the present climatic conditions and management methods employed in *P. pinea* stands in the Northern Plateau, germination can constitute a bottleneck for the natural regeneration of the species. From an ecological perspective, the intensity of regeneration treatments should be reduced and also delayed until a few years after the occurrence of favourable germination/recruitment events in accordance with the light requirements of the species and subsequent natural forest dynamics. In a scenario of global climate change, predictions for future climatic conditions in the Mediterranean basin underline the necessity to consider the recommendations outlined in this paper.

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Chapter 4

Seed predation and secondary dispersal

Based on:

Manso, R., Pardos, M. & Calama, R. (Unpublished data) Plant-animal interactions in *Pinus pinea*, an emblematic Mediterranean species. **Submitted** to *Ecological Applications.*

Specific objectives:

1. Selecting variables to include in the different submodels that are easily-accessible or controllable by forest managers so that the final model can truly constitute a decision-making tool

4. Modelling the spatio-temporal transition probability of non-germinated seeds to be predated, taking into account the ecological factors driving seed predation

6. Identifying the potential bottlenecks that could affect natural regeneration at subprocess level, taking into consideration the silvicultural practices and the ecological processes involved

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Data:

- Predation data series (2009-2011) from plots P2, P7, N1 and N2 from the natural regeneration INIA site in La Pedraja de Portillo and Nava del Rey (Valladolid)

Methodology:

- Zero-inflated binomial mixed model

Main findings:

- *Apodemus sylvaticus* is, by far, the main animal species interacting with *P. pinea*, its role being mainly that of a predator

- A dual climate prey-predator control was found: climate-mediated masting and lack of water availability allow for a period of seed survival in summer. Otherwise, *A. sylvaticus* totally depletes seed crops

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Management implications:

- Providing that summer-dispersed seeds survive during the whole warm period, predation would become a bottleneck only if favourable conditions for germination occur after the recovery of predation activity
- The uncertainty associated to the effects of predation on seed crops may render the strict and intensive current regeneration systems ineffective to achieve their main objective

4. Seed predation and secondary dispersal

4.1. Abstract

Plant-animal interactions are essential for those plant species exhibiting specific traits to benefit from frugivore activity (large seeds, masting habit…). This is the case of *Pinus pinea* L., a widespread North Mediterranean species that plays a key role in arid areas of its distribution, the species presenting serious problems concerning natural regeneration. The present study is addressed to understand the aforementioned interactions through an experimental trial located in the pinewoods of the Northern Plateau of Spain. A camera trap experiment was conducted, revealing that the main frugivore interacting with *P. pinea* was *Apodemus sylvaticus* L. (80% of sightings), whereas corvids were far less important (*Cyanopica cyanus* Pallas, 16% of sightings; *Corvus corone* L., 4% of sightings). *A. sylvaticus* dispersal activity was found to be scarce and potentially inefficient for regeneration of *P. pinea*. Much more relevant was its impact on *P. pinea* seeds as a post-dispersal predator, which was studied through a zero-inflated binomial mixed model. From a temporal point of view, seeds crops were almost totally depleted during the colder months, the summer resulting in a safe period for seeds. Decreasing rodent population (linked to summer droughts) and masting (as dispersal takes place in summer) were found to positively affect seed survival. A Holling Type II predator functional response can be deduced from these results, typical of specialists but also of generalists foraging on highly nutritive/palatable preys, as *P. pinea* seeds. From a spatial perspective, seeds were exploited more rapidly in the vicinity of parent trees and close to shelters (stumps), although further research on *P. pinea* dispersal and seedling establishment indicates that predator activity does not significantly modify the seed shadow. In synthesis, predator-prey interactions predominate in the case of *P. pinea* and the frugivores associated with the species. *P. pinea* persistence may strongly depend on a temporal dual seed predator control that allows germination to take place just before seeds can be potentially destroyed. However, this “survival window” is narrow, resulting in an overall low probability of emergence, which, in turn, could be behind the common regeneration failure in intensively managed, even-aged *P. pinea* forests.

Keywords: Plant–herbivore interactions, *Apodemus sylvaticus*, masting, summer drought, distance dependence, zero-inflated modelling

4.2. Introduction

Frugivore behavior plays a key role in plant distribution and demography (Janzen, 1970; Jordano, 1992; Herrera, 1995a), ultimately even conditioning plant persistence (De Steven, 1982; Andersen, 1987; Hulme, 1997). Therefore, adaptive strategies by plants to either benefit from animal-mediated seed dispersal or to escape seed predation are crucial to guarantee the coexistence of plants and their associated frugivores (Crawley and Long, 1995; Curran and Leighton, 2000; Vander Wall, 2002), although the development of these adaptations is not necessarily dependent on animal activity (Herrera *et al.*, 1998; Kelly and Sork, 2002). Furthermore, the spatial pattern of seed predation and habitat preference for seed hoarding is known to modify primary seed shadow and the spatial arrangement of recruitment (Schupp, 1995; Schupp and Fuentes, 1995).

In the Mediterranean area, it has been reported that seed predation drastically reduces the amount of seed available for subsequent stages of natural regeneration, leading to processes of seed limitation (Hulme, 1997; Castro *et al.*, 1999; Gómez *et al.*, 2003; Gómez *et al.*, 2008). In this respect, much research has focused on the existing plant-animal interactions in the genus *Quercus* (Herrera, 1995b; Gómez *et al.*, 2003; González-Rodríguez and Villar, 2012, among many others). *Quercus* species present particular traits with respect to natural regeneration such as large seeds, a highly aggregated seed shadow or masting habit (Sork, 1993), which may be associated with both mutualist (seed disperser) and antagonist (seed predator) activity.

Contrastingly, little is known about the effect and importance of frugivores on natural regeneration in stone pine (*Pinus pinea* L.), a sympatric and equally representative Mediterranean species sharing some of the aforementioned phenotypic features with the *Quercus* species. *P. pinea* is a masting, large-seeded species which is widely distributed throughout the northern Mediterranean basin, particularly in the western regions, including Spain. One of the most extensive Spanish *P. pinea* woodlands is located in the Northern Plateau where the species occurs naturally, dating back to at least the beginning of the Holocene (Hernández *et al.*, 2011). Because of the highly demanding conditions of the region, including severe droughts, extreme temperatures and sandy soils, the ecological value of *P. pinea* is particularly high. Furthermore, given the commercial importance of its edible seeds, *P. pinea* forests have been managed since the 19th century. However, although seed harvesting restrictions are imposed to favour seed rain, natural regeneration rarely succeeds. The impact of intensive management techniques on the underlying ecological factors affecting regeneration, such as plant-animal interactions, remains unknown.

Therefore, it is important to fully understand the relationships between *P. pinea* and the frugivores which act as mutualists and/or antagonists. In this study, we firstly attempted to identify the potential dispersers/predators and determine their role in the system. Using this information as a starting point, the study then attempts to shed light on the mechanisms that facilitate the coexistence of *P. pinea* and rodents, focusing particularly on the wood mouse (*Apodemus sylvaticus* L.). *A. sylvaticus* is a Paneuropean and North African generalist rodent, widely documented as being central to the exploitation and depletion (and to some extent, the dispersal) of seed crops in different Mediterranean species (Gómez *et al.*, 2003; Gómez *et al.*, 2008; Puerta-Piñero *et al.*, 2010).

For the purposes of the study, a two-year trial was set up in the Northern Plateau of Spain, including camera traps, seed fate and rodent-exclusive seed removal experiments. The data from the latter was used to fit an empirical zero-inflated binomial mixed model which considered all factors assumed to be involved in seed removal. Despite the extensive development of theoretical models focusing on the functional response of predators to changes in prey availability (Nathan and Casagrandi, 2004; van Leeuwen *et al.*, 2007; Kratina *et al.*, 2009), to our knowledge there is no integral empirical approach which deals with seed removal. Four groups of potentially influencing factors were tested in the model based on established ecological hypothesis: (i) predator demographic stage, based on water availability as a surrogate of primary productivity, which in turn controls *A. sylvaticus* Mediterranean populations; (ii) distance and density dependence to seed source; (iii) preferences for foraging habitat, paying special attention to the influence of elements that could be used as shelters in the absence of dense understory vegetation; and (iv) functional response of predator to seed density, which defines the extent to which animals can regulate prey population according to the three Holling's Types (Holling, 1959a; Holling, 1959b).

Overall, our main objectives were (i) to identify the animal species which potentially act as antagonists/mutualists in the case of *P. pinea*; (ii) to characterize the role of *A. sylvaticus* as a post-dispersal seed predator and a possible seed disperser of *P. pinea*; and (iii) to model the process or processes which take place so that the key factors underlying the coexistence of the two species can be identified as well as the extent to which *A. sylvaticus* reshapes the potential seed shadow. We hypothesized (i) that *A. sylvaticus* acts mainly as an intensive (and most determinant) antagonist of *P. pinea*, the latter persisting due to combined climatic and predator-mediated adaptations; (ii) that the spatial pattern of predation will reshape the seed shadow to maximize the survival of established seedlings; and (iii) that current management practices could result in severe constrictions for natural regeneration of the species given the expected potential role of *A. sylvaticus*.

4.3. Material

4.3.1. Study site

The study site is located in two managed *P. pinea* forests (*Corbejón y Quemados* and *Común y Escobares* public forests) on the flats of the Northern Plateau in the municipalities of La Pedraja de Portillo and Nava del Rey at a mean altitude of 700 m above sea level. The study was conducted in two mature even-aged stands at each location (differing in their respective densities as shown in Table 4.1), where restrictions exist on cone collection for commercial purposes and where regeneration fellings have commenced. The climate is continental-Mediterranean with mean monthly temperatures ranging from 4.0 ºC in January to 21.7 ºC in July. Mean annual precipitation is 435 mm, including a period of summer drought (July to September, mean precipitation of 66 mm). Soils in this area are highly sandy.

Table 4.1. Summary of stand features

plot	coordinates	N_s^a(ha^{-1})	BA^b(m^2·ha^{-1})	Dg^c (cm)	H^d (m)
P2	41º28’N, 4º43’W	48	9.76	50.9	15.5
P7	41º27’N, 4º43’W	149	18.42	40.1	13.8
N1	41º26’N, 5º03’W	87	7.65	33.4	8.6
N2	41º27’N, 5º02’W	60	7.04	38.5	8.8

$^a N_s$: stand density; ^{b}BA: basal area; ^{c}Dg: quadratic mean diameter; ^{d}H: average height

The demanding environmental and climatic features described above prevent the profusion of understory vegetation other than a poor herbaceous stratum. Climatic data were obtained from two meteorological stations located at 15 km and 6 km respectively from both forests and at the same altitude (41º17'N, 4º40'W and 41º29’N, 4º59’W; data available in www.inforiego.org). Meteorological data included daily mean temperature and daily total rainfall.

4.3.2. Experimental design

A 60 m × 80 m (0.48 ha) sample plot was set up at each of the four stands considered in November 2008 (P2 and P7, La Pedraja de Portillo; N1 and N2, Nava del Rey). A 7.5 m buffer area was included around each plot, increasing the overall plot surface to 0.7 ha. All trees and stumps within the plots were mapped and their relative coordinates within each plot calculated. Four different experiments were carried out:

Frugivore identification

In order to identify those species that may act as dispersers or predators of *P. pinea* and the seasonality of their activity, a self-activating HCO ScoutGuard SG550 camera, baited with pine nuts, was installed at each plot. The devices were placed approximately 30 cm above ground level, attached to natural elements such as pieces of dead wood. The cameras were equipped with an infrared flash allowing night recording and therefore the possibility for round the clock video capture. They were programmed to capture 20 seconds of video to investigate the behaviour of the animals. The time elapsed between consecutive videos was set to three minutes to prevent multiple recordings of the same visit. Recorded material was downloaded and reviewed monthly, discarding false detections and those videos which were either poorly captured or which captured species unrelated to the objectives of the study. Visiting animals were identified at specific level.

Seed removal patterns

As regards the pattern of seed removal by rodents, a trial consisting of 64 seed points deployed throughout the four plots (16 seed points per plot) was conducted. Seed point location was set such that a wide range of distances among seeds and trees and stumps were represented. Seed points were protected with a 40 cm × 40 cm × 15 cm cage made of hard wire mesh (span 4 cm × 4 cm) to exclude other possible predators/dispersers, such as corvids. From January 2009 to March 2011, 50 sound seeds collected from a nearby stand were placed at each seed point at the beginning of each month. This amount of seeds was considered appropriate as a single average cone produces over 90 pine nuts (Morales, 2009), which are primary dispersed by gravity, leading to a strongly clustered distribution. Given the factors tested, we chose a balanced experiment at temporal (as in Klinger and Rejmanek (2009)) and spatial level (as in Castro *et al.* (1999)), in order to capture both spatial and temporal variability, thus avoiding possible confounding effects related to the experimental design. The number of seeds removed was recorded monthly and intact seeds were eliminated.

Seed fate. All locations

A seed fate experiment was carried out in one plot per stand (plots P2 and N1) in order to evaluate rodent dispersal activity. The aim of this trial was specifically to determine seed fate in all possible locations. For this purpose, 240 seeds were tagged using a 5 cm steel wire with a 2 cm × 1 cm white plastic label attached to its end. A unique code was printed on each label so that the seeds were individually identifiable. The pine nuts were previously immersed in water for 8 hours and then dried at room temperature to permit partial opening of the shell. The free end of the wire was bent and glue-sealed to the seed through the opening in the shell. In previous tests, rodents had not shown a significant preference for untreated seeds. Tagged seeds were systematically deployed in groups of 20 seeds throughout the two selected plots (6 groups per plot). After 10 and 20 days from placing the seeds, the surroundings of each seed group were checked for labelled seeds up to a distance of 20 m. The experiment was then revisited monthly until either emergence or seed depletion occurred. A first lot of seeds was released on 11 December 2009. An extraordinary snow event which took place immediately afterwards prevented us from revisiting the experiment for over a month and therefore we set up a second lot of tagged seeds on 19 January 2010.

The pine nuts were classified into the following categories according to seed fate: predated *in situ*, removed and left intact on the soil surface, removed and buried, intact at original position or missing. Where seeds had been removed, the distance from the points of seed release was measured and recorded.

Seed fate. Burrows and shelters

A second dispersal experiment was conducted to test the numerical relevance of seeds larder-hoarded in burrows or natural shelters and its effectiveness as a dispersal process, since this kind of cache cannot be detected through label-tracking. This trial was based on the main predation experiment and carried out in plots P2 and N1. In December 2009, 12 artificial shelters (Fig. 4.1) were deployed and partially buried in the vicinity of 12 out of the 16 seed predation points (range 1–12.5 m) in the two plots (overall 24 shelters). The minimum distance from one shelter to another was 20 m to minimize interaction from possible relocations. In addition, shelter location was chosen to represent four levels of a spatial factor describing the positions relative to elements in the plot with 3 replications each (shelters placed at: (i) > 5 m from a stump and > 5 m from a seed point; (ii) > 5 m from a stump and < 5 m from a seed point; (iii) < 5 m from a stump and > 5 m from a seed point; and (iv) < 5 m from a stump and < 5 m from a seed point). The artificial shelters consisted of 25 cm × 15 cm × 15 cm boxes made of wood, in which a 5-cm diameter hole had been opened in the front side to permit rodent access. The lower side was removed to allow direct contact of visiting rodents with mineral soil. From January 2010 to January 2011, all the pine nuts released each month at the 12 selected seed removal points (7,800 seeds) were individually numbered on the shell using an indelible pen. The artificial shelters were revisited monthly and seeds as well as empty shells (assumed predated) found within were counted. The number printed on the nutshell, if any, was recorded to identify the seed-point of origin. Empty nutshells were removed whereas surviving seeds were left in the shelters to be tracked the following month.

Figure 4.1. Artificial shelters with pine nuts placed and consumed inside by rodents

4.4. Methods

4.4.1. Camera sightings

Due to slight differences in the intervals between measurements, the number of sightings for each detected species was divided by the number of days of the corresponding interval. The resulting daily frequencies for the observed species were summed over the plots and pooled over seasons (winter: January to March; spring: April to June; summer: July to September; fall: October to December). These averaged values for the different seasons were compared graphically to determine the relative impact of each species foraging on pine nuts and to identify inter and intraspecific temporal patterns of seed usage.

4.4.2. Seed removal

Modelling approach

As in a number of ecological processes, seed survival data from the removal experiment are expected to show a zero-inflated distribution, meaning that on most occasions, the majority of seed points (or at least, more than expected from the corresponding distribution) will present zero counts (all seeds removed or destroyed). The so-called zero-inflated models (Lambert, 1992) can deal with this kind of distributions by simultaneously modelling the probability of event occurrence (e.g. total removal at a seed point) and the intensity of the event conditional to occurrence, also referred as to abundance (e.g. proportion of non-removed seeds at a seed point providing that some seeds escaped rodent activity). In the present study we attempted to model the process through a zero-inflated binomial model (Hall, 2000). This approach combines two binomial distributions. The first distribution acts at seed point level and it is used to model the probability of all seeds being removed from a seed point. The second distribution models the probability of a single seed remaining at a seed point (seed level) conditional to partial exploitation at seed point level. The binomial nature of the abundance process is justified on the grounds that all seeds within a seed point hold the same prior probability of remaining. Simultaneous estimation of parameters defining both processes is attained through the maximisation of the likelihood function (ℓ) of the observations, given by the product of the two abovementioned independent processes:

$$\begin{aligned}\ell\left(y_{jkl} \mid \pi_{jkl}, p_{ijkl}\right) = \prod_{l}\prod_{k}\prod_{j}\prod_{i}\left[\pi_{jkl} + \left(1-\pi_{jkl}\right)\cdot\left(1-p_{ijkl}\right)^{n}\right]^{q_{jkl}} \times \\ \times\left[\left(1-\pi_{jkl}\right)\cdot p_{ijkl}^{y_{jkl}}\cdot\left(1-p_{ijkl}\right)^{n-y_{jkl}}\right]^{1-q_{jkl}}\end{aligned} \quad [4.1]$$

where π_{jkl} is the probability of obtaining a zero count at seed point j within plot k in month l (total exploitation at a seed point); p_{ijkl} is the probability of a seed i remaining at a seed point j, plot k and month l; n is the initial number of seeds (50) at each seed point j, plot k and each month l; and y_{jkl} is the number of seeds remaining at each seed point j, plot k and month l. q_{jkl} is a dummy variable that equals one when a seed point j presents a zero count in month l and zero otherwise.

Covariate selection

Parameters π and p actually define the core processes involved in model formulation. In order to link them to the real ecological processes underlying seed removal, a linear model can be used to model the parameters using a set of explanatory covariates through the logit link function. Different covariates were tested to identify both processes based on established ecological hypothesis:

(i) Demographic stage: Cumulative precipitation over the three months prior to each survival recording ($Pp_{l\text{-}3}$) was tested, as this variable has been found to reflect the availability of resources required to successfully overcome different stages of rodent life (Díaz *et al.*, 2010). We also included the physiological drought of the month in which the measurement was taken as a covariate (D_l) to take into account the extreme summer conditions present in the Northern Plateau. This variable was assessed as the difference between the potential evapotranspiration and the actual maximum evapotranspiration of month l (Thornthwaite and Mather, 1957).

(ii) Spatial location of stand elements: distance to source, seed density and foraging preferences are factors known to possibly modify the seed shadow, and therefore they are likely to influence the resulting distribution of seedlings. Given that foraging choice is generally related to shelter locations, a factor considered was proximity to stumps since these are the only protective elements in this scarce, low diversity understory layer. In order to test these three effects, the influence potential of all trees ($IPOTt_j$) and stumps ($IPOTs_j$) located within an influence area of 15 m radius from seed points was calculated for each seed point. *IPOT* is a competition index based on the concept of ecological field theory (Wu *et al.*, 1985), empirically modified by Kuuluvainen and Pukkala (1989):

$$IPOTt_j = 1 - GPOTt_j, \quad \text{where} \quad GPOTt_j = \prod_{t=1}^{Nt_j} \left(1 - I_{tj}\right) \quad \text{and} \quad I_{tj} = I_{tj}(0) \times \exp\left(-b \cdot d_{tj}\right)$$

$$IPOTs_j = 1 - GPOTs_j, \quad \text{where} \quad GPOTs_j = \prod_{s=1}^{Ns_j} \left(1 - I_{sj}\right) \quad \text{and} \quad I_{sj} = \exp\left(-b \cdot d_{sj}\right)$$

I_{tj} and I_{sj} are the potential influence of tree t or stump s at seed point j, d_{tj} and d_{sj} are the distances from tree t or stump s to seed point j, $I_{tj}(0)$ is dbh_{tj}/(max dbh_t at each plot), dbh_{tj} is the diameter at breast height of tree t in the seed point j influence area, b is a parameter assumed to equal 0.4, and Nt_j and Ns_j are the number of trees and stumps in the seed point *j* influence area. *IPOT* ranges from zero (no competition) to one (maximum competition).

(iii) Functional response: Seed production over the two years of the study for all four plots was predicted by means of the model proposed by Calama *et al.* (2011). The beginning and length of the dispersal period were assessed using the model proposed by Manso *et al.* (2012d). The weight of cones borne by trees divided by the length of the dispersal period on a monthly basis (N_0, in kg·ha^{-1}·month^{-1}) was used as an explanatory variable to test the effect of varying seed production on the functional response of rodents at stand level. The covariate entered the model as a two-order polynomial (*sensu* Juliano, 2001), so that the effect is studied through an empirical approach: Type I functional response implies that neither the linear nor the quadratic terms in the polynomial are significant (independence of N_0); Type II functional response yields a significant and negative value for the linear term in the polynomial (the higher N_0, the lower the proportion of available seeds harvested); Type III functional response arises when both the linear and the quadratic terms are found to be significant and are positive and negative, respectively (comprising a certain value of N_0 that maximizes seed predation). Note that this interpretation of the sign applies directly for the occurrence model as it predicts predation (total exploitation). In the abundance model, opposite signs would lead to similar conclusions because this model predicts seed survival (i.e. proportion of non-harversted seeds). The predicted seed rain was notably higher in 2010 than in 2009 in plots P2 and P7 (plot P2, 33.31 and 3.17 kg of cones·ha^{-1}; plot P7, 34.96 and 3.33 kg of cones·ha^{-1}). Trees in plots N1 and N2 bore slightly more cones in 2009 (14.10 and 18.05 kg of cones·ha^{-1}) than in 2010 (13.18 and 16.87 kg of cones·ha^{-1}). Seeds were predicted to be released from cones from May onwards in all cases.

Overall, the evaluated expression of the two parts of the model is:

$$\log\left(\pi_{\mathrm{jkl}} / \left(1-\pi_{\mathrm{jkl}}\right)\right) = \beta_0 + \beta_1 N_0 + \beta_2 N_0{}^2 + \beta_3 D_l + \beta_4 Pp_{l-3} + \beta_5 IPOTt_{jk} + \beta_6 IPOTs_{jk} \qquad [4.2a]$$

$$\log\left(p_{\mathrm{ijkl}} / \left(1-p_{\mathrm{ijkl}}\right)\right) = \gamma_0 + \gamma_1 N_0 + \gamma_2 N_0{}^2 + \gamma_3 D_l + \gamma_4 Pp_{l-3} + \gamma_5 IPOTt_{ijk} + \gamma_6 IPOTs_{\mathrm{ijk}} \qquad [4.2b]$$

where $\beta_{0\text{-}6}$ and $\gamma_{0\text{-}6}$ are unknown but predictable parameters related to the aforementioned set of covariates.

Model fitting and evaluation

Given the sampling scheme, correlation between observations that belong to the same plot *j*, seed point *k*, and/or year *m* of study, as well as their interactions, might be non-null. In order to prevent this violation of the independence assumption, random effects for the mentioned levels of variability were included as intercept linear terms *u* and *v* in equations [4.2a] and [4.2b], respectively. Random effects were assumed to be normally distributed, with mean zero and variance-covariance matrix *D*. Due to computing limitations, random effects were tested separately starting from the saturated model (including all possible fixed effects) and sequentially on the models resulting from covariate selection. The final models were evaluated in terms of Akaike Information Criteria (AIC).

Model accuracy was evaluated by comparing predicted ($\hat{y}_{jkl}$) and observed (y_{jkl}) values of remaining seeds at each seed point *j*, plot *k* and month *l*. Predictions were obtained through the following expression $\hat{y}_{jkl} = n \times (1 - \pi_{jkl}) \times p_{jkl}$, where *n* is the initial number of seeds at each seed point *j* (50 seeds), $1 - \pi_{jkl}$ is the estimated probability of a seed point to hold surviving seeds and p_{jkl} is the estimated abundance at seed point level. Mean error (*E*), root mean squared error (*RMSE*) and modelling efficiency (*EF*) of the selected conditional model were calculated (equations [4.3a], [4.3b] and [4.3c]):

$$E = \frac{\sum_{jkl} \left(y_{jkl} - \hat{y}_{jkl} \right)}{n} \qquad [4.3a]$$

$$RMSE = \sqrt{\frac{\sum_{jkl} \left(y_{jkl} - \hat{y}_{jkl} \right)^2}{n-1}} \qquad [4.3b]$$

$$EF = 1 - \frac{\sum_{jk\tilde{n}} \left(y_{jkl} - \hat{y}_{jkl} \right)}{\sum_{jkl} \left(y_{jkl} - \bar{y}_{jkl} \right)} \qquad [4.3c]$$

In addition to these indexes, a regression between observed and predicted values ($y_{jkl} = \delta_0 + \delta_1 \hat{y}_{jkl}$) was computed as a measure of the level of concordance between data and model. A successful fit of the seed removal model would imply that this regression would be a 45º line through the origin. Therefore, the null hypothesis of $\delta_0 = 0$ and $\delta_1 = 1$ was evaluated using a simultaneous *F*-test (Montgomery and Peck, 1992).

Furthermore, observed and predicted values were averaged by measurement period at plot level and then graphically compared to test the ability of the model to account for pure temporal variability.

All calculations were done using PROC NLMIXED in SAS 9.2.

4.4.3. Seed fate

Polar coordinates of all recovered seeds were recorded on each revisiting date of the first fate experiment (deployment location was taken as a fixed point). The categories described in the subsection 2.2 were used to classify seed fate. This descriptive analysis undertaken on each visit also included the proportion of recovered seeds and proportion of destroyed seeds. In the second seed-fate trial, distances and final locations were controlled (artificial shelters) and therefore a generalized linear model was fitted to the pooled data to infer the influence of shelter location and distance to the seed source on the process. Shelter location entered the model as a factor (loc_{ikst}) of four levels accounting for the four spatial possibilities observed in the present design. Distance of seed i within an artificial shelter to a seed point j in plot k was included as a continuous variable ($dist_{ijk}$). Given the nature of these data (counts), the Poisson error structure was attempted. Alternatively, the negative binomial distribution was also considered in order to deal with overdispersion problems. For both distributions, the log link function was used. The expanded expression of this model is:

$$\log\left(d_{ijkst}\right)=\lambda_0+loc_{ikst}+\lambda_1 dist_{ijk} \qquad [4.4]$$

where d_{ijkst} is the sum of all seeds i placed within a given artificial shelter in plot k with a closest seed point j, stump s and tree t. $\lambda_{0\text{-}1}$ are parameters to be estimated. A sequential variable selection was carried out. The performance of the two models fitted with the Poisson and negative binomial distribution respectively was tested through the comparison of their resulting AICs. This analysis was performed using R 2.14 (R Core Team, 2011).

4.5. Results

4.5.1. Camera sightings

Overall, 1,335 videos of fauna feeding on *P. pinea* seeds were recorded. The vast majority (80%) corresponded to the wood mouse (*A. sylvaticus*) whereas the azurewinged magpie (*Cyanopica cyanus* Pallas) was observed in 16% of sightings. Much less frequent was the carrion crow (*Corvus corone* L.; 4%) and the common crossbill (*Loxia curvirostra* L.; <1%). Frequencies changed seasonally, with a minimum for *A. sylvaticus* in summer, the opposite being the case for *C. cyanus* (Fig. 4.2). *C. corone* mostly appeared in spring.

From a behavioural perspective, *A. sylvaticus* normally took only few seconds to select a single targeted seed, which was either consumed *in situ* or removed from the field of vision of the cameras. Contrastingly, birds always took seeds to a different location and took longer to make their selection than the wood mice. The number of pine nuts per flight was commonly two in the case of *C. cyanus*, whereas *C. corone* collected up to five seeds.

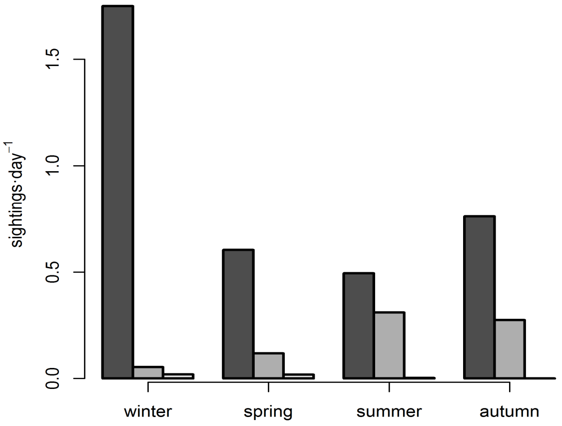

Figure 4.2. Frequencies of daily animal sightings pooled over seasons. Dark, medium and light grey bars represent *Apodemus sylvaticus*, *Cyanopica cyanus* and *Corvus corone* values, respectively

4.5.2. General pattern of seed removal

From a temporal perspective, with few exceptions, most seed points were completely exploited from October/November to May/June in both years of study (Fig. 4.3). Specifically, in 49 surveys (out of 112 = four plots × 28 visits/plot) there were no seeds to be found at the original placement. Additionally, it was found that during certain periods, normally the warmer months (which tend to be a “safe” period for seeds), seed removal either ceased completely or was much reduced (less than 10% of seeds removed). As regards locations, plots P2 and P7 shared a similar pattern, with a longer safe period in 2010 (May to February (2011) and June to January (2011)) than in 2009 (June to September and July to September), the latter exhibiting a lower mean proportion of remaining seeds (mean and standard error for 2009 and 2010, respectively: plot P2, 0.31±0.03, 0.61±0.03; plot P7, 0.42±0.04, 0.81±0.02). Contrastingly, plot N2 showed the opposite trend with a longer safe period and higher levels of intact seeds in 2009 than in 2010 (May to November (0.78±0.03) and July to August (0.46±0.06), respectively). The process in plot N1 emulated the pattern of plots

P2 and P7 in 2009 (May to September (0.35±0.03)) and was closer to that of plot N2 in 2010 (June to October (0.44±0.06)).

As shown in Fig. 4.3, the occurrence of physiological drought loosely coincided with those periods of less removal activity and, in general, seed exploitation increased along with three-month cumulative precipitation.

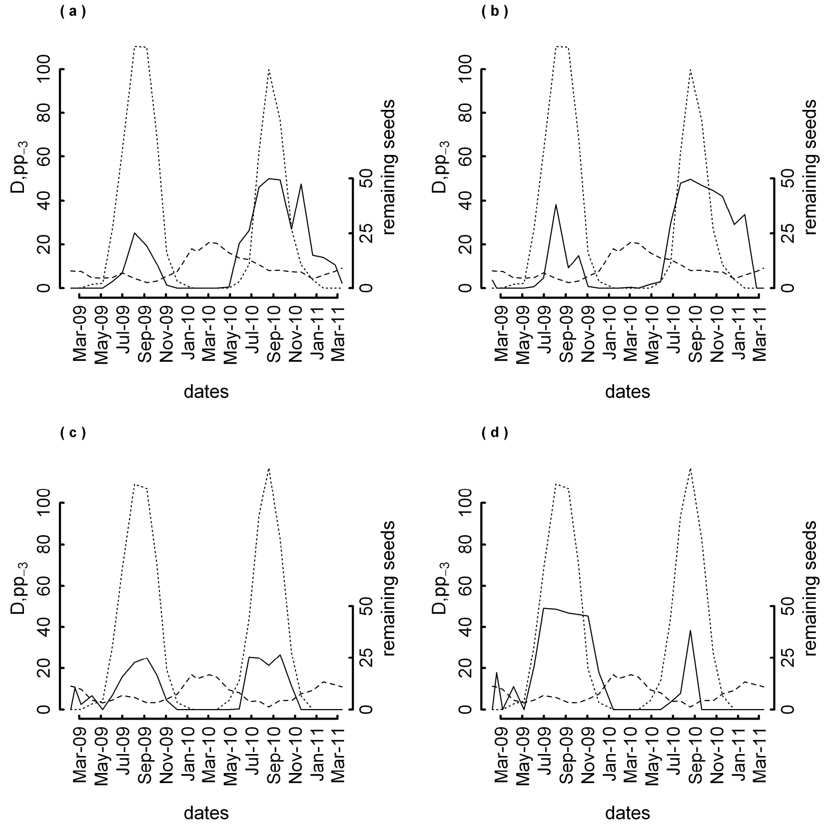

Figure. 4.3. Mean number of remaining seeds (solid line), physiological drought (*D*, in mm, dotted line) and cumulative precipitation of the three previous months ($Pp_{l\text{-}3}$, in cm, dashed line) over time for plots P2 (a), P7 (b), N1 (c) and N2 (d)

4.5.3. Seed removal model

The variance structure accounting for seed point × year random variability proved the most appropriate for the current data set in terms of AIC (Table 4.2). In the sequential fixed effects selection carried out under this structure, different covariates resulted non-significant and therefore were dropped from the model. Regarding the occurrence part of the model, the parameter linked to *IPOTs* was not found to statistically differ from zero. Consequently, the probability of absolute predation occurrence in a seed point j and plot k for a given month l (π_{jkl}) is explained by seed production (N_0), physiological drought (D_l) and cumulative precipitation three months prior to predation event ($Pp_{l\text{-}3}$) at temporal level, and proximity to trees (*IPOTt*) at spatial level. The sign of the parameters indicates that the higher the physiological drought and seed production and the lower the precipitation (Table 4.3), the lower the likelihood that total exploitation will occur. A positive *IPOTt* parameter implies higher removal in the proximity of trees.

Table 4.2. Fit statistics for the different random structure alternatives tested. In bold, values corresponding to the preferred model

random level	seed point	plot	year*	year × seed point	year × plot
–2LL [a]	38,509	38,728	-	**36,641**	37,378
AIC[b]	38,531	38,750	-	**36,665**	37,402

*[a]–2LL: minus twice the logarithm of the maximum likelihood estimate; [b]AICb: Akaike Information Criterium; *: lack of stable convergence*

Table 4.3. Summary of parameter estimates and significance for the selected model, including variance components of the random effects

	occurrence of zero counts (β)		abundance of survival (γ)	
covariate	estimate	p-value	estimate	p-value
Intercept	1.9769	< 0.0001	– 0.9589	< 0.0001
N_0[a]	– 0.6301	< 0.0001	0.2946	< 0.0001
D_l[b]	– 0.0547	< 0.0001	0.0164	< 0.0001
$Pp_{l\text{-}3}$[c]	1.8830	0.0024	-	-
$IPOTt_j$[d]	0.0087	0.0003	-	-
$IPOTs_j$[e]	-	-	– 0.6410	< 0.0001
σ^2_u[f]	1.5904	-	-	-
σ^2_v[g]	-	-	1.1562	-
σ_{uv}[h]	– 0.6858	-	– 0.6858	-

[a]N_0: variable linked to seed dispersal;[b]D_l: physiological drought; [c]$Pp_{l\text{-}3}$: cumulative precipitation of the three previous months; [d]IPOTt and [e]IPOTs: tree and stump IPOT indexes; [f]σ^2_u and [g]σ^2_v: estimated variances associated to the random intercepts (see point × year level); [h]σ_{uv}: covariance between both random effects.

As regards the abundance of remaining seeds (p_{ijkl}), $Pp_{l\text{-}3}$ and $IPOTt_j$ were non-significant. However, in consistence with the effects observed in the occurrence subprocess, increasing drought intensity and large crop size limit seed removal. Furthermore, seeds are harvested more rapidly in the proximity of stumps, as the parameter related to $IPOTs_j$ adopted a negative value. Finally, in both occurrence and abundance submodels, the quadratic term in the polynomial function of seed production was non-significant, inferring a Type II functional response at stand level. The final parameterization is shown in Table 4.3. Note that opposite signs in parameters linked to the same covariates in equations [2a] and [2b] reveals a common tendency, as π_{jkl} represents the probability of total exploitation whereas p_{ijkl} stands for the probability of seed survival conditional to 1 – π_{jkl}. This is also consistent with the negative value obtained for the covariance between random effects affecting the respective intercepts of equations [2a] and [2b].

The model proved highly accurate, with *EF* = 68.61%, *E* = 0.1171 surviving seeds·(seed point·month)$^{-1}$ and *RMSE* = 10.2286 seeds·(seed point·month)$^{-1}$. As regards the regression between observed and predicted values, the null hypothesis of intercept and slope parameters not differing from zero and one respectively was not rejected (*F* = 1.0093; *p*-value = 0.3647), confirming that the model was unbiased. At temporal level, Fig. 4.4 shows how the model closely mimics the pattern of seed removal, perfectly capturing the existing seasonal variability in each plot.

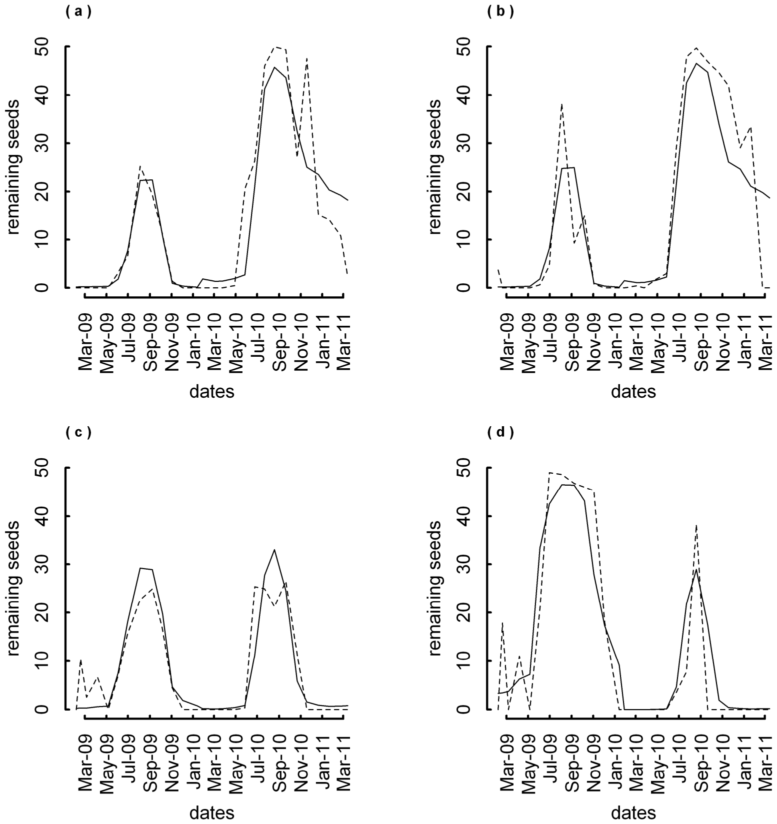

Figure. 4.4. Observed (dashed line) and predicted values (solid line) of mean number of remaining seeds per seed point over time in sampling plots P2 (a), P7 (b), N1 (c) and N2 (d)

4.5.4. Seed fate

As regards the first experiment, all seeds recovered following release on 11 December 2009 had been completely exploited by rodents when the plots were revisited on 19 January 2010. The fate of seeds from the second attempt (set up on 19 January 2010) was checked on 28 January, 8 February and 16 March 2010. In this case, the small number of seeds that escaped rodent predation during the first week of exposition was found to be either unaltered at the original position, larder-hoarded or scattered on the ground at short distances from the deployment point (mean distance 3.16 m). Surviving seeds were mostly exploited by rodents in subsequent visits. These results are detailed in Fig. 4.5.

In the second experiment, 1227 seeds (out of which 79% were marked) were recovered from the artificial shelters. 89% of cached seeds were consumed within the boxes immediately after relocation and those that survived were found to have been predated within the next month. One exception to this pattern was a shelter containing 38 seeds, which was undisturbed for two consecutive months. The seeds in this shelter germinated and consequently escaped predation. The number of cached seeds over time shared a common pattern from one plot to another, with higher values in autumn and spring. Seed caching was maximum in plot P2 in March 2010 (3.86 seeds·day^{-1}) and in December 2010 (1.27 seeds·day^{-1}). Maximum values in plot N1 were reached in December 2009 (5.2 seeds·day^{-1}), May 2010 (5.6 seeds·day^{-1}) and November 2011 (5.3 seeds·day^{-1}). The monthly ratio between non-predated and predated seeds was only higher than one in summer. As regards the fitted model, the Poisson distribution could not account for the overdispersion present in our data and therefore the negative binomial distribution proved significantly more adequate (Table 4.4). In the final model, only distance from the shelter to the closest seed point was significant. The associated parameter was negative, meaning that there is less likelihood of finding dispersed seeds as distance from the place of collection increases (Table 4.4).

Table 4.4. Selection process for the seed fate model. *p*-values of the different variables and parameter values for the preferred model are given (in bold)

	Poisson model		negative binomial model		**parameter value**
variable/statistic	1	2	1	**2**	
Intercept	< 0.0001	< 0.0001	< 0.0001	**< 0.0001**	**4.6049**
$loc_{ikst,2}^{a}$	0.0007	-	0.5200	**-**	**-**
$loc_{ikst,3}$	0.2181	-	0.8060	**-**	**-**
$loc_{ikst,4}$	0.0371	-	0.9650	**-**	**-**
$dist_{ijk}^{b}$	< 0.0001	< 0.0001	0.2730	**0.00859**	**– 0.1517**
θ^{c}	1*	1*	1.248	**1.222**	**1.222**
$-2LL^{d}$	868.73	888.07	229.90	**230.46**	**-**
AIC^{e}	878.73	898.07	241.9	**236.46**	**-**

$^{a}loc_{ikst}$: 4-level factor accounting for seed location in regard to trees and stumps; $^{b}dist_{ijk}$: distance from seed location to the nearest seed station; $^{c}\theta$: parameter modelling overdispersion: when set fixed to 1 (*) a Poisson distribution is used; otherwise, a negative binomial distribution is utilized. ^{d}– 2LL is minus twice the logarithm of the maximum likelihood estimate and ^{e}AIC is the Akaike Information Criterium

4.6. Discussion

4.6.1. The role of *A. sylvaticus* in *P. pinea* natural regeneration

In the present study, we attempted to describe and predict the spatio-temporal interactions between *A. sylvaticus* and *P. pinea*. This general purpose gives rise to the first question addressed in this paper: what role does this rodent species play in the natural regeneration of *P. pinea* forests throughout the Northern Plateau of Spain? Although we found evidence suggesting a marginal (and potentially effective) dispersal activity, our seed fate experiments provided overwhelming evidence that confirmed our hypothesis of a predominant predator-prey interaction. This fact appears to be a common trend in other Mediterranean large-seeded tree species. In this respect, our results are consistent with those reported by Gómez *et al.* (2003) for ecological interactions between *Apodemus spp.* and *Quercus pyrenaica*. Identically, Gómez *et al.* (2008) determined that *A. sylvaticus* consumed over 98% of the *Quercus ilex* seeds deployed and also pointed to the potential benefits associated with the dispersal of a small (albeit minimal) fraction of the seeds. Hulme (1997) observed the same behavior in this species when foraging on different food sources in south-eastern Spain. In the following paragraphs we shall further discuss the association of *A. sylvaticus* with *P. pinea* and attempt to analyze the plant developed strategies underlying the coexistence of both species.

4.6.2. Seed removal

Seed predation temporal pattern

Our results reveal that seed predation is indirectly controlled by climate on a temporal scale through two mechanisms. On the one hand, water availability appears to account for within-year seed predation rates, leading to a safe period during the months of water shortage. The reason for this is the strong dependence of *A. sylvaticus* populations on short-term prior precipitation conditions, which in turn are a surrogate of primary productivity, as reported by Díaz *et al.* (2010) for north-western Spain. This dependence on climatic conditions is also revealed by the significant influence of drought intensity as an additional factor explaining food limitation, probably resulting from the more extreme conditions of central Spain. Rodent population reduction in the study area during the summer period is confirmed by the consequent decrease in the number of *A. sylvaticus* individuals in our recorded videos. On the other hand, *A. sylvaticus* proved highly sensitive to the occurrence of masting events, a between-year climate-mediated process in *P. pinea* (Mutke *et al.*, 2005a; Calama *et al.*, 2011). Dual climate prey-predator control of this type has been identified in alpine ecosystems, enhancing fitness in European larch (Poncet *et al.*, 2009), which suggests that the described pattern may be common, at least in limiting environments. Nevertheless, it should be noted that a non-negligible fraction of the observed between-year and spatial variability in seed predation is attributable to the stochasticity of the process, as indicated by the non-null random variance at seed point × year level.

The resulting parameterization of seed production as a covariate explaining predation also shed light on the shape of the functional response of *A. sylvaticus* at stand scale. On the one hand, the predicted Holling Type II response indicates that there is a greater chance of seeds escaping predation with increasing seed production (for instance, when mast seed crops are produced). This supports the predator satiation hypothesis (Salisbury, 1942; Janzen, 1974), which is expected in low diversity plant communities where among-individual synchrony in fecundity occurs (Nilsson and Wastljung, 1987; Homma *et al.*, 1999) and where the frugivore present is not primarily a mutualist (Hulme and Hunt, 1999; Vander Wall, 2002), as is clearly the case in our study. On the other hand, Type II response would also suggest that the studied predator is a specialist (Andersson and Erlinge, 1977), in contrast with the behaviour commonly exhibited by *A. sylvaticus* (Díaz *et al.*, 2010). The most likely explanation in this case is that *A. sylvaticus* is acting as a specialist with respect to this particular source of food. In this regard, generalists are able to switch from one food source to another when the preferred source is scarce. However, when the preferred food is notably more palatable/nutritive than others, it is possible that frequency dependence does not occur at low crop densities (Hulme and Hunt, 1999) and therefore the generalist continues foraging preferentially on the same crop, leading to total exploitation of exposed seeds and even to instability of the system (Murdoch, 1969; Murdoch and Oaten, 1975). This may be the case of *A. sylvaticus* and the highly nutritive *P. pinea* seeds in periods of pine nut scarcity.

Seed predation spatial pattern

From a spatial perspective, *A. sylvaticus* was distance dependent with respect to seed sources. As a consequence of the higher predation rates in the close vicinity of trees, recruitment might be expected to occur at relatively large distances from seed sources (Janzen-Connell hypothesis; Janzen, 1970; Connell, 1971). However, Calama *et al.* (2012) identified a clumped distribution of one-year-old *P. pinea* seedlings beneath the tree crowns, suggesting that the spatial distribution of predator activity does not qualitatively alter the *P. pinea* seed shadow. This fact is ecologically consistent with the findings of these authors, who stated that seedling survival was also higher under the canopy. Therefore, those locations which offer the highest probability of offspring survival are also those with the greatest probability of seed occupation after predation.

Seeds were also more rapidly predated in the proximity of the potential natural shelters identified (stumps). This finding is consistent with those reported in other studies concerned with spatial foraging preferences in *A. sylvaticus*, reflecting the preference of this species for protected feeding areas (Hulme, 1997; Fedriani and Manzaneda, 2005).

4.6.3. Secondary seed dispersal

It has been reported that masting promotes animal-mediated seed dispersal because hoarding animals are able to cache excessive amounts of food in order to withstand unfavourable periods (Vander Wall, 2002). No evidence of such behaviour was detected in our experiments, which supports the results of other studies conducted in the Iberian Peninsula (Hulme, 1997; Gómez *et al.*, 2003; Gómez *et al.*, 2008) even though in its southernmost distribution area, *A. sylvaticus* usually coexists with masting species. The fact that *A. sylvaticus* acts mainly as a predator would suggest that cached resources are not further required, as the seed dispersal period in *P. pinea* (warm period) is immediately followed by the favourable period for the rodent species (colder period) (Torre *et al.*, 2002; Díaz *et al.*, 2010).

Despite the limited extent of animal-mediated dispersal according to our data, a number of conclusions can be drawn with regard to the effectiveness of the small fraction of surviving, animal dispersed seeds. Scatter-hoarding of *P. pinea* seeds seems to be a rarely used mechanism in *A. sylvaticus*, as previously suggested by Hulme (2002) with regard to rodents (excepting squirrels). Furthermore, when scatter-hoarding occurs, our observations revealed rapid pilfering and immediate consumption of the cached seed. Larder-hoarding was much more frequent although probably ineffective as a dispersal mechanism. Such hoards were normally used as very short-term reserves. Moreover, those seeds that remain in caches at very high densities (until the arrival of the unfavourable period for rodents, escaping predation through early germination) are not expected to produce viable seedlings due to interspecific competition (Hulme, 2002; Gómez *et al.*, 2003). Furthermore, the model fitted using the artificial-shelter data indicates that *A. sylvaticus* only larder-hoards up to very short distances, displaying no particular habitat preference, which suggests that the impact on final seedling shadow would be of little importance.

As regards other guilds of possible dispersers, there were far fewer camera sightings of *C. cyanus* and *C. coronae* than of *A. sylvaticus* and therefore the impact of potential dispersal on managed forest dynamics would be limited. However, corvids are well-known dispersers (Vander Wall, 2002; Gómez, 2003) and most visits coincided with the dispersal period of *P. pinea*, suggesting possible hoarding behaviour of birds, presumably attracted by seed abundance as described in Vander Wall (2002). The behaviour exhibited by the birds in the recorded videos, in which seeds were never predated *in situ* but removed somewhere else. Although beyond the scope of this particular study, the importance of these birds should not be overlooked from an ecological viewpoint.

4.6.4. The *Apodemus sylvaticus-Pinus pinea* interaction

The results of this study highlight the strong influence of climate in regulating the coexistence of *A. sylvaticus* and *P. pinea* through two complementary strategies: on the plant side, seeds are able to escape predation for a period of several months (i) concentrating dispersal in the unfavourable period for rodent populations; and (ii) producing mast pulses that notably increase the fraction of non-predated seeds during the aforementioned period. Therefore, it may be inferred that the dispersal strategy developed by *P. pinea* is an adaptation mediated by the specialist-like behaviour of *A. sylvaticus* when feeding on *P. pinea* seeds. This selective pressure of *A. sylvaticus* would be more important at within-year level, given the climatic origin of *P. pinea* masting habit.

The abovementioned strategy alone, however, does not guarantee the persistence of *P. pinea*: on the animal side, fluctuations in *A. sylvaticus* populations mainly depend on primary productivity, the numerical recovery of which at the end of the dry period results in rapid depletion of previously dispersed seeds. Given the strict conditions required for seed germination in the species (Manso *et al.*, 2012c; in press), conditions which normally coincide with early fall (Calama *et al.*, 2012), the window for emergence and subsequent establishment is especially narrow. Due to the high stochasticity generally associated with ecological processes, it can be concluded that the predatory pressure exerted by *A. sylvaticus* could dramatically condition *P. pinea* natural regeneration at annual level.

However, the intense and non-progressive fellings carried out in the managed *P. pinea* forests of the Northern Plateau of Spain, severely reduce the likelihood of adequate conditions for establishment in the long term. This situation may underlie the observed natural regeneration failure in managed forests. As regards a future climatic scenario of increasing drought intensity and length in central Spain (De Castro *et al.*, 2005), predation levels might be expected to decrease although seed production and germination may also be seriously constrained (Manso *et al.*, 2012c; in press). Therefore, further research needs to be conducted in this field in order to shed more light on this particular matter.

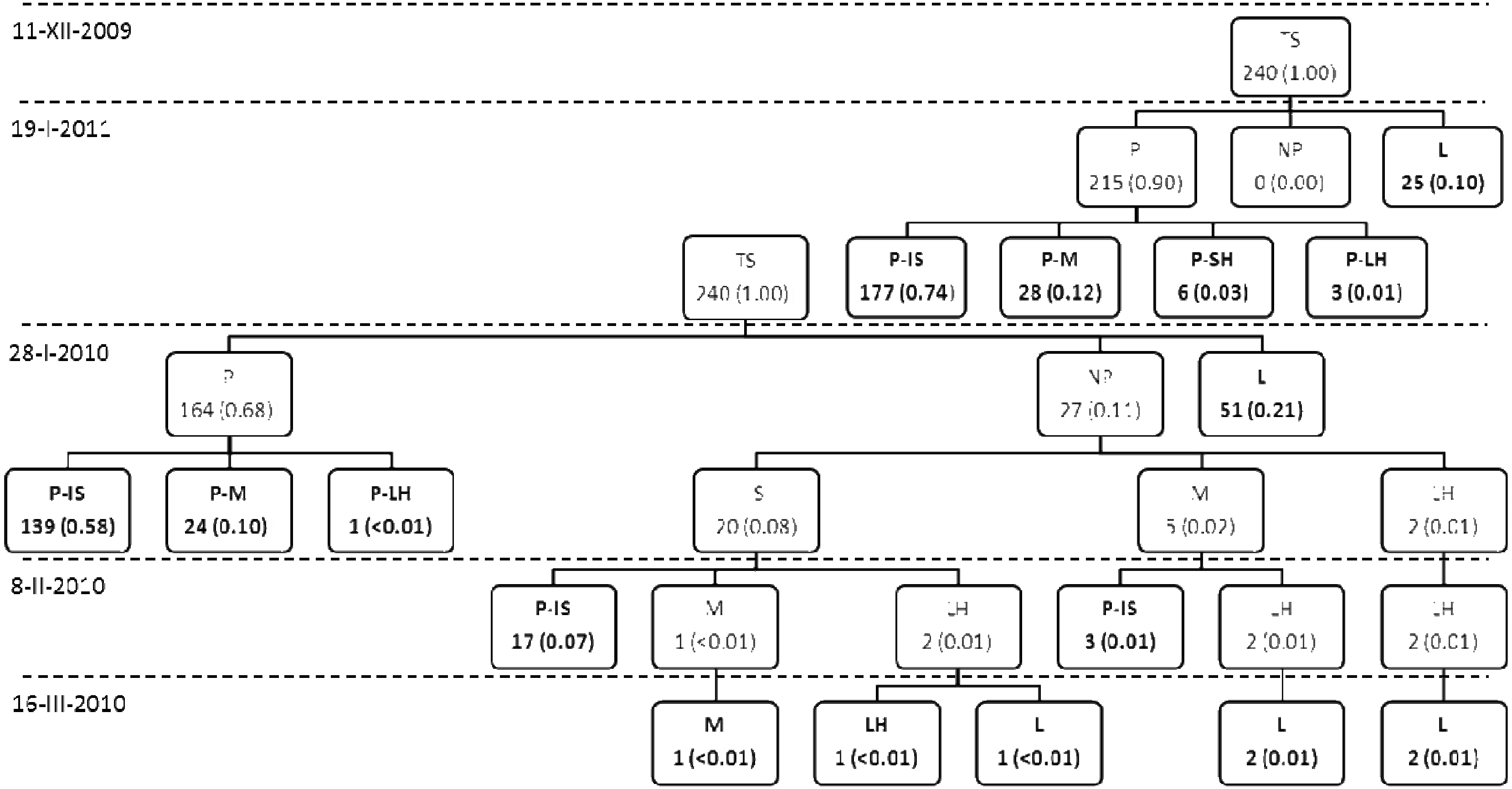

Figure 4.5. Results of the seed fate experiment. Each box represents a specific state for a particular number of seeds and specific date (left). In brackets, the corresponding proportion over the total. Possible states: TS: Total Seeds; P: Predated; NP: No Predated; L: Lost; P-IS: Predated In Situ; P-M: reMoved and Predated; P-SH: Scatter-Hoarded and Predated; P-LH: Larder-Hoarded and Predated; IS: In Situ; M: reMoved; LH: Larder-Hoarded. In bold, terminal states

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Chapter 5

Seedling survival

Based on:

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

Specific objectives:

1. Selecting variables to include in the different submodels that are easily-accessible or controllable by forest managers so that the final model can truly constitute a decision-making tool

5.- Modelling the temporal transition probability of seedlings to survive

6. Identifying the potential bottlenecks that could affect natural regeneration at subprocess level, taking into consideration the silvicultural practices and the ecological processes involved

Data:

- Seedling occurrence and survival data series (2004-2011) from plots P1 to P6 from the natural regeneration INIA site in La Pedraja de Portillo (Valladolid)

Methodology:

- Proportional-hazards model

Main findings:

- When cohorts are generated in fall, seedling mortality was extremely high during the first months, the number of surviving seedlings being stabilised after two years

- Contrastingly, almost no seedling appeared in spring survived the summer season, suggesting that drought is a limiting factor for seedling survival

Management implications:

- Given that only abundant cohorts occurred in fall are expected to produce a relevant number of persistent seedlings, seedling survival could become a bottleneck for natural regeneration

- Present strict and intensive regeneration fellings are currently conducted without considering these findings and, therefore, flexibility is needed in this respect until cohorts can be considered as established

5. Seedling survival

5.1. Abstract

The current study intends to model seedling survival of *Pinus pinea* L. in the Northern Plateau of Spain, as well as to identify the key factors that determine seedling mortality. These findings will make it possible to infer recommendations for silviculture under both the present and future climate. For the purposes of this research, survival of different cohorts has been surveyed from 2004 to date in *P. pinea* even-aged stands located in the sandy flats of the province of Valladolid. Data were analyzed through a proportional-hazards model, based on the cohorts occurred in fall. The effect of drought on these cohorts was also considered. The use of the latter as an explanatory variable leads to unrealistic predictions, which suggests that most of the variability is accounted for seedling age. Survival of autumn seedlings during the first year is lower than 20%, the surviving individuals being stabilized in 4% of the emerged seedlings from the second year onwards. In the case of seedlings appearing in spring, almost none of them overcame the first summer, suggesting that drought is behind mortality in these cohorts. In a scenario of climatic change, it would be likely that drought impact would also affect the seedlings from the previous fall period. Given the predicted high mortality rates, current silviculture schedules should become more flexible, allowing the occurrence of an enough number of cohorts to guarantee successful recruitment.

Keywords: survival analysis, seedling mortality, drought, stone pine

5.2. Introduction

Seedling mortality represents a major cause for natural regeneration failure in Mediterranean forests (Calama and Montero, 2007). In the case of *Pinus pinea* L., where bottlenecks for regeneration are expected in all the processes involved (seed production (Calama *et al.*, 2011); seed dispersal (Manso *et al.*, 2012d); germination (Manso *et al.*, 2012c; in press); and seed predation (Manso *et al.*, 2012b), seedling survival has become a major concern for forest managers. Specifically, it is of crucial importance the impact of summer drought on seedling survival, as water availability is acknowledged as the most serious constraining factor in the Mediterranean (Blondel and Aronson, 1999).

As a consequence, there is an urgent necessity of modelling the process through realistic and accessible models as a management tool. Regression models based on survival analysis techniques have been successfully used for that purpose in studies on seedling survival (Selander, 1993).

The main aims of the present paper are (i) modelling the seedling survival process; (ii) identifying the variables involved; and (iii) providing silviculture alternatives that guarantee natural regeneration. We hypothesized that (i) summer drought drastically conditions recruitment; and that (ii) seedling mortality could be partially behind the natural regeneration failure of the species in the Northern Plateau of Spain.

5.3. Material and methods

5.3.1. Study site

The study site is located in the *Tierra de Pinares* county, province of Valladolid, in the municipality of La Pedraja de Portillo (41º28’N, 4º43’W), at an altitude of 700 m above sea level. The study was conducted in a *P. pinea* pure even-aged stand (*Corbejón y Quemados* public forest), representative of the regional average conditions (Mediterranean-continental climate and sandy soils). Specifically the experiment was set up in a 120-years-old regeneration block and site index 15–16 m at 100 years, characteristic of a II class quality (Calama *et al.*, 2003). Seeding felling were carried out in 2002–2003.

5.3.2. Experimental design

The experiment, set up in 2003, consists of six 60 m × 80 m plots (0.48 ha each), with a 7.5 m buffer area outwards, where two regeneration systems were applied (the shelterwood system (SW; plots P4-P6) and the seed-tree system (ST; plots P1-P3)), implying three replications each. Additionally, a control plot was also established. Stand density and basal area (*BA*) in the control (P7) is 149 stems·ha^{-1} (18.42 m^{2}·ha^{-1}). Otherwise, stand density ranges from 73–75 stems·ha^{-1} (*BA* 9.70–12.26 m^{2}·ha^{-1}), in the plots where the SW system was applied, to 46–48 stems·ha^{-1} (*BA* 6.99–9.37 m^{2}·ha^{-1}) in those plots were the ST system was used. Trees in all plots were mapped and their *dbh* (1.30 m) measured.

Twenty 3 m × 3 m subplots were established on a regular grid across all plots (140 subplots; Fig. 5.1). From February 2004 to date, two inventories of seedling emergence and survival have been conducted each year at each subplot (except in 2010, when only one survey was carried out). New seedlings were counted and identified, recording separately also the mortality of the different cohorts.

Daily climatic data including temperature and rainfall corresponding to the whole period of study were gathered from a nearby meteorological station (41º17’N, 4º40’W; data available in www.inforiego.org).

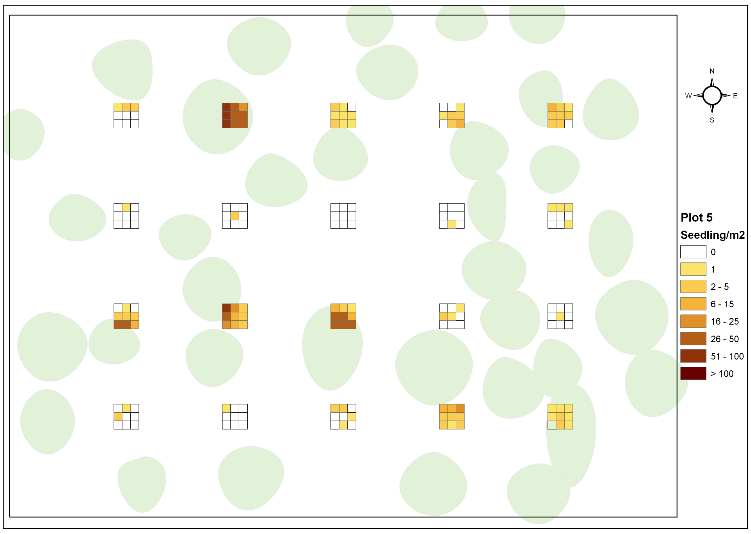

Figure 5.1. Example of subplot deployment within plot 5 (P5). Source: Calama *et al.* 2012

5.3.3. Modelling approach

Modelling of seedling survival was conducted through a non-linear regression based on survival analysis techniques. According to Lawless (2003), in this kind of approaches the probability of survival of a seedling *i* up to time *t* is defined as:

$$S_i(t) = \exp\left(-\sum_0^t h_i(x) \right) \quad [5.1]$$

where $h_i(x)$ is the instantaneous mortality rate or hazard for the subject i in the time t, conditional to survival up to t; and x is a vector or suitable covariates. Therefore, the probability of survival is a decreasing function of the sum of all hazards previous to t.

In the present study, a functional form for $h(x)$ corresponding to the proportional hazards-model (Cox, 1972) with daily basis was adopted. Generically, the hazard can be expressed as:

$$h(x) = h_0(t) \cdot f(x) \quad [5.2]$$

where $h_0(t)$ is the mortality baseline, a function of time, and $f(x)$ is a function of the considered covariates. Both terms must be positive. The shape of the baseline depends on the distribution function assumed for the time T to occurrence of the event of interest (death of subject i, in this case). In the present study, the Gompertz distribution was assumed, which is widely used due to its notable flexibility (Lawless, 2003). Consequently, equation [5.1] can be reformulated as:

$$h_0(t) = \gamma_1 \cdot \exp(\gamma_2 t) \quad [5.3]$$

where γ_1 and γ_2 are estimable parameters, the former strictly positive.

Two different parameterizations were tested. In the first of them, the hazard is set to the baseline (equation [5.3]) and then mortality will be only dependent on seedling age. As an alternative, a second model is presented, where a function of the daily physiological drought (sf, assessed as in Thornthwaite and Mather (1957)) directly affects the baseline:

$$h(x) = [\gamma_1 \cdot \exp(\gamma_2 t)] \times [1 - \beta_1 \cdot \exp(\beta_2 sf)] + [\gamma_3 \cdot \exp(\gamma_4 t)] \quad [5.4]$$

where β_1 and β_2 are parameters to be estimated. β_1 and β_2 necessarily must adopt positive and negative values, respectively, so that the drought function ranges from zero to one. An auxiliary baseline was included through an additive term with parameters γ_3 and γ_4 to prevent the hazard to be necessarily null when $sf = 0$. γ_3 must take positive values only.

The parameters were estimated through maximum likelihood fit. The nature of the observations was taking into account in the formulation of the likelihood function:

the death of a seedling can occur before the first measurement (left truncation), between two measurements (interval censoring) or the seedling can remain alive longer than the experiment time (right censoring). Therefore, the likelihood function is defined as:

$$\ell = \prod_i \left[S_i\left(t_{i,\sup} \mid T \geq t_{i,u}\right) - S_i\left(t_{i,\inf} \mid T \geq t_{i,u}\right)\right]^{q_i} \times \left[t_{i,\sup} \mid T \geq t_{i,u}\right]^{1-q_i} \qquad [5.5a]$$

with

$$S_i\left(t_{i,\sup} \mid T \geq t_{i,u}\right) = S_i\left(t_{i,\sup}\right) / S_i\left(t_{i,u}\right) \qquad [5.5b]$$

$$S_i\left(t_{i,\inf} \mid T \geq t_{i,u}\right) = S_i\left(t_{i,\inf}\right) / S_i\left(t_{i,u}\right) \qquad [5.5c]$$

where equations [5.5b] and [5.5c] stand for the probability of survival of a seedling i until the last time it was found alive ($t_{i,sup}$) and the time it was found dead ($t_{i,inf}$), respectively, conditional to survival until the first observation ($S_i(t_{i,u})$). $t_{i,u}$ was predicted by means of the germination model by Manso *et al.* (2012c; in press). Thus, seedling emergence for cohorts installed in autumn can be assumed to occur on 1 December. Concerning spring cohorts, there is a wider between-years variability. Finally, q_i is a dummy variable adopting the value of one if the seedling i dies during the experiment time and zero otherwise.

Both parameterizations were graphically evaluated and compared in terms of their respective Akaike Information Criterion (AIC) value. All calculations were carried out in R 2.14 (R Core Team, 2011).

5.4. Results

In a number of occasions, no seedling was observed when the experiment was revisited. Moreover, only individuals from four cohorts were able to persist, at least until the next visit. Consequently, only these cohorts were used to fit the model. These seedlings were detected in the spring of 2005, 2006, 2007 and 2010, respectively, all of them emerged in the previous autumn. The progression of survival seedlings across cohorts is shown in Table 5.1. Contrastingly, when emergence took place in spring, none of the recorded seedlings survived during the time elapsed until the next measurement.

Table 5.1. Evolution of seedling survival (in number of remaining seedlings) from cohorts occurring in fall 2004, 2005, 2006 and 2009

	cohorts			
date of measurement	fall 2004	fall 2005	fall 2006	fall 2009
28/05/2005	42	-	-	-
14/06/2005	3	-	-	-
27/05/2006	0	34	-	-
10/01/2007	0	9	5665	-
17/07/2007	0	3	2179	-
23/03/2008	0	3	623	-
30/08/2008	0	2	519	-
27/02/2009	0	2	480	-
25/07/2009	0	2	456	-
17/04/2010	0	1	422	40
18/03/2011	0	1	401	6
21/11/2011	0	0	395	3

The model solely consisting of the baseline presented a better fit than that considering drought (AICs 11,943.46 and 12,471.54, respectively). In Fig. 5.2 it is shown that the predictions from the first of these models closely mimic the corresponding observations, particularly for the cohorts of 2006, 2007 and 2010. In respect to the cohort of 2005, there exists a trend to underestimate mortality. Differently, the second model proved less realistic (data not shown) and therefore the simplest model was selected for the purposes of the present study. The values of parameters γ_1 and γ_2 of the preferred model were 0.01 and – 0.0031, respectively. Mean estimated survival prior to first measurement ($S(t_u)$) varies between years proportionally to the time elapsed from emergence (assumed 1 December) to t_u: 53.58%, 21.83%, 31.00% y 66.79% for years 2005, 2006, 2007 y 2010, respectively. The resulting curve monotonically decreases, depending only on time. Given the nature of the proportional hazard models, there is a constant relationship between consecutive observations in terms of hazard, namely exp($\gamma_2(t_{sup}$-$t_{inf})$). Consequently, 25% of the seedlings emerged in autumn would die a month after emergence; 50%, after two months and three weeks; 75%, after six months. The curve of survival levels off after two years, predicting 4% of survival in respect to the predicted initial value at t = 0 (1 December). This value represents 8% of surviving seedlings out of those observed in the first visit each year.

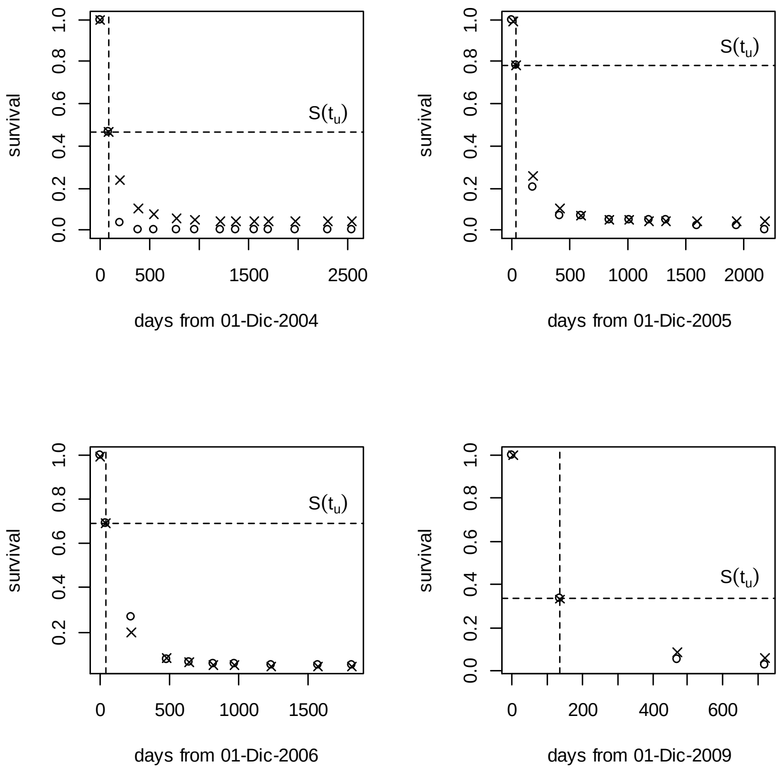

Figure 5.2. Observed (circles) and predicted (crosses) seedling survival over time for the four used cohorts. The horizontal line represents the estimated survival up to time of cohort detection (*S(t_u)*). The vertical line stands for the instant t_u. Note that observations have been scaled so that they coincide with predictions at t_u

5.5. Discussion

The model presented in the current study precisely predicts seedling survival of *P. pinea* for those cohorts emerged in fall as a function of seedling age.

Despite being only few, a fraction of the seedlings originated in fall finally became established. The successfully establishment of these recruits contrasts with the almost total mortality of the seedlings emerged in spring. This fact indicates that summer drought is a strong limiting factor for recruitment for just-emerged seedlings, such as suggested by Calama *et al.* (2012). On the contrary, and according to the results from our models, drought appears not to affect those seedlings that had already faced the winter period. This feature informs a relevant ecological adaptation of *P. pinea* to xeric environments, in contrast to other pine species in the Mediterranean, where severe summer droughts lead to the complete destruction of two-years-old cohorts (Tíscar-Oliver, 2007). From a spatial perspective, other factors, such as the influence of overstory, needs to be tested in the future. In this respect, the medium shade-tolerant behaviour exhibited by *P. pinea* (Awada *et al.*, 2003) suggests a better performance of seedlings when relatively high stand densities are present, as demonstrated for other Mediterranean shade-tolerant species (i.e. *Pinus nigra*; Ordóñez *et al.* (2004)) and already pointed out for *P. pinea* by Calama *et al.* (2012).

All processes involved in regeneration of *P. pinea* are partially responsible for regeneration failure through either low transition probabilities between consecutive stages or the occurrence of a bottleneck (Calama *et al.*, 2011; Manso *et al.*, 2012b; Manso *et al.*, 2012c; in press; Manso *et al.*, 2012d). Along with this circumstance, the observed high mortality rates suggest that current intensive and strict regeneration fellings (Montero *et al.*, 2008) severely condition recruitment, as cuttings are commonly conducted before seedlings could be considered as established. In this respect, flexibility is needed in the application of fellings.

In a context of climatic change, where summer droughts are thought to increase (De Castro *et al.*, 2005), more difficulties to successfully achieve natural regeneration in the Mediterranean are expected (Valladares *et al.*, 2005). Consequently, the impact of more drastic and persistent droughts on seedlings emerged in fall may be relevant. The extent at which this circumstance will affect natural regeneration should be study in detail, given the dramatic consequences for the persistence of the species.

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Chapter 6

Multistage stochastic model

Based on:

Manso, R., Pukkala, R., Pardos, M., Miina, J. & Calama, R. (Unpublished data) A multistage stochastic regeneration model for *Pinus pinea* L in the Northern Plateau (Spain), ***in preparation.***

Specific objective:

7.- Formulating the integral model, from where (i) different silviculture alternatives can be evaluated under varying climatic scenarios; and (ii) the optimal schedule for regeneration fellings can be found out

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Data:

- Outputs from (i) models based on those developed in Chapters 2, 3, 4 and 5 of the present dissertation and (ii) cone production model by Calama *et al.* (2011)

Methodology:

- Multistage stochastic model
- Stochastic simulation
- Stochastic spatial optimisation

Main findings and management implications:

- Multistage stochastic regeneration models are a suitable tool for simulating regeneration performance under different silviculture alternatives and climatic scenarios; also, they permit to optimise management in regard to regeneration success
- Current stand densities at rotation age are insufficient to guarantee adequate dispersal, the optimal value being around 150 stems·ha^{-1}. Rotation length needs to be extended up to 120 years
- In addition, flexibility is required in the scheduling of the regeneration fellings, which could comprise even longer regeneration periods
- In consequence, *P. pinea* regeneration dynamics in unmanaged stands may lead to uneven-aged structures
- Under a scenario of climatic change, *P. pinea* shows an acceptable behaviour concerning natural regeneration, which reveals a notable ecological value of this species to be considered in the future

6. Multistage stochastic model

6.1. Abstract

Natural regeneration represents an essential factor in sustainable forest management. *Pinus pinea* L. woodlands located in the Northern Plateau of Spain have been object of modern management for over a century but, unfortunately, natural regeneration has not always been successful. Regeneration has not thrived either under the seed-tree system or under the shelterwood system without complementary seeding. Moreover, serious concerns arise in the perspective of a changing future climate. In order to quantify recruitment under different silviculture alternatives and varying climatic scenarios, and to optimise management scheduling, a stochastic multistage regeneration model is presented. The model consists of a multiplicative structure where each factor represents the transition probability between the different stages, from seed production to definitive seedling establishment. Outputs of a seed production submodel are therefore multiplied by the transition probabilities assessed through the submodels of dispersal, germination, post-dispersal seed predation and seedling survival. All submodels include stand and climatic variables. Model simulations show that current stand densities at rotation age are insufficient to guarantee adequate dispersal, the optimal value being around 150 stems·ha^{-1}. Identically, rotation length needs to be extended up to 120 years, in order to benefit from higher per tree seed production. These results are confirmed by the stochastic optimisation, which additionally suggests that more flexible regeneration felling schedules are needed to achieve natural regeneration in the species. This fact may indicate that *P. pinea* would spontaneously grow in semi-uneven-aged stands, accordingly to its medium shade-tolerant behaviour. Regeneration performance does not appear to worsen under a scenario of climate change, as long as relatively high rotation lengths and stand densities are permitted. This acceptable behaviour under climatic change conditions informs an additional ecological value for the species in Mediterranean sites threatened by an increasingly severe drought occurrence.

Keywords: natural regeneration, transitional probability, stochastic spatial optimisation, climatic change

6.2. Introduction

Natural regeneration in forest species has been modelled from two main perspectives. A first approach consists of the so called recruitment models. They predict the abundance or occurrence of established seedlings directly from environmental, climatic or silvicultural explanatory variables (e.g. Eerikäinen *et al.*, 2007; Fortin and DeBlois, 2007; Barbeito *et al.*, 2011). Thus, the response variable aggregates all previous processes relevant for establishment. Recruitment models are simple but show limitations when the mechanisms involved in regeneration at subprocess level (e.g. seed production, dispersal, etc.) require special attention (Price *et al.*, 2001). This is the case of critical variables affecting only a single stage in the process during a short time interval and that could be unnoticed when modelling regeneration marginally. Also, when bottlenecks at some stages are expected, recruitment models may prove inadequate.

Multistage regeneration models constitute an alternative approach to overcome these shortcomings (e.g. Leak, 1968; Ferguson *et al.*, 1986; Pukkala and Kolström, 1992; Ordóñez *et al.*, 2006). This approach considers regeneration as a multistage process consisting of underlying consecutive subprocesses that usually can be identified as a series of successive survival thresholds for potential seedlings (Pukkala and Kolström, 1992). Therefore, the probability of regeneration occurrence in space and time can be seen as the product of the transition probabilities corresponding to each involved sequential subprocess. Consequently, multistage models are, at least partly, process-based models, presenting mechanistic basis at subprocess level. In multistage models transition probabilities are separately assessed. They can be empirically obtained, being unique for a specific subprocess (Rey and Alcántara, 2000) or exhibiting a discrete number of values corresponding to different possible states of a particular phase (Ordóñez *et al.*, 2006). A more complex but rather more flexible possibility is to model each transition probability as a set of explanatory variables. Moreover, from a management standpoint, it is convenient to include climatic and silvicultural variables among the explanatory variables.

Regardless of the modelling approach, regeneration models can be used deterministically (i.e. model response produces an unequivocal output) or stochastically (i.e. model response is subject to random variability inherent to the process). The numerous sources of uncertainty arising from the subprocesses involved in regeneration often render deterministic models insufficient for management purposes. Hence, the use of stochastic models is essential to produce accurate and unbiased predictions (Miina and Heinonen, 2008).

This background was taken into account when we undertook the effort of modelling natural regeneration in *Pinus pinea* L. in the Northern Plateau of Spain, a particularly complicated case of unsuccessful regeneration in managed forests. *P. pinea* is an essential species in Mediterranean ecosystems, often occupying sites where few tree species are able to thrive due to the typical Mediterranean weather conditions, continental winters and sandy soils. In addition, the species provides important economic benefits to local populations from its timber and edible seed production. There are over 50,000 ha of managed *P. pinea* forest on the Northern Plateau. Natural regeneration in these forests is rarely successful when using the existing regeneration methods 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* (seed production (Calama *et al.*, 2011); seed dispersal (Manso *et al.*, 2012d); germination (Manso *et al.*, 2012c; in press); seed predation (Manso *et al.*, 2012b) and seedling mortality (Manso *et al.*, 2012a; in press)), concluding that all these subprocesses can potentially become a bottleneck for regeneration. However, the challenge remained to ensemble this information into an integral model for the species.

In order to accomplish this task, a multistage stochastic model was developed. Transition probabilities were independently modelled, based on the aforementioned partial studies for the species, through climatic, environmental and silvicultural variables. This model formulation is particularly useful as it makes possible to conduct predictions in order to evaluate the effect on regeneration of different climatic scenarios and varying silvicultural alternatives at spatial and temporal level. In this respect, the model can be used as a complement of the growth and yield simulator PINEA2 (Calama *et al.*, 2007). So far, we are not aware of any multistage regeneration model comprising these options. In addition, the model was implemented in an optimisation routine addressed to find out the management schedule that maximizes the probability of uniform recruitment occurrence. Although optimisation has been widely used in forestry studies to maximize the production of different resources (Valsta, 1992; Hyytiäinen and

Tahvonen, 2002; González-Olabarría *et al.*, 2008; Pasalodos-Tato *et al.*, 2010), to our knowledge the target has never been natural regeneration.

The main aims of this study were (i) to evaluate suitability of different silviculture alternatives in regard to natural regeneration under different climatic scenarios in *P. pinea* even-aged stands in the Northern Plateau of Spain; and (ii) to optimise the regeneration fellings schedule. For these purposes, a multistage stochastic regeneration model for the species was developed. Our prior hypotheses to be tested from the resulting simulations and optimisations are that (i) more flexible management schedules would be the key aspect to successfully achieve natural regeneration in the species; and (ii) future climate may negatively impact on natural regeneration, although adequate management schemes could mitigate these effects.

6.3. Material and methods

6.3.1. Regeneration model

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

$$S_{i1} = \sum_{k} N_{kl} \cdot Pd_{i1k} \cdot Pg_{i1} \cdot (1 - Pp_{i1}) \cdot Ps_{i1} \qquad [6.1]$$

It can be easily followed that the generalized equation for any time j yields:

$$S_{ij} = \left[S_{ij-1} + \sum_{k} \left(N_{kl} \cdot Pd_{ijk} + N_{ij-1} \right) \cdot Pg_{ij} \cdot \left(1 - Pp_{ij} \right) \right] \cdot Ps_{ij} \qquad [6.2]$$

The submodels explaining the transitional probabilities considered in the present paper are briefly detailed below. Given the temporal precision of the submodels, a monthly time step was set for the regeneration model.

Seed production

Based on Calama *et al.* (2011), this submodel provides annual predictions of seed production at tree level. The original model was formulated as a zero-inflated lognormal linear mixed model, meaning that: (i) it predicts the probability of a given tree to bear cones in a specific year through a binomial process, considering the species' masting habit; (ii) conditional to cone occurrence, lognormal predictions on cone weight per tree for that year are provided. The weight of cones for a given tree was transformed into our interest variable N_{kl} (seeds·(year·tree)$^{-1}$) using the dimensional correction deduced by Morales (2009). Covariates accounting for cone occurrence and cone weight are of four types: tree variables, stand variables, site variables and climatic variables. In this respect, different factors can limit seed production, including (i) too low or too high densities, which could lead either to seed limitation or to a reduction in the per tree cone production, respectively (Calama *et al.*, 2008b; Calama *et al.*, 2011); (ii) tree age, as the younger the individual, the lower the production, up to an age of 120 years; and (iii) intense dry conditions and extreme frost events affecting the key periods of cone formation, which gives rise to *P. pinea* masting habit (Mutke *et al.*, 2005a; Calama *et al.*, 2011) .

Dispersal

The spatial pattern of dispersal of *P. pinea* seeds was parameterized by Manso *et al.* (2012d) based on the 2Dt model developed by Clark *et al.* (1999a). In this submodel, Pd_{ik} is defined through the kernel, or Poisson-distributed probability of a seed from a particular tree *k* to drop in a specific location *i*. The kernel is a monotonic decreasing function of the distance between the tree *k* and the considered point *i*. Thus, the number of seeds N_{ikl} from tree *k* reaching the location *i* during year *l* would be the product of the kernel Pd_{ik} and the nut production of tree *k* for that year N_{kl}. The total number of seeds expected in point *i* is assessed as the sum of N_{jk} over all trees. Providing year *k* is a mast year, low values of Pd_{ik} are due to stand densities below a certain threshold and/or a highly aggregated pattern of adult trees' spatial distribution, resulting in dispersal limitation, given the very short dispersal distance characteristic of *P. pinea* (Barbeito *et al.*, 2008; Manso *et al.*, 2012d)

The submodel accounting for the temporal pattern of seed release in *P. pinea* is detailed in Manso *et al.* (2012d). Once a suitable thermal threshold for cones to open is reached (mean monthly temperature>16 ºC), the model produces monthly predictions on the proportion of released seeds out of those remaining in the cone in the previous month. This proportion is a linear function of the square root of total monthly precipitation.

Germination

The utilised germination submodel was that proposed by Manso *et al.* (2012c; in press). In the mentioned study, germination modelling in *P. pinea* was approached through a proportional-hazards mixed model. The probability Pg_{ij} of a seed to germinate in a specific time interval j at location i can be interpreted as a binomial process and it is predicted on a daily basis via integration of the hazard function. This function describes the daily germination rate conditional to no prior emergence. The hazard function was defined as the product of a generic germination baseline and several nonlinear functions of covariates ranging from zero to one. Covariates controlling germination were climatic (thermal) and stand-related (overstory influence). An additive autoregressive term was included in the model to deal with daily correlation in the hazard. The model takes into account the interval and right censoring nature of observations as well as the lack of independence within years through the inclusion of random effects affecting the baseline. From this submodel it can be inferred that at temporal level, germination is favoured by occurrence of adequate –though rare– thermal conditions in fall and it is limited by frost events, the optimal period for germination being limited to few days in late fall and spring. Moreover, occasional dispersal to large enough overstory gaps can motivate Pg_{ij} to significantly decrease (Manso *et al.*, 2012c; in press).

Predation

The seed predation submodel used in the current study is based on that described in Manso *et al.* (2012b), producing monthly predictions of predation probability Pp_{ij} for *P. pinea* seeds. As zero records (no seed survival due to predation) occurred in more units than expected from the correspondent distribution, it was assumed that two different mechanisms affected the probability of seed predation: occurrence of absolute predation in a given location and abundance of survival conditional to no absolute predation. Abundance was considered binomial-distributed, as it can be assumed that all seeds hold the same probability of being predated, providing they have not been destroyed before. The aforementioned features were accommodated through a zero-inflated binomial linear mixed model, considering data correlation within years. The covariates accounting for both mechanisms described the main environmental trophic characteristics that control predator population: water availability (system primary productivity) and food inputs, independent of current weather (*P. pinea* masting habit). Only predation by rodents is considered, as seed losses caused by birds can be assumed as negligible (Manso *et al.*, 2012b). 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. This effect is partially mitigated along with increasing seed production.

Seedling survival

In order to consider mortality of emerged seedlings in the regeneration process, a simplification of the model developed by Manso *et al.* (2012a; in press) was employed. The daily probability P_{sj} of a seedling to survive is predicted through a proportional-hazards regression model. In this model, the hazard function was assumed to be a Weibull mortality baseline affected uniquely by the age of the seedling, thus daily mortality rate decreases monotically over time. This model predicts high mortality rates of seedlings during the first year since emergence, strongly limiting recruitment in the species. Therefore, 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.

Given the multiplicative structure of our model, regeneration failure will be motivated by the existence of a bottleneck in at least one of the considered sequential subprocesses. 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; and to (ii) the occurrence of adverse climatic conditions. A summary of the covariates included in all models as well as their influence in the correspondent subprocess is shown in Table 6.1.

Further information on experimental design and data collection can be found in the referred literature and the previous chapters of this dissertation.

Table 6.1. Description of the used models

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]	+		
			NU[e]	categorical		
		temporal	pp[f] (may to jun 3ybd)	+		
		(climate)	pp (oct to nov 3ybd)	+		
			frost[g] (dec to mar)	–		
	abundance	stand	log(N)	–		
		tree	d	+		
			d/dg	+		
		site	SI	+		
			NU	categorical		
		temporal	pp (may to jun 3ybd)	+		
		(climate)	pp (oct to nov 3ybd)	+		
			pp (jul to sep 2ybd)	+		
			pp (feb to may)	+		
			frost (dec to mar)	–		
dispersal (spatial)	-	stand	distance to trees	–	-	-
		tree	seed production	+		
dispersal (temp)	-	temporal	pp	+	-	month
		(climate)	thermal cut-off	+		
germination	-	stand	IPOT[h]	+	year	day
		temporal	max temperature	optimal		
		(climate)	time from last frost	+		
		-	autorregressive term	+		
predation	non-occurrence	temporal	drought	–	year	month
		(climate)	cumularive pp 3mbp	+		
	abundance	stand	seed production	+		
		temporal	drought	+		
		(climate)	cumularive pp 3mbp	–		
seedling survival	-	-	time	+	-	day

[a]N: stand density; [b]d: dbh; [c]dg: mean squared dbh; [d]SI:site index; [e]NU:natural unit; [f]pp: precipitation (ybd: years before dispersal; mbp: months before predation); [g]frost: number of days with severe frost; [h]IPOT: influence potential (competition index)

6.3.2. Stochastic simulation

In order to evaluate the effect of management on recruitment, the described model was used to simulate natural regeneration for different silviculture alternatives. Specifically, the influence on regeneration of varying stand stockings and rotation lengths existing at the beginning of the regeneration period was tested during an interval of 10 years. In order to achieve realistic results on final recruitment, mortality was allowed to occur for an additional 10-years 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 current climatic conditions and also considering the predictions for central Spain in the last third of the 21st century under the A2 climate-change scenario (De Castro *et al.*, 2005).

As a starting point, deterministic stands holding typical conditions of the end of the rotation within the range of application of all submodels have to be defined to compute simulations in. To accomplish this task, we simulated twelve 100 m × 100 m plots where tree location was the result of a Poisson process. A buffer strip of 12 m was also taken into account. Single tree development was simulated using the growth module of the software PINEA2 projecting up to an age of 80, 100 and 120 years an initial common 20-years-old even-aged *P. pinea* stand with 500 stems·ha^{-1} and site index 15 m. Besides rotation length age, simulated plots differed in the applied thinning schedule, which led to densities at rotation age of 50, 100, 150 and 200 stems·ha^{-1}, resulting in twelve age-density combinations.

The regeneration process was stochastically simulated at each of the twelve 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 will provide a weighted outcome to be used to generate a probability regeneration map for the plot. Therefore, for each of our twelve initial, deterministic plots, 500 simulations (corresponding to one scenario each) were computed at 1 m^2 scale. As a result, 500 regeneration Boolean maps were generated where those 1 m^2 quadrats where at least one seedling was predicted to establish were assigned the value of one. Otherwise, a zero value was given. Finally, the average value over the 500 maps for each quadrat was calculated, producing as a result a regeneration map where each cell value ranges from zero to one, representing the mean probability of holding at least one seedling at the end of the regeneration period. Additionally, the average probability μ across all 1 m^2-quadrats of the resulting regeneration map and the standard deviation σ of the probability among all cells in the same map were assessed.

The stochastic scenarios to be simulated were defined as follows:

(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 climatic records. In order 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). In each simulation, 14 annual records were randomly chosen to create a climatic scenario: four of them characterized pre-regeneration weather conditions determining seed crops of the first years, whereas the 10 annual series left were utilized to carry out simultaneous predictions from all submodels where climate is involved.

(ii) Cone production submodel: for each chosen annual record, the probability of every tree in the plot to bear cones was predicted. 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 productive trees was estimated and a random realization of a normal distribution of mean zero and model residual error variance was added to each prediction.

(iii) Dispersal submodel: for each randomly sampled annual record, cones were assumed open when the monthly mean temperature reached 16 ºC. Starting in the month fulfilling this thermal condition, seeds are released and dispersal is spatial and temporally distributed according to the predictions of the dispersal models. At a spatial level, 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 is predicted at monthly scale. Stochastic components are included in two ways. First, a realization of the year random effect of the germination model was added to the germination baseline 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 distribution U(0, 1). When the predicted probability was lower than the generated random number we assume that the seed did not germinate, while we assume germination otherwise.

(v) Predation submodel: Dispersed and non-germinated seeds are vulnerable to predation. The predation model predicts first the monthly probability of having total predation in a 1-m^2 quadrat in a specific meteorological annual record. This probability

was compared with a random number sampled from the uniform distribution and total predation was predicted to occur if the probability value was higher than the random realization. Conditional to quadrat-level survival, probability of seed-level survival during that month was predicted and randomized through the same procedure, given its binomial nature. An additional source of stochasticity is given by the year random effect affecting both processes within the model. As the estimated covariance of both random components is non-null, randomization cannot be carried out directly from uncorrelated random numbers generation. Therefore, 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. 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 accordingly to the climate-independent predictions from the survival submodel. No randomization was carried out in this model.

Table 6.2. Changes in mean temperature (ºC) and total precipitation (%) under the A2 climatic scenario in Central Iberian Peninsula in the last third of the 21st 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

6.3.3. Stochastic optimisation

Besides evaluating the impact of the silviculture applied through the cycle on regeneration via simulations, the regeneration felling scheduling can be optimised in order to maximize sufficient and well distributed recruitment for a given stand.

Initial stand

A 250-stems·ha^{-1} stand with a bimodal diameter distribution was simulated. 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 lesser than a random realization of a Weibull distribution (shape parameter = scale parameter = 1), leading to an aggregated distribution of trees.

Objective function

A function to maximize representing the interest of managers concerning natural regeneration is to be defined. Successful regeneration is expected to be abundant and evenly distributed. These two features were summarized in this study through the following objective function (*OF*):

$$OF = \mu + (1 - \sigma) \qquad [6.3]$$

μ and σ being defined in subsection 6.3.2. Higher values of μ imply in general 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. Optimisation 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 so as to take into account main stand conditions affecting regeneration. The tree-selection algorithm developed by Pukkala *et al.* (1998) and modified for optimisation purposes by Pukkala and Miina (1998) was adopted. When using the original algorithm, less competitive trees are removed first. The aforementioned modification includes two parameters b_1 and b_2 that are optimised along with the rest of decision variables. The effect of these parameters is to provide a high degree of flexibility in felling tree-selection, which in turn makes it possible to accommodate the optimal spatial organisation of tree diameter in regard to regeneration. The number of fellings (N_{fell}) was not optimised but a feasible schedule was set consisting of two operations taking place in the first and fifth year of the regeneration period, respectively ($N_{fell} = 2$). As a conclusion, in the present optimisation problem decision variables were felling intensity (in percentage of removed trees) and parameters b_1 and b_2 at each intermediate harvest operation, which yields $3 \times Nf_{ell}$ decision variables.

Optimisation method

The optimisation algorithm utilised 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 non-smooth and non-differentiable objective functions. It consists of two differentiated steps: exploratory search and pattern 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, so that 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 optimiser based on 500 scenarios. In order to test the effect of using different starting points, optimisation was initialized from two different base points, defined by two sets of decision variables. The first of them corresponds to a light management (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 management (intensity of fellings of 70% and 50%; $b_1 = -1$ and $b_2 = -2$). The optimisation was assessed through the software RODAL 5.0.

6.4. Results

6.4.1. Stochastic simulations

Effect of stand structure

The mean probability of holding at least one seedling·m^{-2} (μ) increased after a 10-years period along with both stand final density and rotation age (Figs. 6.1 and 6.3a). The increment in μ was lower as the tested densities became larger, with a tendency to level off when density was higher than 150 stems·ha^{-1}. This pattern was similar for all rotation ages, whose effect was basically to evenly intensify the effect of density in all situations. μ values averaged 0.50 for the 50 stems·ha^{-1} plot, 0.74 for the 100 stems·ha^{-1} plot, 0.82 for the 150 stems·ha^{-1} plot and 0.85 for the 200 stems·ha^{-1} plot, across rotation ages.

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

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 through a gradient of increment of μ values in respect to those predicted for the current climate along with decreasing densities and increasing rotation ages. In the opposite extreme of this tendency, simulations carried out considering rotations of 80 and 100 years and densities over 50 stems·ha^{-1} showed an reduction in terms of μ (Table 6.3; Figs. 6.2 and 6.3b). Overall, μ reached maximum values of 0.74 and 0.82 when simulating 80 and 100 year rotations, respectively, as the leveling off was appreciable at densities as low as 100 stems·ha^{-1} and the tendency of μ was even to decrease beyond 150 stems·ha^{-1}. On the contrary, for the longest rotation, μ exceeded 0.90 at the highest stocking. Contrastingly, σ values presented little changes under the A2 climatic scenario.

Table 6.3. Proportion of variation in predicted mean probability of establishment between the A2 climate scenario and current climate for different densities and rotation lengths. Negative values represent decreasing future probabilities and positive values stand for increasing future probabilities

	density (stems·ha^{-1})			
Rotation (yr)	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

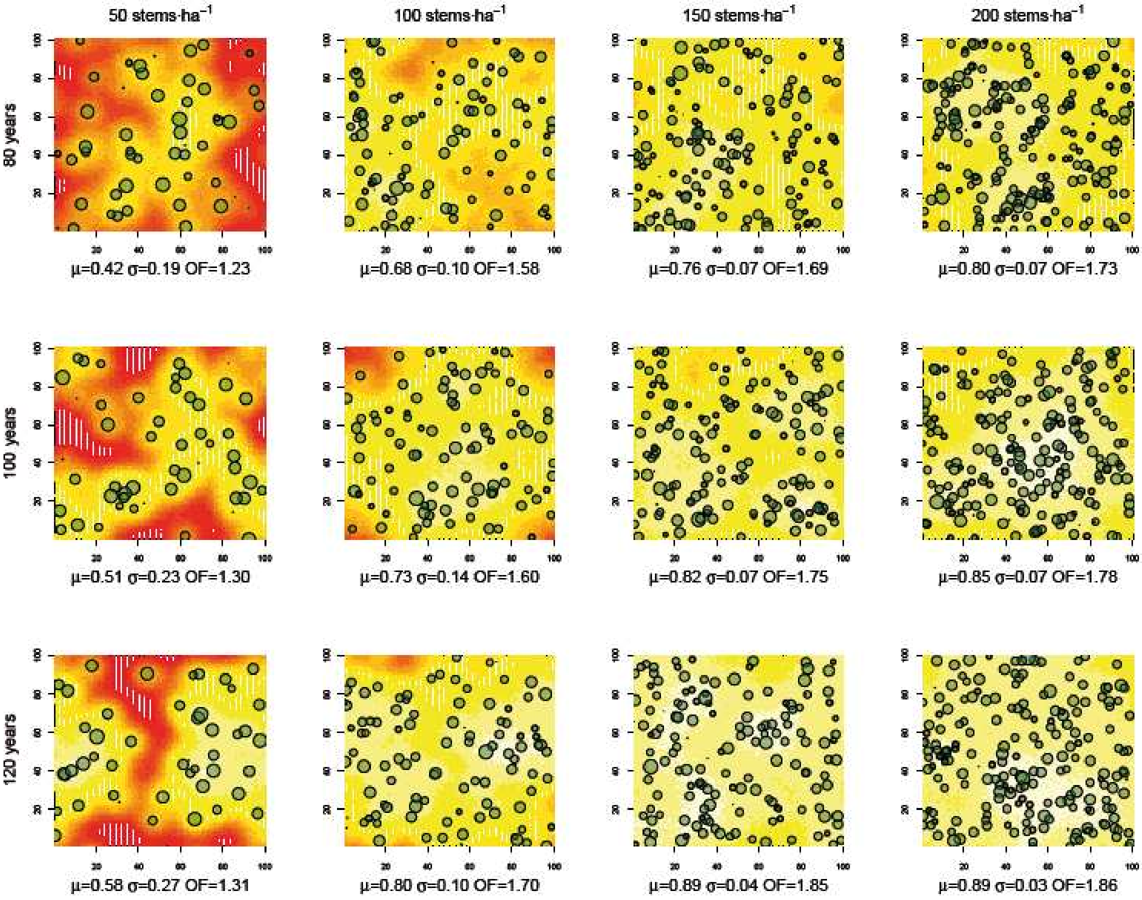

Figure 6.1. Maps of the simulated probabilities of achieving at least one established seedling at 1 m^2 scale in 100 m × 100 m plots at the end of the regeneration period for varying densities and rotations under current climatic conditions. Dark colours indicate lower probability whereas light colours stand for higher probability. Circle positions represent tree locations and circle size is proportional to tree's *dbh*. μ and σ are, respectively, the mean and standard deviation of the probability among 1 m^2 quadrats. $OF = \mu + (1 - \sigma)$

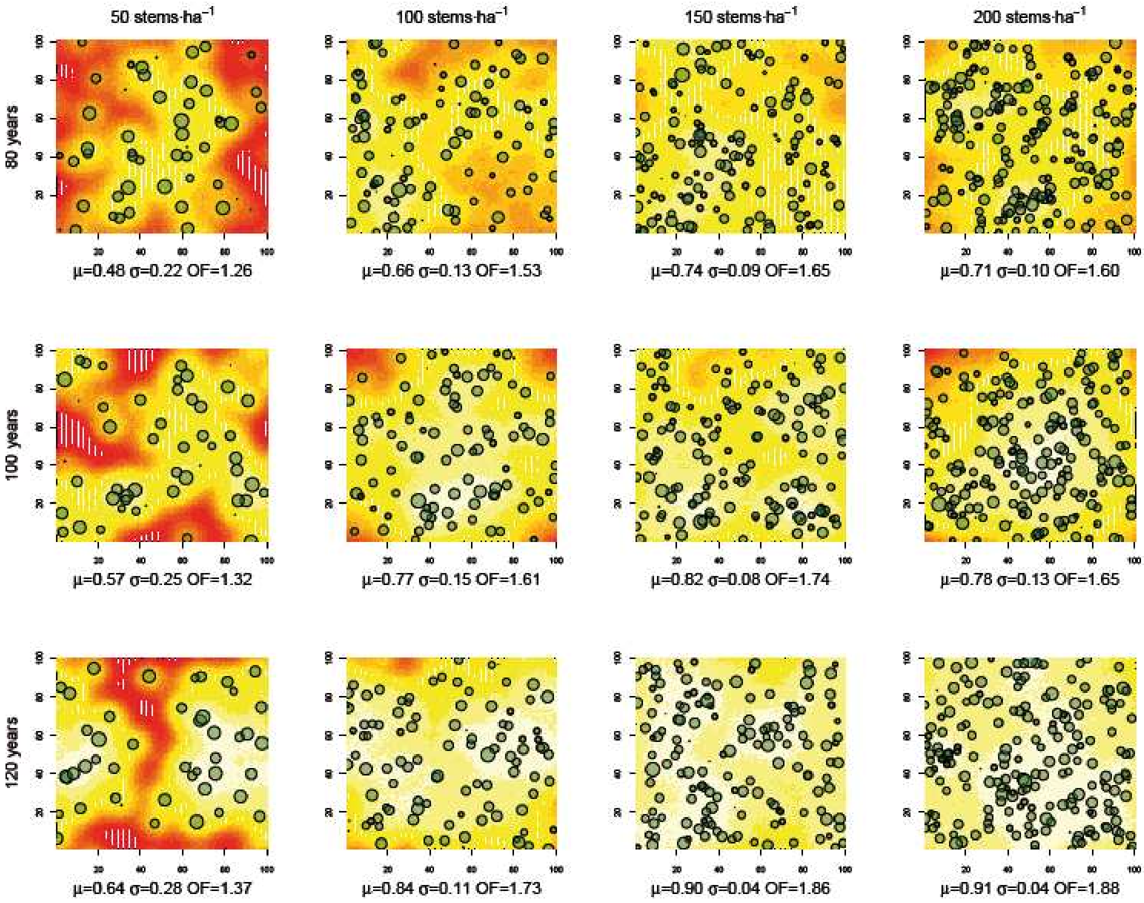

Figure 6.2. Maps of the simulated probabilities of achieving at least one established seedling at 1 m^2 scale in 100 m × 100 m plots at the end of the regeneration period for varying densities and rotations under predicted climatic conditions in the A2 scenario. Circle positions represent tree locations and circle size is proportional to tree's *dbh*. Dark colours indicate lower probability whereas light colours stand for higher probability. μ and σ are, respectively, the mean and standard deviation of the probability among 1 m^2 quadrats. $OF = \mu + (1 - \sigma)$

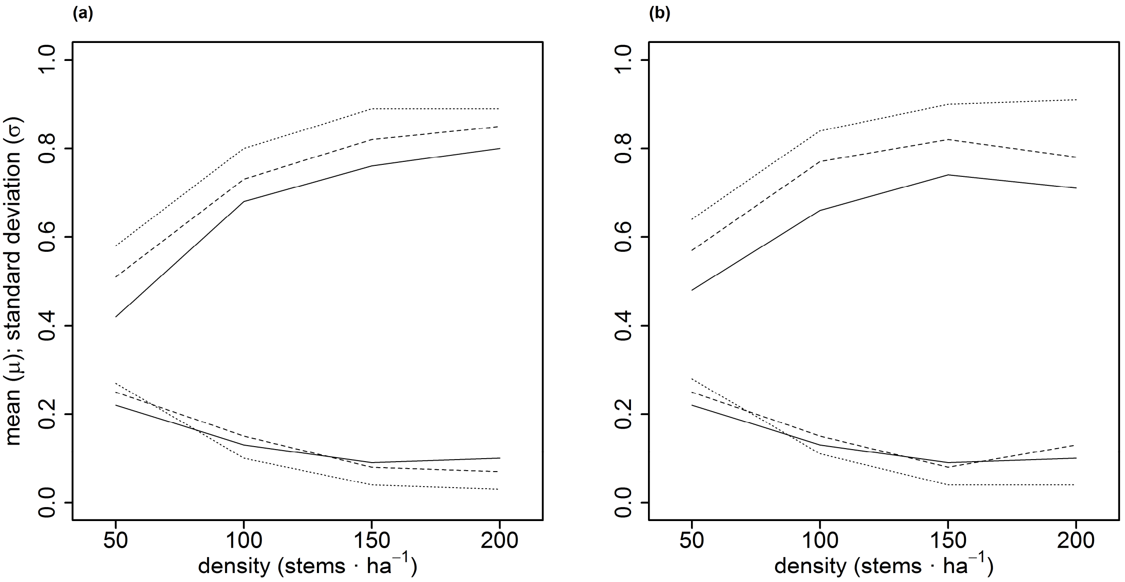

Figure 6.3. Mean (μ, higher lines) and standard deviation (σ, lower lines) probability of establishment for varying densities and rotations (dotted line, 120 years; slashed line, 100 years; solid line, 80 years) under current (a) and future (b; A2 scenario) conditions

6.4.2. Optimisation

The optimisation algorithm converged regardless of the defined starting point. Convergence criterion was reached for the base point representing light management when the objective function was $OF = 1.6608$ ($\mu = 0.8250$, $\sigma = 0.1642$). This maximum of the objective function corresponds to the decision variables' optimal solution consisting of fellings intensity of 30.16% and 18.75%, for the first and second felling, 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, 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 stand initial density and an even less intensive second felling, both of them removing thinner trees located in the densest areas (Figs. 6.4 and 6.5). The progress of the objective function and the decision variables over the iterative process is shown in Fig. 6.6. The provided light-management initial solution resulted to be a close-to-optimal solution, as the search in the surroundings of the given values for the decision variables did not seemingly produce a substantial improvement in the objective function. Only 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 spent up to 20 iterations before the objective function leveled off, the initial values of decision variables being noticeably modified.

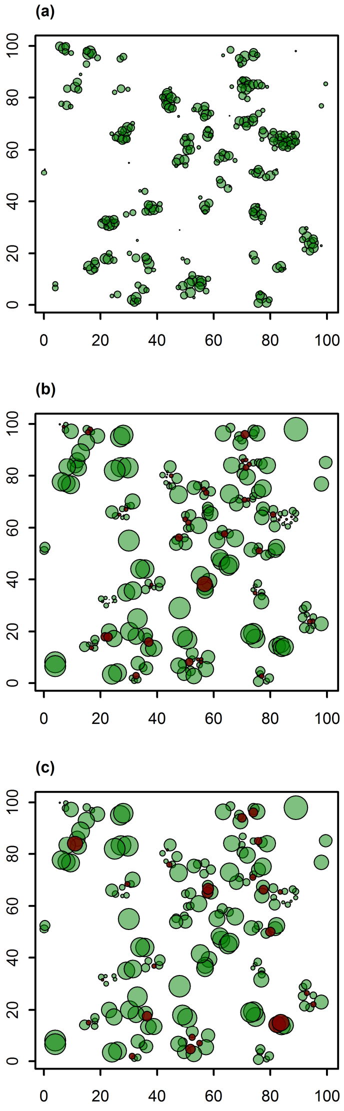

Figure 6.4. Optimised order of tree logging for the optimisation initialized from close-to-optimal initial values. In (a), circle sizes represent the logging order (larger circles are to be cut first); in (b) and (c) circle sizes are proportional to tree's *dbh* and darker circles stand for the logged trees in the first and second harvest operation respectively

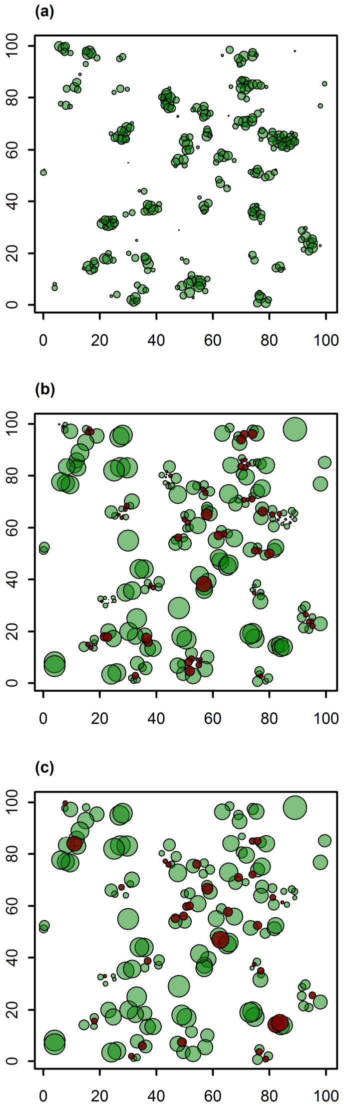

Figure 6.5. Optimised order of tree logging for the optimisation initialized from sub-optimal initial values. In (a), circle sizes represent the logging order (larger circles are to be cut first); in (b) and (c) circle sizes are proportional to tree's *dbh* and darker circles stand for the logged trees in the first and second harvest operation respectively

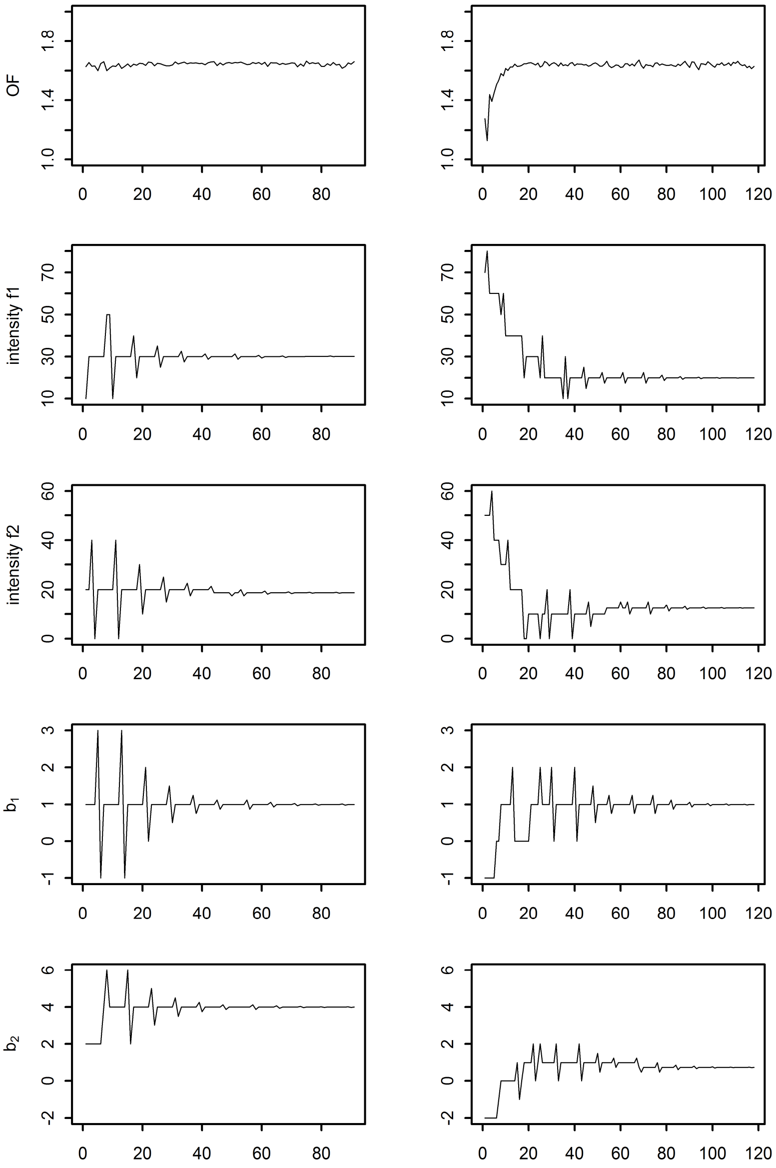

Figure 6.6. Evolution of the utility function (*OF*) and decision variables (felling intensities and parameters b_1 and b_2) through iterations in the optimisation initialized from close-to-optimal (left) and the optimisation initialized from sub-optimal values of decision variables (right)

6.5. Discussion

In the current study we presented a multistage stochastic model for natural regeneration in *P. pinea*. There are two main aspects contributing to the originality of this paper. On the one hand, the key environmental and climatic effects and the random variability associated to each subprocess were thoroughly defined and modelled. 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. On the other hand, the further implementation of an optimisation algorithm based on the model represents a novel tool for decision making in managed *P. pinea* stands.

6.5.1. Stochastic simulations and stochastic optimisation

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 years period (i.e. high μ), mainly due to dispersal limitation and seed shortage. Identically, stockings 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, σ only noticeably changed over varying stockings (the higher density, the lower σ; Fig. 6.3a and 6.3b). In the light of these results, μ seems to be strongly dependent on factors driving seed production and dispersal, whereas σ is only closely related to the spatial arrangement of parent trees. This fact is also observed when considering the effect of rotation length, which only affects μ: shorter rotations (i.e. 80 years) would reduce μ due to seed limitation as younger trees are less productive (Calama *et al.*, 2011).

The best results for natural regeneration, considering only a 10 years interval, are attained for the highest rotation tested (120 years; μ = 0.89, σ = 0.04), when the optimal stand density is met (150 stems·ha^{-1}). In spite of not being straightforwardly comparable due to dimensional incompatibility, these results largely improve the records from manager inventories under current felling schedules, where seedling density was below 200 seedlings·ha^{-1} in 44% of the surveyed area and only in 10% it was over 1,600 seedlings·ha^{-1} (Gordo *et al.*, 2012).

The abovementioned finding of an optimal stand density of 150 stems·ha^{-1} is confirmed by the outputs resulting from the first and second optimisation, where the programmed fellings at algorithm convergence reduced the initial density (250 stems·ha^{-1}) in 39% and 32.5% of the stems in 5 years, respectively. Moreover, from a spatial perspective, final b_1 and b_2 values indicate that fellings should be addressed to remove first those trees of lower diameter from denser areas. Seed production and dispersal subprocesses mainly drive this circumstance. On the one hand, smaller trees are potentially less productive and account for a decrease in the per tree productivity at stand level (Calama *et al.*, 2011); hence, they are to be cut rapidly. On the other hand, trees located in open areas are preferred to remain, even if low productive, given the short dispersal distances of the species (Manso *et al.*, 2012d), as the final seedling distribution should be as uniform as possible. Accordingly, in optimisation problems where the per tree value is not relevant, resulting b_1 and b_2 usually lead to the removal of large trees first, as in Pukkala and Miina (1998).

The two different starting points led to final management schedules qualitatively equivalent, although not exactly the same. The reason behind this fact is that the used algorithm does not necessarily converge to the global maximum (Miina, 1998). There are two particularities in this study case that potentially can hamper the finding of this 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 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 similar final values for the objective function, as long as the cuttings are light enough to just cancel out the unfavourable effect of over-dense stands in seed production. 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 parameters' value.

The objective function used in the present optimisation problem combines two features of interest for regeneration: the mean (μ) and the standard deviation of (σ) of the probability of regeneration for a given plot at 1 m^2 precision. Although these two variables are obviously correlated, none of them can be neglected. Whereas very high values of μ will lead unequivocally σ to be null, lower μ are possible under different spatial distribution of seedlings (varying σ), some of them being more adequate than others. Nevertheless, caution must be taken when using this objective function below realistic stand densities and spatial arrangement. The relationship between μ and σ is not monotonic for the full domain of the two variables. However, this relation was found to be always decreasing within the range used in the present study (μ over 0.35).

6.5.2. Current implications for management

Current management in *P. pinea* in the study area primary focuses in pine nut production. 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 highly intense 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 in 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 density should be maintained as long as needed, until the occurrence of successful establishment events. Actually, first 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 a –nowadays unsustainable– artificial regeneration-based silviculture model, including strip clearcuttings (Gordo, 1999). Indeed, seedlings need to be released from parent tree's shade at some point, which implies that a longer maintenance of relatively high stockings 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 bear relatively high stand densities at least during few years, these stockings favouring the establishment of new recruits. Subsequently, parent trees should be progressively removed to release from shade those cohorts with increasing light requirements. The present multistage model does not include a seedling survival submodel taking into account the effect of shade on long-term established seedlings. Further improvements in this respect will make possible to optimise also the progressive removal of the remaining trees as their role as a constraining factor for regeneration becomes more important than those beneficial of seed source (Manso *et al.*, 2012d) and shelter in the first seedling stages (Calama *et al.*, 2012).

Concerning rotation length, current values are also often below the proposed optimal (120 years). Surprisingly, it is not uncommon that regeneration in managed forests is perceived as unsuccessful due to too short rotation lengths (Tíscar-Oliver, 2007; Kerr *et al.*, 2008). In these cases, if parent trees were allowed to remain longer (increasing the length of the regeneration period), 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 (bottleneck). 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. Identically, for those locations of very low quality, longer periods might be required. A high degree of stochasticity in unfavourable conditions for regeneration was also found for Mediterranean *Pinus nigra* by Tíscar-Oliver (2007), who concluded also that flexible (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 the region for the species, achieving reasonably good results (Finat *et al.*, 2000).

Differently, from a spatial perspective, our results do coincide with current silviculture practices. The present cone production-oriented management highlights the importance of maintaining large trees as evenly distributed as possible, the condition being fulfilled during the whole rotation through both thinnings and fellings (Montero *et al.*, 2008).

6.5.3. Future climate and future management

Interestingly, the application of the multistage model including simulated climatic data for the A2 scenario did not reveal a worse performance of the system concerning natural regeneration. On the contrary, the mean probability of establishment increases 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 clearly cancelled out or even reversed in the longest rotation and lower densities by reduced seed predation: because rainfall is expected to decrease all over the year, the predation-free period is to increase (Manso *et al.*, 2012b). Consequently, predation may be a less severe limiting factor, as seeds would be available to germinate during a wider period. This pattern would be reinforced by the more drastic precipitation decline taking place from July to August, which implies a negative lagged response for rodent abundance in fall, the period where germination typically occurs. Germination, however, is only thermal-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 frost decrease. Consequently, suitable conditions for germination would be both more probable and extended longer.

The cases where probability of regeneration diminishes are those of higher densities and shorter rotations. Given the definition of successful regeneration, it is equally thriving to hold one seedling·m^{-2} than a higher quantity. Most probably, under the current climate these plots contain a relevant number of quadrats successfully regenerated but not far from the defined threshold. Considering seed production reduction in the A2 scenario, it is most likely that a fraction of the stand comes in seed limitation problems that in average are not compensated for by the increasing number of successful seedlings right beneath the crowns.

As it has been showed, a sensible management of seed production (extending rotation length) and dispersal (maintaining adequate stocking) can mitigate the impact of climate change on the regeneration of *P. pinea* and even improve regeneration performance in respect to current probabilities. Therefore, the same recommendations as those stated for the current climate apply for the future: emphasis should be taken in rotation age 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 mountainous forests and therefore shortening of rotation length will 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 silviculture paradigm. Moreover, when silviculture techniques are aimed to achieve the natural regeneration of stands, lowered rotations are generally regarded as inadequate (Lindner *et al.*, 2008). In respect to stand density, recommendations to mitigate drought effects through evapotranspiration control and increasing individual vigour point out to a more intensive thinning schedule, aimed to reduce stand density (Kellomäki *et al.*, 2000; Spiecker, 2003). Because management of *P. pinea* woodlands is oriented to seed production, current stand density is among the lowest in pine forests throughout Spain (Montero *et al.*, 2008), meeting the aforementioned proposal. Nevertheless, the conclusions from our study must be considered prudently. At first, although precipitation reduction appears to be a beneficial factor for natural regeneration, water shortage may also imply negative effects on tree growth (Lindner *et al.*, 2008). This circumstance indirectly affects regeneration through seed production, modulating the effect of the different proposed rotation lengths on natural regeneration. Secondly, the prey-predator system consists of complex interactions (Kratina *et al.*, 2009) and therefore predictions based on current behaviour should not be deterministically admitted. Third, the effect of more intense drought in 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 predictions and therefore they are subject to some degree of uncertainty (De Castro *et al.*, 2005). Additionally, our results are conditioned by the selected climatic scenario (A2; high emission increment). Would the B2 scenario (moderate emissions increment) prove more realistic, our conclusions may differ. In this respect, an advantage of the proposed stochastic model is that it considers all feasible scenarios providing also multiple solutions for the different posed 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). Furthermore, tools such as that developed in the present paper are strongly encouraged by the European Union Forest-Based Sector Technology Platform, which highlights the importance of forest decision support systems (DSSs).

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 frugal character, makes of *P. pinea* a potentially resilient species of remarkable interest throughout different areas in Inner Iberian Peninsula susceptible of aridification.

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Chapter 7

Conclusions

7. Conclusions

I. The spatial primary dispersal pattern of *Pinus pinea* proved strongly aggregated, only 1% of the seeds being expected to drop beyond 2 crown radii. Consequently, currently-applied regeneration fellings prevent seeds be to uniformly dispersed throughout the stand. From a temporal perspective, seed release is climate-controlled: cones break open when mean monthly temperature reaches a thermal threshold (usually in May), whereas the subsequent release rate is positively related to precipitation, taking place during the summer until early fall.

II. Germination of *P. pinea* seeds is governed by thermal and stand variables in the Northern Plateau. On the one hand, the absence of climatic optimal conditions severely limits the process, resulting in a narrow window for seed germination, which occurs either in late fall or spring. On the other hand, extremely poor overstory cover leads to low probabilities of germination. Additionally, there is a relevant time-lag effect in the process, meaning that precedent environmental conditions significantly influence current germination performance.

III. *Apodemus sylvaticus* is the main frugivour removing seeds of *P. pinea*, whereas corvids affect seed crops to a much lesser extent. *A. sylvaticus* mainly acts as a predator, exploiting almost all available seeds out of the dry period. The favourable period for seed survival is a consequence of both the decreasing rodent populations due to the effect of drought and the higher seed availability in summer, when dispersal takes place. This fact suggests the existence of a dual climate prey-predator control, driven by summer conditions and the climate-mediated masting habit of the species. From a spatial perspective, seeds are more intensively predated in the close vicinity of trees and potential shelters.

IV. The vast majority of emerged seedlings are expected to perish two years after emergence. In the case of individuals from cohorts occurring in fall, a small fraction can survive, the mortality rate being irrespective of any specific climatic event.

When considering those seedlings appeared in spring, none persists. Emergence rapidly followed by severe summer drought could be behind this circumstance.

V. As it can be seen, all processes involved in natural regeneration of *P. pinea* are subject to a high degree of uncertainty, including seed production, given the species masting habit. This circumstance results in low transition probabilities between consecutive stages or even leads to the collapse of the system (bottleneck). These bottlenecks can occur as a consequence of dispersal limitation, high predation rates before germination takes place, lack of suitable conditions for germination, and intense mortality. However, an adequate management scheme can mitigate these difficulties.

VI. Simulations and optimisations undertaken through the developed multistage stochastic model demonstrate that current intensive and strict regeneration fellings lead to processes of dispersal limitation before a sufficient number of evenly distributed recruits has been established. Longer rotation lengths, an optimal stand density at the beginning of the regeneration period and more flexibility in the scheduling of subsequent fellings are the key factors that would lead to successfully achieve natural regeneration in even-aged stands of *P. pinea* in the Northern Plateau of Spain.

VII. According to model predictions, regeneration of *P. pinea* is expected to show an acceptable behaviour in a context of a climatic change. In this respect, the species proves highly valuable from an ecological point of view, as it will be able to occur in demanding sites where other tree species probably will fail to persist.

VIII. The findings of the present dissertation indicate that, ideally, natural regeneration of *P. pinea* would occur as follows: (i) seeds are dispersed in summer during a mast event, mainly beneath parent tree’s crowns; as long as stand density is high enough, no dispersal limitation should rise; (ii) seed germination thrives to take place by early fall; (iii) seed predation diminished rates hold until emergence; (iv) seedlings are then uniformly arranged in a sufficient number throughout the stand, so that at least a surviving fraction of them definitely becomes established.

IX. Providing that parent tree's crowns facilitate performance of established seedlings for several years given the medium shade-tolerant behaviour of the species, regeneration dynamics would rely on the regeneration under cover, until gaps in the overstory occur. This feature and the characteristic low transition probabilities could lead to various regeneration failures over time and therefore an uneven-aged stand structure is expected.

X. Advanced statistical methods are required in order to precisely model the subprocesses involved in natural regeneration, given the nature of data. Furthermore, providing all subprocesses have been adequately modelled, the multistage stochastic approach is a powerful approach to model the entire process of regeneration.

XI. Regardless of formulation complexity, the variables included in models addressed to provide tools for forest management must be easily measurable/modifiable by forest managers, such as climate and/or stand variables. This is the base of silviculture and, consequently, the development of accurate but not accessible models would be completely senseless.

Epílogo

Epílogo

1. Motivación

El presente epílogo no es una sección de agradecimientos. Antes bien, se trata de una crónica de los últimos cuatro años de vida… o de agonía.

2. Caso práctico de modelización mediante análisis de supervivencia

La probabilidad de que el doctorando sobreviva como tal en el periodo en el que se desarrolla su tesis es un caso típico de aplicación de modelos basados en análisis de supervivencia. Si bien se puede definir una línea base de supervivencia que agrega un amplio abanico de variabilidad estocástica indefinida tal como la desidia, el aburrimiento o la desesperación, existen ciertas variables que aceleran o ralentizan el riesgo de que el doctorando lo mande todo a hacer puñetas.

Pero la supervivencia del sujeto está condicionada a la propia ocurrencia del proceso. Cuatro fueron las circunstancias que permitieron que el factor que define esta ocurrencia adoptara el valor de uno. En primer lugar, aunque ponerse con una tesis doctoral me sigue pareciendo que no es nada del otro barrio, lo cierto es que muy pocos “chicos de barrio” hacen tesis doctorales. Este mérito corresponde exclusivamente a mi casa (sin rodeos, el binomio padre-madre) que, sin seguramente saber muy bien cómo, han edificado sobre los escombros de un pasado en ruinas, común al de una generación de perdedores de guerras, una sólida estructura basada en el conocimiento, el esfuerzo y la dignidad. En segundo lugar, la actitud no sirve de nada si no se tiene acceso a la información sobre financiación para personal predoctoral. Imperativo es en este punto saludar a Salvia García y agradecerle el envío de esta convocatoria, demostrando que el apoyo mutuo es mucho más eficaz que la paralítica competencia. Como tercera condición en esta interacción a cuatro bandas se sitúa la osadía del salto al vacío: una vez dados todos los pasos hasta el borde del abismo, aún hay que atreverse a arrojarse. Mucha, mucha gente, tanta que no cabe aquí, escuchó mis dudas. De entre las personas que aún merecen que se les recuerde hay que destacar a aquellos zaragozanos/as de origen o de acogida como Belén Sirviente, Sergio Co!, Arantxa Lorente o David Gil “el Calata” y a alguna gente de la difunta EUIT Forestal como Alfredo Bravo y, una vez más, Valentín Gómez. Finalmente, cierran este grupo de elementos determinantes los, entonces, potenciales directores de tesis, Rafa Calama y Marta Pardos, que dieron un voto de confianza a una historia que podría no haber sido cierta (aunque lo era), creyendo seleccionar (digo yo) a un paradigma de la honestidad y “cráneo previlegiado”. Sólo se acercaron algo a la verdad en lo primero.

A partir de aquí, ya nadie regala nada. Entonces, ¿cómo definir la función de riesgo, esa tasa instantánea de “mortalidad de doctorando” cuya suma día a día nos permite evaluar el grado de frustración de aquél? La forma más sencilla es considerar de forma aditiva todas las variables influyentes y meterlas en una exponencial, acorde a la magnificación que de todo –dicen– hace el doctorando. Algunas de estas variables dependen del tiempo; otras no tanto. Estudiaremos la cuestión, en cualquier caso, considerando diferentes grupos de factores. Por otra parte, existe una parte de variabilidad que no podemos relacionar directamente con nada y que es intrínseca a distintos niveles. Es aquí donde se hace necesaria la inclusión de los efectos aleatorios: el efecto aleatorio despacho, el efecto aleatorio lo contentos que estén los jefes, el efecto aleatorio precio del café,. Los EBLUPs podemos asumir que son realizaciones aleatorias de una Normal, en el caso del precio del café-solo-con-hielo-para-llevar, de media 0.65€ y desviación típica 0.1€, de acuerdo al criterio de esa genial camarera llamada Tere.

3. Factores intrínsecos

En los comienzos, Rafa Calama, el cerebro de la Operación Pinea, tenía una idea de tesis que, retrospectivamente, vemos que respondía a un plan bien trazado, habida cuenta de que esa estructura sigue siendo la que sustenta el documento. Eso fue siempre una ventaja que amortiguó la caída de la probabilidad de supervivencia del doctorando antes mencionada: saber, sin fisuras, qué quedaba por hacer y a dónde queríamos llegar. La estructura de la que hablo, sin embargo, fue fuertemente zarandeada en esos primeros tiempos por el alto grado de entropía del entorno, hasta el ecuador de la beca, en el que Marta Pardos puso un poco de orden y se fijaron unos plazos que al final hemos ido cumpliendo. Entretanto, un factor positivo nada desdeñable fue el apoyo presupuestario para todo tipo de idas de pinza en relación a los experimentos vallisoletanos.

Como quiera que fuera muy rápido cuando yo lo empecé a percibir, cabe hablar ya del efecto INIA. El INIA tiene una envidiable disponibilidad de recursos, desde los coches a la reprografía, y de personal. Pero también tiene sus cosas, que terminan por afectar a la supervivencia del doctorando, de los contratados por el antiguo Régimen Especial Agrario en fraude o no de ley, del capataz, del tecnólogo, del investigador, y al mismo tiempo, son todos estos sujetos los que lo componen y lo retroalimentan. El efecto INIA en este sentido es semejante al bosón de Higgs: una especie de campo de ácido butírico y dimetil, en el que cada uno de nosotros no es sino una simple perturbación, parte integrante del mismo, como igualmente lo es este párrafo. Esperemos que, al contrario que el campo de Higgs, el efecto INIA no tenga vocación de eternidad y esté sujeto a cambios para bien.

Pero volvamos al resto de variables. Íbamos por los comienzos, cuando al llegar tempranito sólo se escuchaba, muy bajito, rock&roll en la radio de Estrella y la tos, menos bajito, del Kike. Las salidas de campo a tientas entre la niebla y los valores siempre negativos de la temperatura de la Tierra de Pinares se sucedían por entonces. Esto cambiaba cíclicamente según avanzaba el tiempo con episodios de insolación norteafricana. ¿Y aún alguien se preguntaba por qué el piñonero pasaba de regenerar por allí? Lo de acumular aproximadamente 12000 km en salidas de un día por allí arriba en su momento tuvo un impacto negativo. También para el pobre Guillermo Madrigal, cuando venía conmigo, que tenía que fingir durante horas lo muy interesado que estaba en mi imparable verborrea. En realidad, el problema de las salidas de campo no sólo correlaciona con el bosón de Higgs-INIA en forma de trámites, el tráfico de la A6 y con el clima, sino también con la preocupación de burlar como burlamos todos los controles de la Benemérita para poder meter en Madrid las dos fanegas de farlopa que siempre nos bajábamos de los pinares, así como las muchas “9 mm Parabellum” destinadas a reiniciar la lucha armada en Egoalde. En esto era especialista el bueno de Santi de Blas, más que yo si cabe, fiel aliado mío en muchas “excursiones” y en la lucha contra las alharacas de Valsaín. Siempre de signo positivo en este modelo de supervivencia, excepto el día que cruzó el Terrano en la pista aquella, el mismo día que se nos rajó una rueda. Un emocionado saludo desde aquí a aquel retén que nos sacó por dos veces del fango aquel día (aún estarán descojonándose, me imagino).

Positivo, igualmente, que Javier Gordo sea de los pocos gestores de Hispanistán que confía en la investigación. Y en consecuencia, también favorable el poder encontrarse de vez en cuando con los guardas de Tordesillas, Alejandro y Eugenio, ambos dos, antagonistas de los Romera. Eugenio, además, es un ecólogo de verdad, sin necesidad de publicar en revistas importantes ni saberse la última genialidad teórica de algún listo genérico al que todos nos toca citar. Disculparme desde estas líneas porque el dispositivo de predación aún debe andar descomponiéndose por sus propios medios en el pinar de la Nava. Los guardas, asimismo, echaron una mano con los datos cuando yo “andaba de vacaciones”, como se suele afirmar cuando estás en el extranjero trabajando como si no hubiera un mañana. En este sentido, gracias a la gente del INIA que anduvo al quite: Rafa, Guille y el personal de prácticas. Puntualmente también hasta se pringaron Carolina Mayoral, María Pasalodos (hauska tutustua, Marrrrria!) y Eduardo López, notable francófilo y frecuente consejero en asuntos morales y edáficos (gracias también a Salva por esto), con el que esperemos algún día podamos colaborar para aplicar mi amplia experiencia en el análisis de datos con exceso de ceros (sentimentales, sobre todo) a los falsos ceros en la ocurrencia de especies.

Otro efecto positivo, enlazando con lo anterior, es el de nuestra “plantilla flotante”, los famosos capataces en prácticas o cómo aprovechar(nos) del fraude de la formación. Aún a riesgo de olvidar a alguien: Sergio, Maribel, Susana, Paula, Rodri, Eduardo, Adrián y, especialmente Merche, mil gracias. Mar Conde, la más guapa del INIA y de Carabanchel Bajo, va aparte, aunque sólo sea por haber soportado más chapas que nadie en sus sucesivos contratos. Negativa, en cambio, la sensación de que este hecho esclavista no llega a entenderse como tal. Así nos va con eso de las conquistas sociales. Pero si de campo y de conquistas (de todo tipo) hablamos, ¿cómo obviar la función sinusoidal que describe mi buen amigo Enrique Garriga, el Kike? Cambiando una rueda, lijando rodajas, estudiando física, intoxicándose (conmigo) con la ración aquella de oreja en Mojados, escondiéndonos de los pelotazos de los antidisturbios en Tirso o vaciando un tercio de Mahou verde, un tipo siempre valiente, que si hace falta le mete “un rodamiento del 9 a la Secretaria General en el entrecejo”. Y no es broma. Pendiente queda el cochinillo y la botella de Ribera en Segovia, rediós.

En aquella primera fase forzosamente hay que hablar también de los cursos de doctorado, enfoque decididamente deficiente para la formación. No obstante, se trata del típico factor con diferentes niveles, algunos de ellos afectando de forma positiva a la variable respuesta. Entre estos debo resaltar a Miguel Ángel Ibáñez, de Agrónomos, Diseño de Experimentos, siempre dispuesto a ayudar en los cortocircuitos mentales de los alumnos sin el más mínimo interés por la estadística (sé que es aquí cuando queréis que hable de la Prêt. Pues no, os jodéis). Y a Carlos Morla, entrañable, en cuyo curso, además, tuve la ocasión de retomar el contacto con Raúl Iglesias, el Ruli, más conocido como el Sabio de Tubilla. Gloriosas jornadas del alpinismo-torocismo ibérico quedaron atrás empujadas por las suelas de nuestras botas. Primera mención especial para Sven Mutke, ("Eh'ben", voz carpetana), quien me facilitó la bibliografía, me aconsejó y me revisó un trabajo infumable de historia medieval pinariega para uno de esos cursos, del que he tenido la deferencia para con los miembros del tribunal de sólo incluir algunas pinceladas en la introducción de esta tesis. Segunda mención especial: con qué poca gente se puede hablar de religiones ecológicas, sectas ácratas y otras minucias, con la seguridad de que además se está aprendiendo algo (y encima, en el bello castellano del siglo XVII). Tercera mención especial: remarcable excepción en las reuniones de grupo, levantando la mano para pedir la palabra; se nota el "background", majo.

Por aquellos entonces también hubo un intento de transformación masiva a R, sospecho que con poco éxito. Aunque a Mathieu y a Rafa les rechinen los dientes yo voy a valorar positivamente que R exista, a pesar del bando dogmático que sustenta el sistema. Creo que Andrés Bravo estará conmigo.

Para terminar con la primera fase de la tesis, caracterizada por los palos de ciego contra la cabeza propia, particularmente con el tema de los bichos, hay que indicar que fue un elemento positivo la enorme amabilidad y disponibilidad de José Luis Tellería (Biología de la Complu) y Eduardo Mezquida (antes Montes Madrid, ahora en otros entornos más propicios, espero). No obstante, pese a las aportaciones de ambos, de María M. Jáuregui y de Alberto Hurtado (EUITF, aúpa), para mí, amigos, los bichos siguen siendo variables aleatorias y poco más.

Los "biodiversos" vinieron un poco después. La interacción con ellos (ellas, mayoría absoluta de chicas) a nivel laboral es poco significativa a causa de nuestras muy distintas orientaciones "pofesionales" del momento, pero debo incluirla en el modelo porque ahora me sabe francamente mal no haber aceptado nunca el cafelito y la magdalena que Marcelo amablemente me ofreció cada día. Ah, y porque los pantalones que le dieron a Laura me quedan increíblemente bien. Y aprovecho el momento histórico, aunque no pegue ni con cola, para mencionar que por ahí tuvo lugar el asalto al centro de una avanzadilla de la EUITF, Álvaro y Raquel.

Una interesante variable cuyo efecto mutó de positivo (por los vínculos) a negativo (por el seguimiento) según avanzaba el tiempo y que, por tanto, cabe introducir en nuestro modelo como una interacción cuadrática con aquél, es el de la (nada) famosa Asamblea de Becarixs. Mientras me entretenía pintando piñones, hecho objeto de mucha burla (englóbese en efecto Higgs-INIA), también perdíamos el tiempo principalmente Marina de Miguel, Quique Sáez y yo mismo (aunque en menor medida, también todos los de nuestra planta en el CIFOR y alguna gente "del otro lao") en remitir un escrito al Director Particular (porque ya no era General) del INIA solicitando cinco tonterías de forma (paréntesis para Bea: siempre fuimos, somos y seremos; ¡salud!), en connivencia con Marisa Barragán, que siempre nos apoyó. Con la misma cintura con la que este Director Particular pasaba del escrito, el grueso de los becarios del INIA ignoraba, rechazaba y hasta despreciaba con alevosía hasta una raquítica hoja de firmas. Yo, que no soy rencoroso, les deseo todo lo mejor a esos esquiroles miserables con los numerosos artículos que habrán publicado mientras otros se preocupaban por su propia dignidad en el centro. Luis Alté estará de acuerdo conmigo, la única persona de por aquí que conoce el daño que hicieron los Pactos de la Moncloa.

Siguiendo esta línea, por lo que representa, por lo que le debemos, por lo que le admiramos, debo evaluar como variable aparte un fenómeno único en la naturaleza: JB. Estimado amigo, te dedico estas líneas. Aun con tu enorme parecido al Ministro De Guindos, éste no te llega ni a la suela en lo que se refiere a la defensa de los intereses del Estado. Serías un antidisturbios formidable, si dimensionalmente fuera posible. Te sugiero que leas el preámbulo de la Ley 30/1992, donde se indica para qué están los funcionarios públicos. Tampoco dejes de ojear el régimen sancionador. Eso de andar pidiendo barrenas de Pressler por el CIFOR para cargarte con sal un árbol colindante a tu parcela se llama malversación de fondos públicos. Y pobre árbol.

Menos mal que siempre estuvieron Dori y Toñi para evitar males mayores mediando con semejante individuo. Aparte, a mi modo de ver, estas dos mujeres ejemplares e infatigables en su capacidad administrativa son el verdadero motor del CIFOR. Su competencia, aliviar la parálisis que produce el entramado burocrático del centro y del INIA, así como su absurda rigidez, diríase de origen napoleónico. Curiosamente, me he encontrado Doris y Toñis en cada estancia. Creo que es el puesto más importante en un centro de investigación. Del mismo modo, aunque en general poca gente las considere compañeras de trabajo, y quizá por eso, debo incluir en este párrafo a quien hace que el

CIFOR no sea un estercolero: Juani, por la que no pasan los años, e Isabel, que a pesar de los mismos, tiene diligencia para limpiar por las tardes, co-gestionar un bar por las mañanas y sacar adelante todas las plantas del centro.

Otro grupo de variables a considerar es aquél que engloba al resto de becarixs de selvicultura, que por proximidad, representan un colchón sobre el que recostar las miserias diarias y, por tanto, detienen la caída al vacío. Lástima que mi paso por el INIA ha sido en este sentido un poco como un paseo por las parameras de la Meseta Norte: al llegar yo, ya se iban Nacho Barbeito y Darío Martín, y ya se había ido Guillermo Gea. Me alegro sinceramente de la vuelta de este último, ¿o con quién podría yo discutir del verdadero significado de un mínimo relativo en la función de verosimilitud en un espacio n-dimensional sin llegar a la conclusión conjunta de que la ciencia es un negocio deshonesto y lamentable? Gente con tablas en cualquier caso.

Y por otra parte, las nuevas incorporaciones tardaron mucho en llegar para estar en el mismo momento del proceso de supervivencia. Los eché siempre en falta, incluso antes de saber que existían. Sin embargo, estos compañeros que dignamente recogen el testigo Pinea –Carolina Mayoral (experta musicóloga y envidiable "viviora" que estoy seguro debí ya haber conocido en el Crápula de Zgz) y Javier de Dios (¡un biólogo! ¿Será el principio del fin (por fin) de las masas puras DE forestales?)– son funciones de riesgo en sí mismas (para eso hacen la tesis a tiempo completo) que limitan el riesgo de mortalidad condicional del resto de doctorandos. Sin olvidar en este epígrafe, claro está, a Laura Fernández y Víctor Mora. Una pena que haya sido tan sorprendentemente complicado lo de compartir con ellos despacho, que es donde creo me correspondía.

Y, por cierto, a pesar de que los comienzos no les han sido del todo fáciles a ninguno, estoy seguro de que encontrarán su lugar en esto de la ciencia (también en el avispero) y que sus trabajos serán excelentes. Con la excepción del de Víctor, claro, que nos dio una admirable lección de humildad y creo que nos hizo a todos preguntarnos si esto merecía realmente la pena. Un tipo tremendamente válido, por lo demás, que no sólo jugaba bien al basket sino que en el fondo sabía de sobra por qué la inversa de la matriz hessiana de la función de verosimilitud es equivalente a la matriz de varianza-covarianza de los parámetros a estimar. Y es que el coincidir con gente más lista que uno mismo yo lo entiendo como una ventaja, no como una amenaza: el ingenio se lanza hacia delante y la eficacia se incrementa, superándose más rápido la fase de chapuza científica. En este sentido, la profesionalidad y la capacidad de computación tipo i-7 de Alicia Ledo, otra chica de barrio, son parte fundamental de la robustez de últimos pisos de esta tesis, aunque se discrepe en algo tan fundamental como es la preferencia de los empalagosos tintos de verano sobre un buen tercio de Mahou verde.

Y enlazando con eso de los últimos pasos del proceso, debo mencionar el interesante fenómeno (no muy positivo en esta formidable ecuación que propongo) que advertí según el entorno se iba oliendo que el final se acercaba: el ambiente súbitamente se torna todo paternalismo, paternalismo que recuerda a cuando el aguerrido ciclista pre-EPO, que se aferraba a su manillar para no caer al asfalto en el último y desesperado esfuerzo por coronar los Lagos de Covadonga, justo recibe la palmadita en el lomo de cientos de aficionados. Se agradece con sinceridad la atención, queridos, pero un punto de mesura, un punto de mesura…

Como vemos, son muchos los factores que afectan la supervivencia. La salud ha quedado hecha mierda en este periodo (cuánto se agradece que Rocío (Rotxi), mi compi de clase en el Gaudí, fuera tan determinada en escoger medicina y se convirtiera así en médico particular cuando a uno más lo necesita). Me pregunto si la tesis deja taras. Yo creo que sí: ahora soy peor persona. Me temo que algún día tenga que seguir las recomendaciones de José Pablo para ingresar en el centro de desintoxicación de Los Molinos.

4. Factores extrínsecos científicos

Las estancias. He aquí que el Ministerio a veces acierta, muy a pesar de JB. ¿Qué hubiera sido de esta tesis sin las estancias? Muy probablemente algo bien administrado pero no muy distante un puñado de pintones modelos mixtos generalizados. ¿Qué hubiera sido de la idea del doctorando sobre la investigación? El bosón de Higgs como teoría única. En suma, hubiera supuesto tasas tan elevadas de riesgo de perecer, que quizá hubieran catalizado un abandono definitivo del ámbito científico en algún momento.

La primera de les estades va ser a Barcelona, Cerdanyola del Vallès, al Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), amb en Josep Maria Espelta, en Tete, a qui vaig trobar un tio veritablement eficient, ordenat, professional i supersimpàtic. Tot i que va ser només d'un mes, vam aprofitar moltíssim, i no solament pel que fa de l'avanç a la tasca dels bichos, sino també per treballar des del punt de vista dels ecològs: cal n'aprendre molt! Tengo que agradecer también a José Luis Ordóñez el rato que echó conmigo para explicarme cómo iba el modelo estocástico de su tesis, porque fue así cómo entendí enteramente el objetivo de la mía. També he d'agrair el consells del Lluis Comas sobre els ratolins. A nivell personal, va ser un period força agradable amb en Tete, però també amb tota la gent del CREAF, particularmente con Roberto Molowny i el mon de becaris que hi havia. És bastant dificil oblidar-se'n, però és també complicat recordar tots els noms: el Guille, la Jara, Laura... Merci a tots per la vostra hospitalitat i molt especialment a la Lucia per fer més fàcil el camí cap a Montana.

En Barcelona vivía en Sans, gracias a los contactos talibanes movidos por la pequeña Soyarina. Allí compartía casa con el Nacho, el Popi, compañero castellanista y notable pensador que me hizo descubrir los bajos fondos barcelonís y los grifos de cerveza Voll-damn. Dentro de este bando de la casa estaba también Sawali, egipcio economista y abogado tetralingüe (árabe, inglés, francés y castellano) que trabajaba en un bar. Y el Manolín, que como si fuera de la casa. En el otro bando, el pulsar (hispano)navarro Laura-Lorea, del cual la primera llevaba la voz cantante. Nunca conseguimos que bajaran a Ciutat Vella a darle al alpiste.

També molt d'altres amics van contribuir a que l'estada fossi un èxit personal: moltes gràcies a la Marta i l'Andrea per fer-me sentir com a casa tot el temps. Mai podria jo haver pensat que la nit aquesta del partit del Barça fossi a acabar a aquella festa del copón al Gòtic (d'on, malauradament, es va escapar la Rosa de foc...) i d'allí, a la fi, a una casa modernista del Passeig de San Joan. Un plaer també sortir a la muntanyeta amb la Neus i el seu xicot, quedar amb en Dani-Alacant de Montes UPM, la Elena de Tarragona i de veure tan, tan bé a la Desireé. Espero que tot vagi igual ara...

The second stay was kind of exotic, in Missoula, University of Montana, with Chris Keyes. Chris was always a devoted host who did his best to make me feel as at home. And definitely, he succeeded. I strongly appreciate his efforts on our paper on dispersal. I think I improved quite a lot with scientific compositions in English at that time. Also I am sincerely grateful for the opportunity to travel with Tom (heart-breaker man!) to the forests of Mediterranean California as well as to the IMPRESSIVE sequoia forest at Reddish. Back in the lab, thanks also to David Affleck for solving my agonic doubts with R programming and to Bob Keane, from the Missoula Fire Lab for his interest in our work. Among the students, it was a pleasure to share room with Kyle, I'm sure nowadays a remarkable forester, and Woongsoon (sorry if the spelling is incorrect), a South Korean gay who can be listed among those who are intelligent beyond the average. Y como lo mío es juntarme con gente brillante, por ver si se pega algo, no podía ser de otra manera que llegara a trabar buena amistad con Adrienne Keller, brillantísima hispanófila "oregonesa". Definitely, I like type-A people. Greetings also to my neighbours, Suyama, Helgue and his girlfriend, with whom I shared amazing beer-evenings. Y gracias, ante todo, a Juan Abarca, por crear y mantener en ese estado de pureza escatológica el virtuosismo de Mamá Ladilla, que me acompañó en cualquier momento de debilidad, estreñimiento o parálisis mental.

Però, és clar, cal parlar del Dani i la Margarita, dos fenómenos valencianets de la vida social missouliana, grands competidors en l'art de fer tortilles de patates. A més, si coneixes al Dani ja coneixes a tothom! I quina grand surpresa, quand va venir ca meva en Josep, ja conegut de un congress a Montpellier. Un tio excellent en Josep, critic i internacionaliste que, amb l'Albert (campion dels pedos!) i l'Anna, em van deixar un sitio al cotxe per poder anar a Yellowstone. Y en este contexto no podemos olvidar, por supuesto, a la Sole, (Soledad Jimena Inés, concretamente, no sé si ese era el orden), montañera patagónica excepcional. El Trapper Peak fue coser y cantar para nosotros tres and however we and the others would have found our death in the Missions but for the incredible sense of orientation of Charley. Hei, man, I still own you some pictures of the last hike we did! Finalment, he d'enviar una abraçada forta a l'Anna Sala, a la seva filla i al seu marit: estava collonut el pavo d'acció de gràcies!

Le troisième stage a été au centre INRA de Nancy (France). Je ne voulais pas. Je vraiment ne voulais pas. Mais il sembla que le destin avais fait un chemin unique, direction la Lorraine, bien difficile à ne pas le suivre. Je me suis aperçu à ça après voir, par hasard, un film de la Mélanie Laurent. En fait, j'étais bien sûr que je la rencontrerais sur Nancy. Pas de tout. Dommage. Mais par contre j'ai trouvé Mathieu Fortin. Ce n'est pas le même, mais de toute façon, je vraiment le dois beaucoup et on pourrait dire qui il y avait deux phases en la thèse: Before Mathieu et After Mathieu. Pour ce qui est de la statistique, pour ce qui est de la programmation, pour ce qui est de l'efficacité, pour ce qui est de la génialité, pour ce qui est de la capacité didactique et linguistique et sur tout, pour ce qui est de sa disponibilité.

Et, en France, un autre mythe que tombe. Oui, semblant chez les catalans, les françaises, quand même les lorraines, sont des gens qui ne perdent pas le temps à penser comment enmerder les espagnols. Bientôt, tout le contraire, spécialement si on considère leur patience avec mon très déficient français. Comme exemple, les chercheurs de l'INRA, un d'entre eux me donnant même une bouteille de vin excellent ou les étudiants de la résidence de l'Engref: Matilde et beaucoup d'autres. Ou mes amis Tony (formidable cuisiner et magicien des eaux de vie), Haykel et Johannes (capable de pas mélanger le catalan, le castellan, le française et le português). Ou le groupe de stagiaires a l'INRA, particulièrement Vivien, palentino de acogida, como yo. Ou les très sympathiques filles du bus à Champenoux, avec particulier attention à la Leslie, jeune lorraine-alsacien qui toujours s'a excusé de boire une bière à cause de sa thèse (mis cojones 33). D'hors de l'environ INRA, ils ont été bien agréables avec moi Florent et Florence (brouillardé journée aux Vosgues!) et aussi Gabi. Et beaucoup plus loin du truc académique, il faut se rappeler à l'hospitalité de Coco et Sonja (¡no pasarán!). Y, por si fuera poco, hete ahí que coincidí en esta estancia con Marina, quien absorbió, como más cercana hispanoparlante, parte de la tensión que supone andar en dos artículos de lo mismo perfectamente a la par.

Ja Suomi! Rafa sanoi että täytyin mennä Joensuun. Ein halua mennä siellä uudelleen! Minusta Pöhjois-Karjala on liian kylmä ja seillä ei ola valo talvissa! Mutta Timo Pukkala ja Jari Miina olivat Joensuussa. And I wonder what kind of simulator I would have carried out and how long it would have taken without their selfless help, their deep knowledge on the underlying stochasticity of the processes to study, the formulation of such problems and, overall, their incredible capacity to solve any question, suggestion or shortcoming in a record time, regardless of the difficulty of the targeted objective. In this respect, I sincerely appreciate the confidence and rapid response of Jari to provide a favorable report for my thesis. Truly, this is optimization.

No menos increíble es la resiliencia del grupito español "finófilo" en Carelia del Norte. Y que a pesar del friazo de por allí, reciban con extraordinario calor a los viejos conocidos. Después del chiste tonto, debo pedir el aplauso más fuerte para uno de esos perpetuos hispano-fineses, Javier Arévalo, que me hizo la vida más fácil en todos los aspectos, integrándome en la farándula joensuusta y en las memorables pachangas de baloncesto del Metla. Asimismo, y por antigüedad, merece un hueco en este apartado el Jaume a qui no hi havia vist des d'una llunyana nit al Meksiko, ja fa sis anys. Y en otro orden de cosas, realmente agradable las charletas, cervezas y paseos con Isa (EUITF Madrid, dejando huella), Juha (Espanjalainen en el fondo), Sergio, Víctor, Antonio, Rubén, Javi Pasalodos y espero no olvidarme de nadie. En cualquier caso, quizá sea la maximización de las experiencias negativas, quizá sea este ambiente propicio, quizá sea el trabajar con gente seria, quizá sea esa luz boreal que no deja que el ánimo baje (ni dormir tampoco deja), quizá sea la Vía Carpetana pero la verdad es que la cuesta de Niinivaara nunca volvió a ser un obstáculo penoso para llegar a ese rincón del Pyhäselka llamado Hukanhauta.

Por cierto, que en Hukanhauta tenía dos compañeros finlandeses. Antti, carélico pura sangre, parco en palabras, digamos, pero un tío majo que creo que me tenía en buena estima. El death metal hace amigos. Y la tortilla de patatas y el salmón al horno, más. El otro, el Markus, en el fondo también me tenía aprecio, porque si no, no hubiera intentado evangelizarme con tanto ahínco.

And, concerning Finns, it was a pleasure to visit Tampere to meet Kapa and Adrien (français-finnois), one of the most expected encountering of all times. Sure there will be more, hopefully in the "warmness" of Lorraine! And to finish with Finnish people, it is compulsory, though the word may be inconsistent to some extent in this context, to identify the significantly positive effect of Johana and Jakko, representing the generational succession to JOA in Joensuu, in an effort for demonstrating that human beings only can be integrally free. Do not hesitate, it is always worthy to keep on.

Et un autre stage encore. Hors du temps de la thèse, mais reliée à la thèse de toute façon. Voilà que j'ai me rendu une autre foi en Nancy, pour finir quelques choses et développer une autre model avec des données de Rafa en suivant une autre idée brillante de Mathieu. Et c'est à ce moment-là quand j'ai intégralement eu le document intégrativement intégral de la thèse, comme François dirait. Tout ce que j'ai déjà dit sur Nancy est applicable ici, sauf que aussi on est allé à Freiburg, pour rencontrer Axel, le windthrow-modelling-man et le Valhala. También era diferente en Nancy que ahora la liebre ibérica, Nacho Barbeito, andaba, o más bien corría, por la Lorraine, a quien tengo que agradecer mi rapidísima reintegración en la localidad, los platos, los vasos y la tabla que luego se partió. Y también lo del segundo informe de experto que faltaba. La próxima St Georges será con entrenamientos más intensivos en la Pépinière. Se van a cagar los nancienses. No así los keniatas: el centro de África siempre corrió mejor que el norte del continente.

A nosotros, por el contrario, nos visitó menos gente. Como interacciones significativas, mencionaré la de Luke, que estuvo a punto de morir de frío en el Ocejón, y la de César, que me recomendó el escribir unos agradecimientos orientados a objetos, pero programar las complejas interacciones de los elementos del bosón de Higgs-INIA está más allá de mis capacidades. Y aunque no se tratara de una estancia, por el tiempo que coincidimos, como si lo fuera: Ana Rincón, que resultó ser famosa por Nancy y que me dijo que le enviara el primer artículo tan pronto como saliera. El parto fue tan largo, que me olvidé.

Pero no sólo hubo estancias. También el Ministerio acierta con lo de los congresos, en general positivos en esta construcción estocástica de la supervivencia del doctorando.

El primero, el Congreso Forestal E'hhpañol de Ávila, buen sitio para pasearse y dejarse ver. Allí se coincidió con tanta gente que necesitaría un disco duro externo para acordarme, pero debo mencionar, al menos, al núcleo palentino, con Irene, Josu, Celia, Oli, etc., etc., a la Miriam Piqué, a Joserra, que me salvó el pellejo en Finlandia la primera vez, a Serrada, con el famoso símil de los pliegos y, en otro orden de cosas, a Pedro "el de Monflorite" y a Íñigo Oleagordia.

El segundo fue una cosa de la IUFRO en Palencia, donde ni que decir tiene que estaban los autóctonos dirigiendo. Me parece que fue aquí cuando Ricardo Ruíz-Peinado, pobre, debió flipar con "mi vida paralela" y los comentarios talibanes de mi amiga Ana, que suscribo íntegramente.

El tercer congreso fue en Francia, en Montpellier, una cosa de bichos y ecólogos. Aquí tengo que agradecerle a Rafa la búsqueda de financiación. Pensaba yo que el congreso no iba a tener relevancia para "lo nuestro". Pero vaya que sí. Entre otras muchas cosas, supe que el queso francés es cojonudo, que Akiko Nakahasi era una chica de menos de 30 años, que a Kim V. le afectaba suficientemente "one point five bottles of white wine", que Pedro Jordano es un tío llanísimo, que a Dani, el de Oviedo, espero encontrármelo otras muchas veces, que Carolina Puerta, quien me había dado amables consejos para la primera estancia, era de carne y hueso y que Juanjo Robledo Arnuncio es un verdadero crack que trabaja en el INIA.

La cuarta reunión fue la de transferencia del piñonero y el pináster en la capital financiera de Castilla, Pozal de Gallinas. Aunque fueron unas jornadas con regusto triste, creo que fueron a la vez una buena oportunidad para poner en práctica lo que, en mi opinión, debería ser un centro público de investigación y tecnología como el INIA: si enfocamos los recursos públicos sólo a sacar artículos sobre "trendy topics", los verdaderos beneficiarios, gestores y sociedad, se van a terminar por mosquear. Además, fue un gusto reencontrarse con el núcleo palentino una vez más, escuchar la copla de Gregorio sobre el Caballero de Olmedo y asaltar la barra con el Kike (sí, fuimos nosotros).

La quinta fue una de la SECF, de modelización en Lugo. Creo que Mariola temió por su vida cuando me cortó el 40% de mi tiempo por orden de la superioridad dado que la Conselleira de Judías Pintas, Sardinas Arenques y Gusanos de Seda había llegado tarde al mitin de apertura. También tuvimos que escuchar algunas barbaridades sobre modelos mixtos contra las que Javier Vázquez y Rafa se batieron el cobre con el disgusto de entender que nadie ha terminado de entender nada después de 10 años de esto. Un requetegusto recoincidir por cuarta vez con el núcleo palentino y con la gente del CREAF. No tan agradable el discutir con mis ex-coincidentes laborales sobre cuáles son las normas tácitas que el doctorando asume al firmar su contrato. Me imagino que una vez reducido el sueldo un 11% y subidas las tasas un 100%, podemos dejar claro que aquí no hay convencionalismos que valgan, ya que el propio Estado no cumple ni siquiera las normas explícitas.

El quinto, de pinos, en Avignon. Yo ya no sé si había alguien de Palencia o no. Els que si que estaven a tot arreu van ser els del Centre. Quina capacitat! No fue un congreso muy allá y además me tiraron el artículo para el número especial. Pero boicotear la charla de aquella francesa presumida que revoloteaba alrededor de Sergio de Miguel estuvo bien, así como la cena de clausura y la borrachera subsiguiente, que tampoco fue desdeñable.

El sexto, el Agropine de Sven, en Pucela, unas buenas jornadas técnicas sobre el piñonero a las que acudimos la flor y nata, la élite, la más avanzada representación de la ciencia piñoneril, mención no muy complicada de obtener habida cuenta de lo limitado de semejante parroquia.

Séptima, otra de la SECF, en el INIA, donde copamos las charlas, que para eso jugábamos en casa con el bosón de nuestro lado. De Palencia estaba Encarna, a quien, por cierto, también agradezco sus buenos consejos para la primera estancia y que, de hecho, me terminaron llevando a Montana. Y de Albacete, cual "Miguelito de la Roda", ¡David Candel!

Y luego el memorable maratón del CIFOR y las aún más memorables Jornadas de Jóvenes Investigadores de Valsaín. Es en estas últimas donde he elegido ubicar a Luis Santos, setero, endrinero, eRrero y escéptico… En fin, de esa gente a la que el Estado de Hispanistán despilfarra con su antipolítica de investigación. Allí también estaba, claro, el núcleo palentino, con un buen número de nuevas incorporaciones. Esperemos ver a Paloma pronto por el INIA.

Y, por último, los cursos, como elemento determinante si uno quiere avanzar algo en cosas nuevas. Realmente bueno el de Carrascal y Seaone, del Museo de Ciencias Naturales, sobre ajuste por PLS. Allí coincidí con Laura Sánchez, otra de las escasas doctorandas cosladeñas, y con Tere, pinchadiscos de categoría en diferentes jolgorios. Sin embargo, el curso más notable fue, sin duda, el que tomé en Bayreuth, chivado por Alicia, con el agua al cuello ya, a cargo de Florian Hartig y otros antifrecuentistas de pro, sobre inferencia bayesiana. Ich will kein scheiβ-Weizen ohne schaum!!!

5. Factores extrínsecos no científicos

Por fuera del INIA, donde aún había vida, anduve rehaciendo la red social después de cinco años de ausencia, elemento que afecta a la supervivencia del doctorando de forma cuadrática (pasado cierto punto de socialización, resulta difícil trabajar, especialmente al final de la tesis). Así nació el núcleo sectario talibán cosladeño-sanfernandino, que igualmente tuvo forma cuadrática, alcanzando un máximo para decaer después, pero sin perder nunca su esencia combativa. El tiempo nos va dando la razón.

Y se fundaron los cimientos de Caterva, con mi inseparable socio musical y cervecero desde el tiempo en el que “ciencia” era sólo parte del nombre de una asignatura de instituto: Jesús Silveira, mejor guitarrista de lo que se cree y prolífico fabricante de pedales de distorsión. El edificio se siguió elevando con la llegada de Álvaro Carrillo, perversamente engatusado por mí en un momento de entusiasmo en las lomas de unos picachos de la montaña cántabra. Y David Flores, que vendió su alma al diablo de la matemática (¡saludos a Cati y al Pablito!). Y Nacho, también vino Nacho. La construcción se vino abajo justo cuando se puso la última teja, broche de oro a la aventura.

Por Madrid se retomaron otros contactos, curiosamente relacionados con el mundo forestal, que siempre fueron vía de escape para el rompecabezas de la tesis. Por ejemplo, con Sira (y a veces con Miriam, ohh) apuntalamos las miserias propias de cada cual, unas contra las otras, en buen equilibrio, que son ya muchos años. Con David, el Torrado, pateamos a lo tonto la sierra de Albarracín y los Ancares, con gran empacho de callos de primero y botillo de segundo en el Bierzo, ganándole al ajedrez a un ex-legionario al frente de un ¿albergue? Con el Miguel (forestal, escalador, montañero, artesano, programador y filósofo), como siempre, aprendiendo más y más cosas, aunque el cociente entre ambos no deja de aumentar a su favor. También vivimos en común con cierta angustia el costillazo del mendrugo anterior contra un muro en la Capadocia. Con César Muñoz trepamos por varios sietemiles del Guadarrama, excepcional compañero en el campo. Como mi tío Paco, que aunque se queja bastante, le quedan piernas para rato. Con Amparo revivimos la esencia del rock de los 90. Con Salvia pasamos muy buenos ratos, valorando, entre otras cosas, el uso de la violencia contra quien se la merece, con desacuerdo, por lo general. Creo que con Rubén Laína estaría más en sintonía; lástima haber coincidido tan poco, quitando la vez aquella en Carabanchel (quién me lo iba a decir). Porque ahí seguimos, en los Carabancheles, merced al precio de amigo de Paco padre, padre de mi amigo sin precio Paco. Seguimos pendientes de darle a la oreja por el barrio, por cierto.

Aquí en Carabanchel las cosas tomaron nuevos derroteros. Para empezar, la tele del Crescente y las voces del Aaaadrian y el I’hmaeeeel arrojaron luz a por qué los griegos representaban el Olimpo con seres eternos, donde no había infancia ni vejez. Y también en relación a las grandes jornadas de ciclismo que se han vivido en los puertos de primera y categoría especial de la Vía Carpetana y C/ Segovia, respectivamente. Lástima que el “Madrid Río” sea semejante chapuza. Sospechaba que su promotor era gilipollas, pero ahora lo ha confirmado a la cabeza del Ministerio de Justicia. Por otra parte, la cercanía al corazón de la bestia talibana, formado por personas de integridad y coherencia fuera de toda duda, da la seguridad de poder decirle las cosa claras al JB, al Director y al Ministro en persona sin ningún tipo de vergüenza. Además, vivir en Carabanchel permite ser sociable en Madrid; las dificultades para esto cuando se vive más allá de la M-40 (i.e. Cojjlada) es algo que los madrileños circunscritos por la misma suelen no comprender. De ahí, que por ejemplo, me animara hasta a ir a la Teatro Real para demostrar lo cultivado que soy en la iniciativa promovida por nuestros representantes germánicos, Katha (Deutschland) y Gregor (Österreich). Pero, sobre todo, es en esta etapa cuando se refunda Caterva, en forma de Hatajo, con el Silveira, Laura y yo mismo. El formato acústico cerca estuvo de provocar una tendinitis, pero mereció la pena.

Como punto final a este apartado de madrileñismo exacerbado, es imperativo mencionar un factor binomial espacial altamente determinante en la función de riesgo: vivir o no en Cojjlada, que es donde antes andaba. Siempre es positiva la presencia de un hermano como Javier, pieza clave para atemperar este factor. También para tomar lo de "O pozu" a coña. "¿Lo viste o lo miraste?". La verdad es que con Javier todo se relativiza y las cosas son mucho más fáciles de lo que parecen. Excepto alcanzarlo cuando corre. Liebre ibérica plusmarquista.

En todo este tiempo, Aragón siempre estuvo muy presente. Así, la visita de Pablo a la Prospe o el reencuentro (mucho después) con Juanjo y Óscar no son al final fruto de la estocasticidad del universo. También en Zgz sufrimos el festival infame del viento, con posada y fonda en casa de Sergio CO! Y con este último, la subida al Moncayo (cara sur, por supuesto, co), los efectos de la deshidratación (yonkización) en el Cercanías pasado El Pozo o los tapeos por lo poco que queda de auténtico en Madrid. De baturra crianza es también Laura, que amablemente me saludaba cada vez que venía a visitar museos a la capi. Lamentablemente, la escasa probabilidad de supervivencia del doctorando al final del trance ha impedido que pueda yo responder con igual gentileza cuando ella recientemente se ha mudado a Madrid. Y el otro Juanjo, virtuoso de la música y de casi todo, a quien debo los numerosos consejos sobre qué guitarra acústica agenciarse en Montana. Notable también la visita especial a Calatayud, a cargo del gentil Calata, y alguna visita turística adicional a cargo de Melisa, también ilustre bilbilitana. Sin embargo, es Huesqueta la ciudad que se lleva la palma, con especial atención a sus Sanlorenzos, donde, más borrachos imposible, Álvaro Mur y yo tuvimos ocasión de repartir buenos tomatazos, antes de llegar (en otro momento) a lo alto del Teide en compañía del Álvaro bajista. Fue un verdadero placer recoincidir además con Carlos, Pablo, César y Alodia, entre otros muchos y muchas, y muy especialmente con Eva/Eba. También con la Jess que, pobre, siempre le toca el lado malo de la barra en fiestas. Y con Marta, cuyo gato asesino esperemos que haya madurado.

También el País Vasco ha tenido su peso (positivo) para la tesis. En Egoalde (sí, es Euskadi Sur, pero seguramente sólo Mirem se lo sabía esto) no nos hemos dejado ni una: Sanse, la quedada en Astigarraga con Samu (extraordinarios fiestorros en Pucela a cargo de la Tere), Rubén Rodolfo y Paula, con consecuente hinchazón de sagardoa, extraña conversación con una joven psicóloga llamada Ainara y pernocta en Intxaurrondo; como en Palencia pero ahora con perras para esos excesos; Bilbao, Barakaldo y fiestas de Ibarretxe, discutiendo con Jaione sobre cualquier cosa que pudiera parecer irrelevante; Vitoria, Jungitu, donde el Gurbindo y Teresa se han apañado una casa de cojones, precedente del remarcable bodorrio en Donostia un poco después (Pasalodos es testigo), con reencuentro incluido con la cuadrilla iruñesa 10 años después en un contexto igualmente etílico y encontronazos como el de la Lore.

6. Hiperfactores

La ciencia como negocio es el peor enemigo del doctorando y de la propia ciencia. En estos días, asistimos atónitos en el campo forestal y ecológico a un sistema de calidad basado en el número de cesiones gratuitas de un producto construido mayormente con financiación pública (artículos) a empresas privadas (revistas). La proliferación de los "lobbies" científicos con sus teorías científicas asociadas y sus estrategias empresariales nos lleva a que el conocimiento sea lo último que nos interesa. Verdaderamente desalentador para cualquier profesional un poco serio.

A otro nivel, el laberinto administrativo de la Escuela Única aumenta significativamente la quiebra moral del doctorando. Las trabas institucionales que hasta el último momento han jalonado el camino y algunas estrategias que no he llegado a entender así lo demuestran. Al final, semejantes malabarismos terminan por pagarlos sólo el alumnado. Afortunadamente, a estos malabares se han opuesto los de dos mujeres de gran valía, Marta y María José, de la secretaría de Montes.

Y no me entretendré en algo que ya sabemos. La lamentable planificación de la economía nacional desde hace 30 años y el querer jugar en una liga que no toca ha dado al traste con cualquier posibilidad de que la investigación convierta a este Estado en algo diferente, y eso desanima enormemente a quien trata de empezar en esto. El derroche educativo va a ser de gran utilidad a la Europa central. Pero no olvidemos que no se trata de algo coyuntural: las crisis son parte del juego en el que todos resulta que al final queremos participar.

Desmotiva, más si cabe, que el reformismo, la coartada responsable de estas crisis, tampón que absorbe la ira del pueblo, más aún que todos los mercenarios terroristas al servicio del Estado, impregne cada rincón de la sociedad. En nuestra mano está el tomar las riendas.

Madrid, diciembre de 2012