Forest Systems
26 (2), eR02S, 20 pages (2017)
eISSN: 2171-9845
https://doi.org/10.5424/fs/2017262-11255
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria O. A., M. P. (INIA)

REVIEW ARTICLE

OPEN ACCESS

Natural regeneration in Iberian pines: A review of dynamic processes and proposals for management

Rafael Calama[1,2], Rubén Manso[3], Manuel E. Lucas-Borja[4], Josep M. Espelta[5], Miriam Piqué[6], Felipe Bravo[2,7], Carlos del Peso[2,7], and Marta Pardos[1,2]

[1] INIA-CIFOR, Dpt. Silviculture and Forest Management, Ctra A Coruña km 7.5, 28040 Madrid, Spain. [2] iuFOR. Sustainable Forest Management Research Institute INIA-UVa. Avda. Madrid 44, 34004 Palencia, Spain. [3]Forestry Comission. Northern Research Station. Roslin Midlothian EH259SY, UK. [4]Castilla-La Mancha University, Technical School of Agricultural and Forestry Engineering, Campus Universitario s/n, 02071 Albacete, Spain. [5]CREAF. 08193 Cerdanyola del Vallès (Barcelona), Spain. [6]Sustainable Forest Management Unit, CTFC. Ctra. de Sant Llorenç de Morunys, Km 2, 25280 Solsona (Lleida), Spain. [7]Valladolid University, ETS Ingenierías Agrarias, Dept. Producción Vegetal y Recursos Forestales. Avda. Madrid 44, 34004 Palencia, Spain.

Abstract

Aim of study: Designing adequate silvicultural systems for natural regeneration of a forest species requires sound knowledge of the underlying ecological subprocesses: flowering and fruiting, seed dispersal and predation, seed germination, seedling emergence and seedling survival. The main objective of the present work is to carry out a review on the current knowledge about the different subprocesses governing the regeneration process for the main Iberian *Pinus species*, in order to propose scientifically based management schedules.

Area of study: The review focuses on the five main native *Pinus species* within their most representative areas in the Iberian Peninsula: *Pinus nigra* in Cuenca mountains, *Pinus sylvestris* in Sierra de Guadarrama, *Pinus pinaster* and *Pinus pinea* in the Northern Plateau and *Pinus halepensis* in Catalonia.

Material and methods: Firstly, currently available information on spatiotemporal dynamics and influential factors is introduced for each subprocess and species. Secondly, current regeneration strategies are characterized and the main bottlenecks are identified. Finally, alternative silvicultural practices proposed on the light of the previous information are presented.

Main results: Different climate-mediated bottlenecks have been identified to limit natural regeneration of the Iberian pine species, with seed predation and initial seedling survival among the most influential. New approaches focusing on more gradual regeneration fellings, extended rotation periods, prevent big gaps and program fellings on mast years are presented.

Research highlights: Natural regeneration of the studied species exhibit an intermittent temporal pattern, which should be aggravated under drier scenarios. More flexible management schedules should fulfil these limitations.

Additional keywords: seed production; seed dispersal; seed predation; germination; regeneration fellings.

Authors´ contributions:RC and MP conceived the idea and structure of the article, and gathered all the previous information, synthetized it and wrote the main corpse of the text; RM, JME, MELB, MP, FB, CDP and MP compiled and prepared information for the different species and processes, and revised the manuscript.

Citation: Calama R.; Manso R.; Lucas-Borja M. E.; Espelta J. M.; Piqué M.; Bravo F.; Del Peso, C.; Pardos M. (2017). Natural regeneration in Iberian pines: A review of dynamic processes and proposals for management. Forest Systems, Volume 26, Issue 2, eR02S. https://doi.org/10.5424/fs/2017262-11255

Received: 19 Feb 2017 **Accepted:** 07 Jul 2017.

Copyright © 2017 INIA. This is an open access article distributed under the terms of the Creative Commons Attribution (CC-by) Spain 3.0 License.

Funding: Spanish Program for R+D (Projects RTA-2013-00011-C2.1, AGL-2010-15521, RTA-2007-00044, POII10-0112-7316, AGL-2011-29701-C02-00, AGL-2014-51964-C2-1-R); EU 7th Framework Program (ARANGE-289437)

Competing interests: The authors have declared that no competing interests exist.

Correspondence should be addressed to Rafael Calama: rcalama@inia.es

Introduction

One of the main aims of sustainable forest management is to guarantee forest persistence over time (Nyland, 2002). This general objective implies that managed stands need to be successfully regenerated. In Silviculture, natural regeneration is defined as the renewal of a forest stand by natural seeding, sprouting, suckering, or by layering seeds that may be deposited by wind, birds or mammals (Pardos *et al*., 2005).

The successful regeneration of a forest conforms a temporal succession of phases that should be effectively realized: seed production, seed dispersal, seed predation, germination, emergence, seedling survival and seedling initial growth. In this way, regeneration can be considered as a multistage process (Fig. 1)

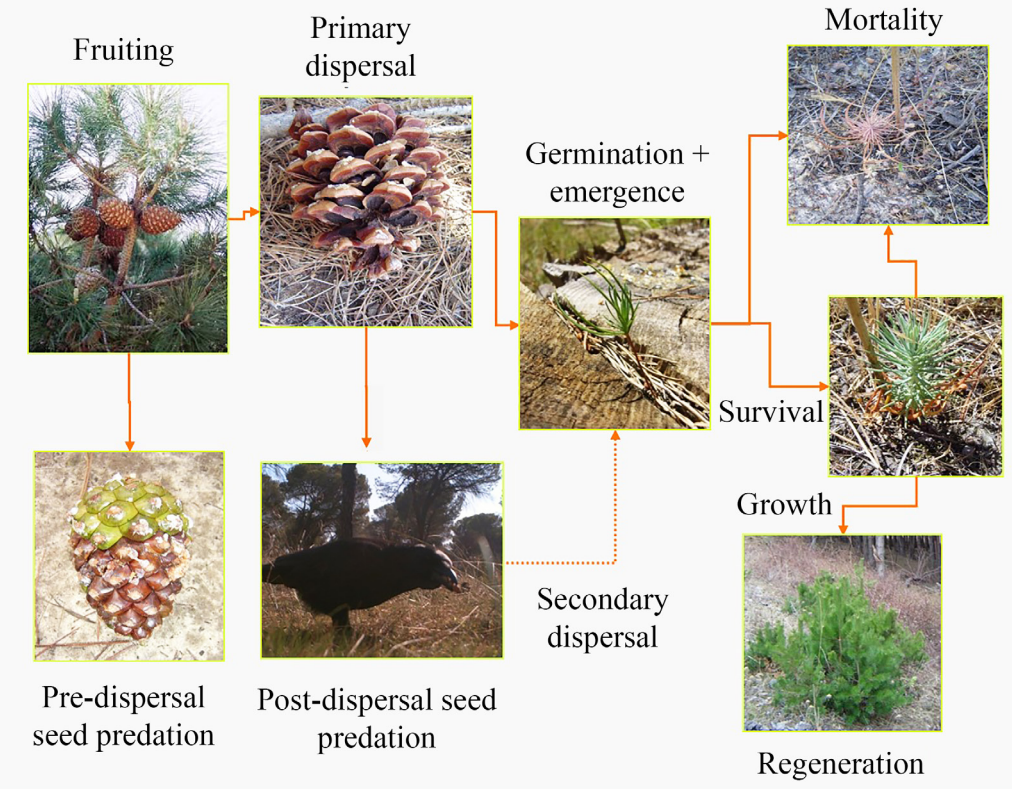


Figure 1. Multistage process of natural regeneration

consisting of underlying consecutive subprocesses that often can be identified as a series of successive survival thresholds for potential seedlings (Pukkala & Kolström, 1992; Manso *et al.*, 2014a). The process begins with the supply of seeds from soil or aerial seedbanks, but seed supply is commonly highly variable at different spatial and temporal scales. Across an interval of several years, several tree species appear to produce many more small crops than large crops, such process being known as masting (Kelly, 1994). Once the seed is available, seed dispersal takes place. Seed dispersal is thought to enable seeds to escape competition (with their parents, with other seedlings and/or with surrounding vegetation) and to colonize favourable sites (Howe & Smallwood, 1982). Both wind and animals play important roles in establishing seed banks in the soil. 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 (Manso *et al.*, 2012). However, on heterogeneous environments the spatial pattern of seed dispersal commonly does not determine the spatial pattern of established seedlings (Meiners *et al.*, 2002). In this sense, seed predators are considered to be major seed mortality agents, structuring recruitment patterns that will depend in turn on the proportion of seeds escaping predation at the source, the mean distance from the source of dispersed seeds and of predators' activity, among others (Nathan & Casagrandi, 2004; Manso *et al.*, 2014b). Frugivore behaviour plays a key role in plant distribution and demography (Jordano, 1992), ultimately even conditioning species persistence (Hulme, 1997). Furthermore, differences in hoarding habits (scatter-hoarding vs larder-hoarding) may impact seed germination and seedling establishment.

Once the seeds have reached the soil, subsequent regeneration subprocesses include (i) the germination of the seeds: defined as the process starting by seed imbibition and ending with the complete elongation of the radicle; (ii) seedling emergence, ending with the complete liberation of the cotyledons; and (iii) seedling establishment, extending up to the initial phases of seedling survival. Germination occurrence and germination timing play an essential role in subsequent seedling survival (Baskin & Baskin, 2001) and therefore, in the overall success of natural regeneration (Manso *et al.*, 2013a,b). In addition, as with seed predation, germination strongly contributes to reshape recruitment patterns. The possibility that a seedling emerges and survives in a given site depends on the metabolic reserves of the seed. Among the specific characteristics of plants, seed size has been defined as the most selective trait, conditioning the spatial and temporal

pattern of recruitment of the species (*e.g.* Calama *et al.*, 2015a). According to the *k* and *r* reproductive strategy (MacArthur & Wilson, 1967) plants must respond to a trade-off, either producing abundant small-size seeds, with limited reserves, or producing less large-seed, with abundant reserves (Westoby *et al.*, 1992). Seedling size is dependent on seed size during the first weeks until the true leaves replace the cotyledons as the primary source of carbohydrates (Greene *et al.*, 1999). In general, large-seeded species show higher initial growth, but lower relative growth rate with time and usually occupy wider geographical ranges (Aizen & Patterson, 1990). Plant performance depends on the underlying patterns of resource availabilities. Resources vary spatially and temporally and species differ in their ability to tolerate resource scarcity. Thus, more than one resource may be limiting simultaneously among microsites or at different times within the same microsite or for different species grown together (Latham, 1992). Differences in performance ranking across resource gradients will result in patterns of seedling abundance that may persist in the composition of adult trees community.

Natural regeneration has been for long a primary concern in the forest management of Mediterranean species. Natural regeneration is commonly unsuccessful in Mediterranean species for different reasons. Some of them are directly related to forest management (the use of silvicultural systems which lead to low densities; long rotations inducing poor seed crops during the regeneration period; excessive grazing and uncontrolled ploughing activities; intensive pruning for providing fuelwood). Others, however, are related to the species themselves (the masting habit and lack of synchrony with regeneration fellings and adequate years for seedling establishment), to the habitat (soil compaction; competition with ground vegetation; inadequate overstorey density and forest fires) or to climate (severe summer droughts and high summer temperatures that lead to regeneration failure). Thus, a deep knowledge of the ecological processes involved in each stage of regeneration would help to identify the bottlenecks in natural regeneration, supporting forest planning under criteria of adaptive silviculture.

The main aim of this work is to thoroughly review the current state of the knowledge on natural regeneration of the five main Iberian pine species. We focus on the most representative areas for these species (Table 1): *Pinus nigra* Arn. ssp. *salzmannii* (Spanish black pine) in Cuenca mountains, *Pinus sylvestris* L. (Scots pine) in Sierra de Guadarrama, *Pinus pinaster* Ait. (Resin pine) and *Pinus pinea* L. (Stone pine) in the Northern Plateau and *Pinus halepensis* Mill. (Aleppo pine) in Catalonia. In a first step, we list the currently observed problems for the regeneration of the species. Subsequently, we make a comprehensive review of the state of art of the different ecological subprocesses involved in natural regeneration: flowering and fruiting, seed dispersal, pre and postdispersal seed predation, seed germination, seedling emergence and initial seedling survival, in order to identify potential bottlenecks. Finally, we present recently implemented silvicultural practices, based on scientific findings, aiming to promote natural regeneration of the species. We have mainly focused this review on the processes and factors leading to the

Table 1. Main characteristics of the studied species and regions

Characteristics	*P. nigra*	*P. sylvestris*	*P. pinea*	*P. pinaster*	*P. halepensis*
Studied region	Cuenca Mountains	Sierra Guadarrama	Northern Plateau	Northern Plateau	Catalonia
Involved provinces	Cuenca	Madrid, Segovia	Valladolid, Segovia	Valladolid, Segovia	Barcelona, Girona, Tarragona
Area occupied by the species (ha)	259,000	130,000	60,000	124,000	290,000
Altitudinal range (m)	1000 - 1600	1200-1800	600-800	750-850	0-1000
Average annual temperatura (ºC)	10.7	8.7	12.5	11.9	13.8
Annual rainfall (mm)	700	882	450	430	525
Bedrock	Calcareous	Granites and gneiss	Quartz	Quartz	Calcareous
Main type of soils	Sandy-Loam	Sandy-loam	Sands	Sands	Carbonated materials
Mean water holding capacity (mm)	30	210	100	100	75
Traditional silvicultural system	Uniform shelterwood	Uniform shelterwood	Uniform shelterwood	Uniform shelterwood	Diameter selection cutting
Rotation (years)	120-150	100	100	80	60-80

successful initial establishment of the species. Thus we have deliberately omitted long term seedling and sapling survival processes as herbivory by large ungulates, despite the potential importance this process has on natural regeneration success in both temperate (Putman, 1996) and Mediterranean forests (Zamora *et al*., 2001).

Natural regeneration in Iberian pines: Current situation in case study regions

Natural regeneration of Iberian pine stands has been a major concern for forest managers of the studied regions since the end of 19th century, when rational and ecologically-based forest management started to be applied. In that early time the main effort focused on homogenising stand composition, increasing forest standing stock and transforming age-heterogeneous stands into even-aged ones. However, serious failure in natural regeneration have also been widely detected for the different species since then, the issue becoming dramatically severe over the last decades.

Since the first management plans for *P. nigra* forests in Serranía de Cuenca, dated in 1895 (*Los Palancares* forest), the commonly proposed silvicultural system for the species was the uniform shelterwood system, with a rotation length of 100-120 years and a regeneration period of 20 years. However, failure in natural regeneration was detected by the decade of 1920's (Tiscar *et al*., 2011). In a first diagnosis of the main causes leading to regeneration failure some authors cited: masting habit, occurrence of consecutive dry summers, excessive grazing and uncontrolled ploughing activities (Serrada *et al*., 1994), soil compaction (Trabaud & Campant, 1991), inadequate overstorey cover and forest fires. Recent studies (Tíscar *et al*., 2011) point out to climate conditions as the main current limitations, being natural regeneration in a typical dry summer largely threatened.

P. sylvestris is a Eurosiberian species, with the southern limit of its distribution area in the Mediterranean mountain environment in Spain. In this region, drought is considered as the main abiotic factor constraining the establishment of *P. sylvestris* in the Mediterranean environment (Barbeito *et al*., 2009), unlike in Northern and Central Europe, where low temperature, biotic factors (invertebrates, herbivores and pathogens) and competing vegetation are the main limiting factors. In Sierra de Guadarrama, some *P. sylvestris* forests, as *Navafría* and *Valsaín,* have been rationally managed and successfully regenerated since 1895 and 1899, respectively. Traditional silvicultural systems in these forests relied on uniform shelterwood fellings over a 100 to 120 year rotation period. In Navafría forest mature stands are completely removed after a 20-years regeneration period, followed by soil scarification. The regeneration period in Valsaín forest is extended to 40 years to assure sufficient natural regeneration, without any additional intervention (Pardos *et al*., 2008). The uniform shelterwood system contrasts with the typical systems in northern and colder regions, even in Spain, where the species is successfully regenerated by means of clearcutting (Montero *et al*., 2008a).

The establishment of natural *P. sylvestris* regeneration in the Spanish Central range shows a great spatial and temporal variability (Pardos *et al*., 2008). Mast & Veblen (1999) suggested that episodes of regeneration might require a combination of several factors such as a good seed year, seedbed conditions and the absence of drought and fire. However, the coincidence of a good prseed year and the absence of drought is not actually so common in central Spain, thus resulting in failure in regeneration. In addition, lack of regeneration has also been observed in both the timberline and the lower altitudinal limit, where *P. sylvestris* is mixed with other species.

P. pinaster and *P. pinea* share territory, ecological conditions and historical management traits within the Northern Plateau of Spain, where both species occur in either pure or mixed stands. By the end of 19th century, the forests of this region exhibited a deplorable state, mainly due to abusive grazing, defective stocking volume, intensive pruning for fuelwood purposes and complete lack of regeneration (Gordo, 1999). Given these circumstances, the main objective of the foresters was to transform these depauperated forests into pure even-aged stands. Clearcutting by strips system, followed by either lateral seed dispersal (*P. pinaster*) or artificial sowing (*P. pinea*) using local seeds was the main method used. This method also permitted the change of species at the stand level depending on the main product being favoured by management: cones and nuts (*P. pinea*) or resin (*P. pinaster*) (Gordo *et al*., 2012a).

In *P. pinea*, clearcuttings were successfully maintained up to the end of the decade of 1970's, where closer-to-nature regeneration systems where applied. Based on the experience from other regions (*e.g*. Andalusia), uniform shelterwood system was proposed (Montero *et al*., 2008b). Under this scheme, the seeding felling is scheduled when the stand reaches 100 years, which ideally reduces stand density up to 60 trees/ha. Two secondary fellings are usually applied within an interval of 5-15 years, aiming to completely regenerate the stand in a period of 20 years at maximum. Cone collection should be restricted, at least during the initial phases of the regeneration process. Unfortunately, this system widely failed throughout the sandiest locations within

the Northern Plateau, mainly due to incapacity for disperse seeds on large gaps, seed predation and summer seedling mortality. As a matter of fact, large areas remained without regeneration years after the fellings, exhibiting large highly-exposed gaps where a deep grass layer was installed instead. Contrastingly, advanced regeneration occupied unmanaged patches, leading to non-viable, bad-shaped trees, with low potential as cone producers. As an alternative, in those locations with abundant advanced regeneration, a conversion into uneven-aged stands by means of group selection system has been successfully applied (Calama *et al*., 2005).

P. pinaster was traditionally favoured in the Northern Plateau up to decade of 1960s, due to the economic importance of the resin collection. This production conditioned the whole management system, resulting in short rotations (80 years) and regeneration periods (10 years). These short periods, together with grazing and the keeping of mature resin producers, which hold low seed production, resulted in failure of clearcutting methods. Artificial sowing was therefore widely applied to ensure the stand homogeneity, even on sites where the species was not well adapted. Resin price dropped by the mid-70s, leading to the successful application of extended rotation periods (up to 100 years) and uniform shelterwood systems in a 20-year regeneration period. Despite this early success, regeneration of the species is becoming challenging over the last decades in some areas. Soil conditions, the more frequent occurrence of extreme droughts and the deepening of the water table due to the increase of irrigation practices in neighbouring lands have been suggested as potential agents behind this failure (Gordo *et al*., 2012a).

Finally, *P. halepensis* represents a singular case within the Iberian pines. As a species very well adapted to wildfires, regeneration massively occurs after an intense forest fire. Strikingly, there are very few experiences about the success of regeneration cuttings in *P. halepensis*. Additionally, the species is a clear shade-intolerant one and therefore management guidelines suggest managing it as even aged forests, by applying clearcutting or uniform shelterwood system (del Rio *et al*., 2008). However, in the main part of *P. halepensis* forests in Catalonia negative selection cuttings, focusing only on large trees, have been commonly applied (Saura & Piqué, 2006). This has resulted in open forests colonized by understory species and *Quercus* sp., while the worst shaped and genetically depauperated pines stay in the forest, hence decreasing stand quality, vitality and seed production. In addition, resulting forest structures are very vulnerable to forest fires due to the vertical continuity of vegetation stratums.

Regeneration processes

In this section we present the current state of the knowledge associated with the different processes involved in the natural regeneration for the species, which will permit a subsequent diagnosis and identification of main bottlenecks for the regeneration of the species in the studied areas. At this point it is noteworthy to mention that while Iberian pines share many common traits – they are obligate seeders, do not form lasting seed sol banks, they show masting events… – there are marked interspecific differences in such features linked with seed size, dispersal strategies, fire evasion and drought resistance strategies, pioneering character

Table 2. Main regeneration traits for the five studied species

Regeneration trait	*P. nigra*	*P. sylvestris*	*P. pinaster*	*P. pinea*	*P. halepensis*
Seed length (mm)	5-8	3-5	7-9	15-20	5-7
Wing length (mm)	15-20	12-17	30	25	15-20
Seed weight (mg)	15-25	10-15	35-65	600-1000	20-25
Maximum dispersal distance (m)	100-150	100-120	50-60	10	120-150
Seed release	January-May	December-March	June-August	May-June	March-May[1]
Main dispersal agent	Wind	Wind	Wind	Gravity	Wind
Serotiny	Low	Low	High	Low	Very high
Sexual maturity age (years)	15-40	25-30	10-15	20-25	5
Shade tolerance	High	Intermediate	Low	Intermediate	Very low
Leaf specific conductivity (m^2/MPa·s)	3.24 E-07	4.98E-07	3.43E-07	2.19 E-07	0.95 E-07
Water use efficiency (‰ $\delta^{13}C$)	-26.6	-27.0	-24.7	-18.9	-16.1

[1]Non-fire associated seed release

and shade tolerance that will define specific natural regeneration processes (Table 2).

Flowering, fruiting and seed production

The first stage in any regenerative process is flowering, fruiting and seed production. Although seed limitation has been reported as a main bottleneck in natural regeneration of forest species (Muller-Landau *et al*., 2002), there still exists a wide gap on the knowledge on specific topics such as total amount of seeds annually produced, climate factors affecting fruit and seed production, initial and final ages for bearing fruits and masting habit.

P. nigra is assumed to be a masting species, with good seed crops occurring every 6 years (Alejano *et al*., 2008), the minimum seed bearing age being between 15 to 40 years. Existing observations of *P. nigra* reproductive ecology may support both the pollination coupling and the predator satiation hypotheses for masting (Lucas-Borja *et al*., 2011). The wind pollination hypothesis states that wind-pollinated plants obtain reproductive benefits by synchronizing large flowering efforts, because it increases the probability of pollination (Smith *et al*., 1990). It has been observed that *P. nigra* produces higher percentages of empty seeds (unpollinated) in low flowering years (Tíscar, 2007). Similarly, the predator satiation hypothesis states that large seed crops are likely to satiate seed predators, which thus would destroy a lower percentage of crop (Kelly, 1994). Moreover, seed production is significantly lower at the altitudinal limit of the species distribution than in the most favourable habitat (Lucas-Borja *et al*., 2012), confirming that pines under stressed conditions tend to produce solely male cones or even stop reproducing (Shmida *et al*., 2000). Seed production in mast years can be up to 10-fold greater than that of a non-mast year, with average values over 70 seeds/m2 on mast years and favourable locations, and less than 10 seeds/m2 on non-masting years and/or altitudinal limits (Lucas-Borja *et al*., 2011, 2012). Larger values of seed production were identified in high dense stands. Nevertheless, these values are notably smaller than those obtained in other non-limiting areas such as Cazorla (average values of seed dispersal over 600 seeds/m^2; Tiscar, 2007). Thus, seed availability is one of the main factors limiting the natural regeneration.

P. sylvestris in the Central Range of Spain starts producing a high amount of cone and seeds at 25-30 years old (in isolated trees) or 40 years old (when growing in canopy) holding this capacity up to very high ages (Ruiz de la Torre & Ceballos, 1979; Rojo & Montero, 1996). According to the classical trade-off theory by Smith & Fretwell (1974) a small-seeded species like *P. sylvestris* will produce a sufficient amount of seeds every year.

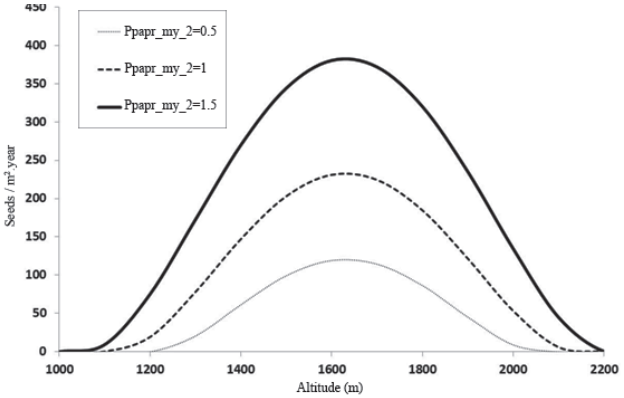


Figure 2. Annual seed production in *Pinus sylvestris* stands in Valsaín forest over the altitudinal range of the species. Lines represent seed production for three different precipitations: half (dotted thin line), the same (dashed line) and twice (solid thick line) the mean value for April and May precipitation two years before cone maturation (PPapr_my_2). Original figure based on Calama *et. al*. (2015b).

Confirming this, during a four-year study (2005 to 2009) annual seed production was high enough to discard either source or dispersal seed limitations (Calama *et al*., 2015a). Annual seed density mean values ranged from 150-300 seeds/m^2 (Calama *et al*., 2015b), except in the lower lands (Fig. 2) where the species occurs in mixed stands with *Quercus pyrenaica* Willd. (average production 36 seeds/m^2). A certain masting is to be found in the species, with about two good crops every seven years (Montero *et al*., 2008a), although null crops are absent (Hilli *et al*., 2008). In the aforementioned four-year study, 16-fold average differences between years were detected, mainly related with the precipitation occurring in the spring two years before cone maturation (Calama *et al*., 2015b). It is worthwhile to mention that the observed values for *P. sylvestris* in Central Range are remarkable if compared with that of the relictic forests of the species in Andalusia (average annual production 2-20 seeds/m^2; Castro *et al*., 1999). Seeds from trees in the timberline stand showed a different interannual variation to those at mid-altitudes (1400 – 1600 m), where seed production seems to be maximized. Despite these spatiotemporal differences, natural regeneration for *P. sylvestris* seems not to be limited by the production of seeds, except on the lower altitudinal limit and/or in years with very low seed production (Calama *et al*., 2015a).

Cone and seed production has been largely studied for *P. pinea*, given the edible character of the nut. In this respect, there is a major feature that makes *P. pinea* different from all other Iberian pines, as cone development occurs over a 3-year period, in contrast to the 2 years of the rest of pines (Calama *et al*., 2012). Additionally, *P. pinea* exhibits a large size seed (over 700 mg ± 200 mg, with 20 mm in length), which

prevents wind dispersal from occurring. Cone and seed production is delayed up to an age of 15-20 years, although it can be anticipated in grafted plantations (Mutke *et al*., 2012). On the opposite, trees hold their productive capacity up to 160-180 years.

Given its large size, and according to the trade-off theory, we should expect smaller seed crops than in other species. This was confirmed by the average seed production of 9.4 seeds/m^2 observed over a 5-year experiment on seed dispersal in *P. pinea* (Calama *et al*., 2015a). However, large differences in cone and seed production are detected within the study area. Lower crops are associated with sandy soils with low water holding capacity (Calama *et al*., 2012). Low density stands, where trees can expand their crowns freely, are more favourable for cone and seed production than overdense stands (Calama *et al*., 2011).

Additionally, the species shows a noticeable, climate-mediated masting habit, which can result in interannual 20-fold magnitude differences in cone production at regional level, largely synchronized within the study area (Calama *et al*., 2012). The rate of trees not bearing cones at all in very bad years can reach values close to 80% (Calama *et al*., 2016). The occurrence of favourable climatic conditions during key phenological stages as bud formation, bud differentiation, conelet survival through first summer and winter and cone enlargement determine mast events (Mutke *et al*., 2005; Calama *et al*., 2011). In addition, masting in *P. pinea* is secondarily ruled by a three-year delayed resource depletion effect, resulting in lower than expected cone production three years after an exceptional bumper crop (Calama *et al*., 2016).

Previous findings indicate that the lack of seed availability could be considered a main limitation for *P. pinea* natural regeneration in unfavourable crop years, especially in overdense stands within low producing sites. The results of the above mentioned seed dispersal study came to corroborate this, as regeneration limitation was related to seed shortage in three out of the five studied years (2005, 2008 and 2009) (Calama *et al*., 2015a).

Contrarily, *P. pinaster* seed availability has never been considered a limiting factor within the Northern Plateau, due to abundant and frequent cone production and the silviculture approach implemented that always left a sufficient number of trees in the stands during the regeneration phase (Gordo *et al*., 2012a). While a serotinous species, this trait in *P. pinaster* is not so marked in the Northern Plateau as in other regions (Tapias *et al*., 2001). However, recent studies have given exact figures by counting cones on standing trees and collecting seed from traps (Ruano *et al*., 2015), resulting on average values around 7-24 seeds/m^2, though showing large spatial and temporal availability (3.6 fold magnitude between years). Juez *et al*. (2014) found that just a small fraction of mother trees are responsible for a high proportion of seed production. Ruano *et al*. (2015) identified a climatic control over masting habit in the species, with the precipitation during the period of secondary growth of the cones positively affecting cone production. Thus, water stress may limit seed production in extreme dry years. Additionally, they identified that following very intensive regeneration fellings, seed availability could be a limiting factor.

P. halepensis presents a combination of several remarkable reproductive attributes related with cone and seed production that helps explaining the great colonization potential of this species and its high resilience to intense fire events (de las Heras *et al*., 2012). *P. halepensis* starts as female the reproductive stage, prior to the appearance of male structures in secondary branches and it shows an extremely short juvenile period, with an early onset of cone and seed production from 3-5 years of age (Tapias *et al*., 2001; Espelta *et al*., 2008). Annual production of cones is often massive and quite regular across years (Verkaik & Espelta, 2006) and part of the crop of mature cones is retained in the canopy for several years as serotinous (closed) cones (45–80% according to Thanos & Daskalakou, 2000). According to these authors, considering both serotinous and non-serotinous cones, canopy seed bank can reach values between 115-790 seed/m^2, with 10-20% (del Río *et al*., 2008) that can be released during summer without exposure to fire.

In fact, serotiny has probably been one of the most analysed reproductive attributes of *P. halepensis*. This pine is a weak or partial serotinous species as rupture of serotinous cones is certainly induced by fire, but it may also occur spontaneously, especially when canopies are suddenly exposed to high radiation levels (Verkaik & Espelta, 2006) or after drought episodes (Espelta *et al*., 2011). Serotiny degree of *P. halepensis* decreases with ageing and tree size, a pattern suggested to be caused by the costs of maintenance for the plant of these long-lasting structures competing with younger cones for resources (*e.g*. water, in Espelta *et al*., 2011). In Spain, a large variability in the degree of serotiny has been observed among populations across geographical gradients revealing that serotiny may increase with stand density and from northern to southern populations (Moya *et al*., 2007, 2008; de las Heras *et al*., 2012). Recently, studies conducted in common garden experiments have demonstrated, after controlling for the effects of tree size, that serotiny has a genetic basis and it is lower in pines from harsh (dry and cold) sites compared with mild sites (Martín-Sanz *et al*., 2016),

while is more abundant on post-fire stands than on stands established in fire-free conditions (Ne'eman *et al*., 2004).

In spite of the well-known importance of the occurrence of fire, the abundant production of cones in *P. halepensis* ensures a massive availability of seeds even in the absence of this disturbance (del Río *et al*., 2008). Therefore seed availability cannot be considered a limiting factor for the species, except in very dry conditions, or when the lapse between two fire events is shorter than the expected time for younger plants to reach sexual maturity (del Río *et al*., 2008; Espelta *et al*., 2008).

Seed dispersal

Seed dispersal is a key process in natural regeneration, determining the arrival of seed to favourable sites for establishment and the spatial location of the seedlings. Wind-dispersed seeds are expected to arrive to every location within the stand, even travelling over long distances. Contrarily, heavy seeds tend to be clustered beneath the crown of mother trees, resulting in a clumper distribution with gaps in those locations where seeds cannot arrive.

P. nigra, *P. sylvestris*, *P. pinaster* and *P. halepensis* are species mainly dispersed by wind, a fact that facilitates its wide distribution, even in low dense stands. *P. nigra* disperses seeds from January through May, with a maximum in March, and seed rain tends to be uniformly distributed throughout soil, especially on dense stands (Tiscar, 2007). Literature in *P. sylvestris* shows that fifty percent of the seeds remain under the crown, while other 40% of the seeds are found at distances as long as 2 to 4 times the tree height (Burschel & Huss, 1997). This means that between 30 and 75% of the seeds are found not more than 18 m from the tree (Montero *et al*., 2008a). In our specific study area only 20% of the seeds were released under the crown, while in a distance of three crown radii the number of dispersed seeds is similar to that beneath the crown (Calama *et al*., 2015b), resulting in a close to uniform distribution of the seed rain on the soil surface. For *P. pinaster* median dispersal distances in the territory varied between 14.1 to 24.5 m, with maximum distances over 54 m (Juez *et al*., 2014). Dispersal events are concentrated in only one period, from June to August, with maximum dispersal events associated with violent summer storms. Finally, in *P. halepensis* spatiotemporal variation of seed rain reveals dispersal curves with ca. 95% seeds dropping less than 20 m away from the mother tree, maximum seed dispersal up to distances of 100-120 m, and occasional long distance dispersal events spreading 0.2 % of the seeds up to distances over 1 km (Nathan & Ne'eman, 2000). Based on the information above, no limitations associated with seed dispersal are expected in these species.

Concerning seed dispersal, *P. pinea* is mainly referred to as a gravity-dispersed species, due to the morphology of the large and wingless seeds produced. Manso *et al*. (2012) found a strongly aggregate spatial primary dispersal pattern in a *P. pinea* stand in the Northern of Spain, only 1% of the seeds being expected to drop beyond 2 crown radii. Similar results are due to Masetti & Mencussini (1991) in their study in Toscana (Italy). This aggregated pattern of seed dispersal will result in a clustered distribution of seedlings and samplings under the influence area of the crown of mature trees, conforming overdense small patches that will require further liberation to enhance development (Barbeito *et al*., 2008). From a temporal perspective, seed release is climate-controlled, at least in central Spain locations: 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 from summer until early fall (Manso *et al*., 2012), showing a similar temporal pattern than its conspecific *P. pinaster*.

Accordingly, low-distance dispersal by gravity prevent seed arrival into large gaps (radius > 10 m), thus avoiding natural regeneration in these areas (Fig. 3). Additionally, though dispersal of *P. pinea* seeds has been often assumed to be secondarily animal-mediated, a belief probably linked to the highly nutritional content of the nuts, this fact has never been clearly confirmed. In fact, Manso *et al*. (2014b) did not find any obvious

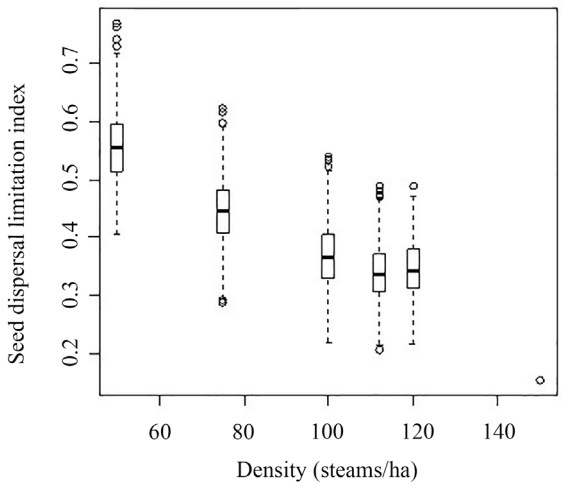


Figure 3. Seed dispersal limitation index (defined as the rate of places where no seeds arrive, assuming that there are no limitations in seed source) for *Pinus pinea* in Northern Plateau as a function of stand density. Original figure based on Manso *et al*. (2012)

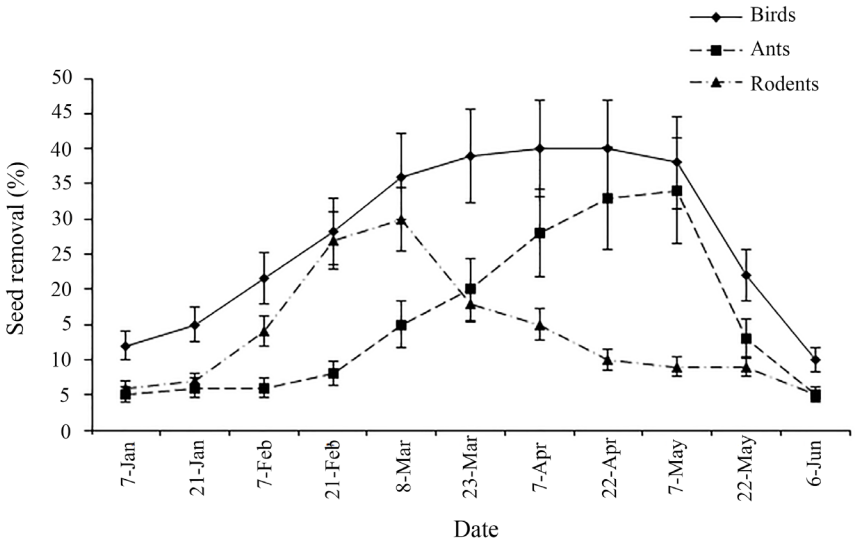


Figure 4. Seasonal variation of seed predation in *P. nigra* by predator group in typical Cuenca mountains forest areas in a masting year. Original figure based on Lucas-Borja *et al*. (2010)

trace of secondary dispersal by rodents within the regeneration blocks. The authors detected a minority seed removing by corvids, though. Although the fate of these seeds could not be tracked, this can be behind the occurrence of isolated seedlings growing in the closer vicinity of managed forests, far beyond the dispersal distance expected from primary dispersal models.

Pre and post-dispersal seed predation

Pre-dispersal predation by birds (*e.g*. cornbills), jays, mammals (*e.g*. squirrels), or insect pests attacking cones and seeds in the early stages of maturation can be responsible for severe seed losses. However, post-dispersal seed predation has been reported as a main limiting factor in many pine species, as the seeds reaching the soil can be consumed in the ground in the different seasons of the dissemination period. A large variety of potential consumers (from insects to mammals and birds) have been identified, thus resulting in spatio-temporal heterogeneity in predation due to factors as abundance of seeds or abundance of predators. Seed predators can severely reduce the total amount of seeds available to create a seed bank, but also change the spatial distribution of seeds after the initial seed rain (Castro *et al*., 1999).

For *P. nigra* in Cuenca mountains three main group of predators were observed (Lucas-Borja *et al*., 2010): ants, birds (*Fringilla coelebs* L., *Parus caeruleus* L., *Parus major* L.) and rodents (*Apodemus sylvaticus* L., *Mus musculus* L.). Predators present different seed removal rates depending on the season of the year, with special incidence on winter and lower rates on spring, coinciding with the uprising of temperatures and subsequent lesser activity of rodents (Fig. 4). Seed predation was related with seed rain patterns (Lucas-Borja *et al*., 2016) being lower in the high seed rain year (11.2±3.7% of removed seeds) than in the low seed rain years (84.3±6.6% of removed seeds), a finding in agreement with the predation satiation hypothesis (Janzen, 1976). For the species, a good year of recruitment has to be preceded by a good seed production year, in which case post-dispersal seed predation is not as important as in low seed fall years. In high seed production years, birds were the most important predators and rodents were the less important predator group in both typical and relict forest areas for this species. Due to the high seed removal percentage by all predator groups, no conclusion can be obtained in low seed production years (Lucas-Borja *et al*., 2010).

Though no specific studies on seed predation on *P. sylvestris* in Central Spain have been carried out, this topic has been widely studied in other locations of the species. For instance, the great spotted woodpeckers *Dendrocopos major* L. is one of the main predators of seeds in closed cones of *P. sylvestris* in central and eastern Europe (Myczko & Benkman, 2011), while the crossbill (*Loxia curvirostra* L.) feeds on ripening seeds in southern Spain (Castro *et al*., 1999). Predation pressure shows an interannual variability that may be related to temporal variation in cone production (Matias *et al*., 2009). Although pre- and post-dispersal predation can reduce the seed pool of *P. sylvestris* to almost 50% (Worthy *et al*., 2006) or even over

90% in relict *P. sylvestris* forests in southern Spain (Castro *et al*., 1999), it is unlikely to be a serious problem for the regeneration of the species in Sierra de Guadarrama, except in the lower limit, where seed production is much more scarce.

In the case of *P. pinea*, it is important to consider the effect of both pre- and post-dispersal predation. Pre-dispersal seed predation has only been described as a serious threat for seed production very recently. Classical native pests, as *Pissodes validirostris* Gyll. or *Dioryctria mendacella* Staud. have been reported to produce damage to a limited extent, damaging about 20% of cones (Calama *et al*., 2017). Moreover, in recent years, a North-American invasive seed-feeding bug, *Leptoglossus occidentalis* Heid., has been postulated as the main cause for the dry cone syndrome, resulting in recent decay in cone production as well as the rate of filled seeds (Mutke *et al*., 2015). In this sense, the rate of damaged seeds in the Northern Plateau has increased up to 50% in the recent years, resulting in both economic and ecological losses. Additionally, it is worthwhile to notice that this bug species is a conifer-specific pest, thus the potential damage over other Iberian pines should not be neglected and the monitoring of its activity and its effect on seed availability it is highly recommended.

The size and nutritional value of *P. pinea* seeds may not go unnoticed by post-dispersal seed predators. Manso *et al*. (2014b) observed that the wood mouse (*A. sylvaticus*) was the main predator of seeds of *P. pinea* in the Spanish Northern Plateau, being responsible for more than 80% of seed removal. Secondary agents for predation were identified as azure-winged mapie *(Cyanopica cyanus* Pall.) and common raven (*Corvus corax* L.). *A. sylvaticus* acts exploiting almost all available seeds during drought-free periods, being able to consume almost 100% of available seeds during winter. The favourable summer 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, predation is slightly higher in the close vicinity of trees and potential rodent shelters (Manso *et al*., 2014b).

A similar process has been identified in the conspecific *P. pinaster* in the Northern Plateau. Ruano *et al*. (2014) showed that predation can reduce seed density up to values below 1 seed/m^2, even in locations where seed rain reached values over 40-50 seeds/m^2. Although no specific experiment for detecting potential predators' species was carried out, the authors indicate that together with *A. sylvaticus*, *C. ciyanus* and *C. corax*, ants should be considered a potential predator for the seed of *P. pinaster*. The authors found a positive correlation among density of seeds escaping from predation at the end of the year and total seed rain, thus higher predation rates occur when the amount of available seed is lower. Additionally, climate variability influences predator populations, showing larger rates in autumn-winter and almost no predation in summer. As for *P. pinea*, predation is favoured in the vicinity of stumps and in denser areas (potential sheltered locations), while the presence of grasses and needles on the floor hide seeds and therefore prevents predation (Ruano *et al*., 2014).

In *P. halepensis*, notwithstanding an initial abundance of seeds, their availability may be reduced by intense seed predation, especially when no other seed sources are available (*e.g*. after a fire event), when seed losses can reach up to 90%. Rodents have been observed to be the main predators of *P. halepensis* seeds, while predation by ants or birds is considerably lower (Broncano *et al*., 2008). Concerning the spatiotemporal patterns of seed predation, Broncano *et al*. (2008) showed that predation by rodents is very high in all situations and seasons.

Germination, emergence and early survival

Seed germination, seedling emergence and early survival success will define the spatial pattern of seedling location, and further spatial pattern of adult plants, redefining the spatial pattern associated with seed shadow. In this sense, different requirements can be identified for each process, thus, conditions and traits beneficial for one developmental process could be disadvantageous for another.

Stand density, soil preparation, dispersal season and site conditions had a significant influence on *P. nigra* seed germination and initial seedling survival, though showing conflicting situations for both processes (Lucas-Borja *et al*., 2011). The effect of the overstory can be summarized as positive for seed germination, with rates reaching values up to 40-60% in denser stands and below 30% in open stands (Lucas-Borja *et al*., 2011). This effect is more evident on drier and warmer years, where germination and seedling emergence is also favoured by shrub protection, factor with no effect on cooler and wetter years. Germination is also favoured in mid-altitude locations, while largely restricted in the upper limit area. Site preparation had a significant influence on seed germination, which was favoured by scalping, but no effect on seedling survival at long term (Lucas-Borja *et al*., 2011).

Higher light availability (low basal area) promotes seedling survival, thus a seed germination-seedling survival conflict can be observed. This conflict is more patent on wetter years, since the probability of summer seedling survival in drier and warmer years is very low, irrespective of crown coverture (Lucas-Borja *et al*., 2011). All the results point out that, for *P. nigra*, annual climate is the major factor controlling seed germination and seedling survival, with a secondary control due to light availability.

Light is a determinant factor for the germination of *P. sylvestris* in Central Spain. The optimal radiation for germination suggested for *P. sylvestris* is 35% of full sunlight, thus germination is favoured under the mid to high shadow conditions that are found when the group shelterwood system is applied and with selective cuttings, while is minimized under the large gaps created after a clearcutting (Calama *et al*., 2015b). Apart from the direct limiting effect of radiation on seed germination, high rates of light are often associated with the presence of a dense herbal layer which prevents seed germination and seedling emergence. Under moderate light levels the presence of this herb layer had a weak effect on seedling emergence, suggesting that seedlings and herbs can occupy the same sites (Pardos *et al*., 2007). On the contrary, an increase in the light levels led to a decrease in regeneration performance because of an increased competition for resources (Módry *et al*., 2004). Although *P. sylvestris* can germinate in many different types of seedbed (Cañellas *et al*., 2004), the litterfall accumulated increases the depth of organic matter and thus improves microsite conditions for germination (Pardos *et al*., 2008), except if layer thickness reach values over 10 cm. This result contrasts with previous findings for the species in Central Europe (Hille & den Ouden, 2004), or even in Northern Spain, where soil scarification is recommended, and reflects the particular ecological conditions for the species in the mountains of Southern Europe.

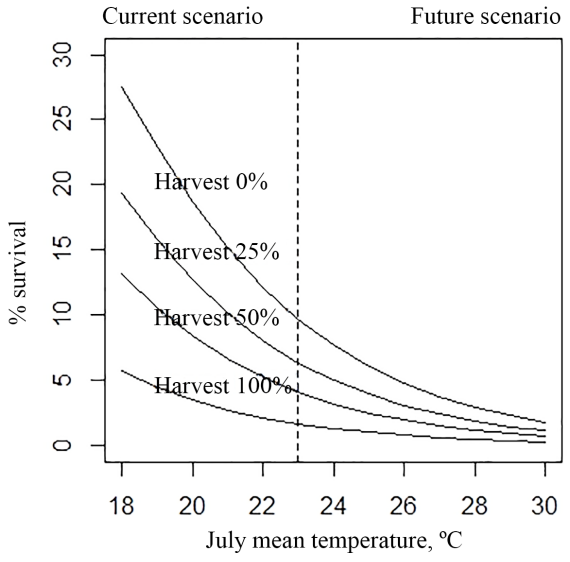


Figure 5. Percentage of summer seedling survival in *Pinus pinaster* as a function of mean temperature of July and rate of harvested basal area. Remaining basal area 8.8 m^2/ha. Original figure based on Ruano *et al*. (2009)

The results from a 3-year (2009 to 2011) study in Valsaín forest also suggested a climate control that limits germination at least in the timberline (Calama *et al*., 2015b), partly related to the occurrence of spring frost events and low water availability during summer (Barbeito *et al*., 2009). In any case, under the current climate conditions, germination rates in *P. sylvestris* are high, with a great variability between years and sites. For instance, germination rates recorded in the studied area were over 70%, the larger rates obtained during spring and autumn at 1600 m. On the contrary, lower rates of germination were observed at timberline areas (Calama *et al*., 2015b).

Despite high rates of seed germination and seedling emergence, the regeneration occurs as a temporary pulse of seedlings, due to seedling mortality that could be close to 100% after a hot and drought summer (Calama *et al*., 2015a). Water availability during the summer seems to be the key factor driving *P. sylvestris* regeneration at Sierra de Guadarrama, similarly to what has been recorded at its southernmost distribution limit (Matias & Jump, 2014). With respect to light requirements, although in the Eurosiberian forests *P. sylvestris* behaves as a light demanding species, results from different studies in central Spain, suggest the preference of the species to moderate light conditions, at least during the early stages of growth (Pardos *et al*., 2008; Calama *et al*., 2015a). Seedling survival is also threatened after extemporal cold springs and in highly shaded environments (Calama *et al*., 2015b). Mortality in *P. sylvestris* steadily increases during the first two years after emergence, but a notable stabilization in seedling survival is found after three years (Pardos *et al*., 2007).

Seed germination in *P. pinea* is governed by thermal variables in combination with different degrees of soil and air humidity. In the field, Manso *et al*. (2013a,b) were able to empirically link seed germination of *P. pinea* seeds to climatic and stand variables in the Northern Plateau of Spain. Optimal conditions occur over few weeks either in autumn (linked with warm conditions) just after seed dispersal, or in the following spring (linked with humid conditions). Large interannual variability in germination rates, conditioned to the occurrence of this optimal conditions, is observed. Over a 4 years study, germination rates varied between 9% and 90%, with two years showing autumn germination

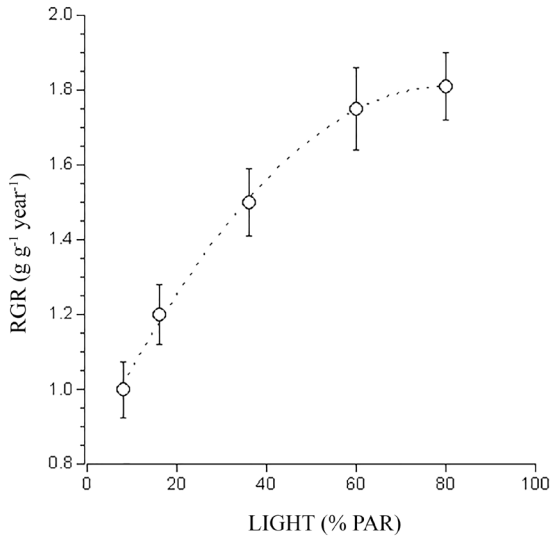


Figure 6. Mean ± SE relative growth rate (RGR) of *Pinus halepensis* seedlings in response to light availability (PAR: photosynthetic active radiation). As a shade-intolerant and pioneer species *P. halepensis* seedlings exhibit a fast growth response to an increase in radiation. Conversely, for this species shading is the main factor constraining seedling recruitment. Based on Espelta (1996).

events, one year with spring germination events, and one year with almost no germination at all (Manso *et al*., 2013a). Moreover, extremely poor overstory cover leads to low probabilities of germination. Implications for natural regeneration in *P. pinea* are relevant as the process becomes seriously limited in the absence of this climatic optimal conditions. Occurrence of cold fall season prevents germination, thus the remaining seeds are highly vulnerable to the action of predators during winter, the season where rodents are more active. Additionally, if a cold winter is followed by a dry spring, germination does not occur (*e.g*. 2008-2009 campaign, germination rate < 9%).

Studies carried out in the Northern Plateau show that seedling mortality of *P. pinea* occurs as a result of a combination of low water potential and negative assimilation rates (Calama *et al*., 2015c). These circumstances usually take place during the summer season, with older seedlings being able to better thrive due to carbon reserves stored in previous favourable seasons. This picture matches up with the empirical evidence found in the same area, where the vast majority of emerged seedlings perished in the first two years after emergence, except if optimal summer conditions occurs. Interestingly, winter frost does not significantly affect seedling survival (Pardos *et al*., 2014). From a spatial perspective, optimisation of the carbon balance and survival is attained when seedlings are placed in mid-shaded locations, which are those locations more favourable for germination. This is in full accordance with the findings of Awada *et al*. (2003), which reveal that *P. pinea* seedlings can actually tolerate some degree of shading in the initial stages of development. The same observations show that individuals emerging in autumn and closer to adult trees are more likely to survive than seedlings from spring cohorts and isolate individuals (Manso *et al*., 2014a).

Seed germination for *P. pinaster* in the Northern Plateau seems not to be a limiting factor, with this provenance showing larger germination rates in response to drought than Atlantic provenances (Núñez *et al*., 2013), and positive response to thermal shocks (Herrero *et al*., 2004). Concerning germination rates on field conditions, Ruano *et al*. (2009) observed, over an 18 months experiment, a significant effect of remaining basal area on germination rates. Higher germination rates (around 60%) were found at remaining basal area of 6.6 m^2/ha (25% of reduction) on harvest operations. Surprisingly, values of germination rate about 40% were obtained both in non-harvested as well as on clearcut areas. Germination occurs in either fall or spring season, seasonality that could explain the observed little effect of summer rainfall on germination rate.

Seedling establishment and survival processes in *P. pinaster* are closely related to seed germination, thus more favorable sites for germination are those more favorable for survival. However, initial seedling survival is largely threatened by water stress during the summer (Fig. 5), as well as interactions with other factors. In particular, mid-shaded conditions, the presence of shrubs acting as nurse plants (Rodríguez-García *et al*., 2011) and needle soil cover (del Peso *et al*., 2012) facilitate *P. pinaster* germination, emergence and initial survival.

Unless severe predation or topographic constraints limit seed availability, germination of *P. halepensis* seeds and early survival is often successful and occurs at high rates (80%) under contrasting environmental conditions: *i.e*. from closed (10% full sunlight) to open (80% full sunlight) canopy cover. In this sense, while shading favours earlier germination (Broncano *et al*., 1998), previous studies in Southern France have reported complete lack of regeneration in very dense stands (Prévosto *et al*., 2012). Germination is favoured in exposed mineral seedbeds while thick layers of organic matter may limit this process (Broncano *et al*., 2008). As a light-demanding and drought-tolerant species, once established, seedlings are able to tolerate high levels of radiation exposure (Fig. 6) and moderate water stress (Eugenio *et al*., 2006). Indeed, these are environmental conditions particularly occurring after intense stand-replacing wildfires and therefore, in this situation, regeneration is often successful (de las Heras *et al*., 2012),

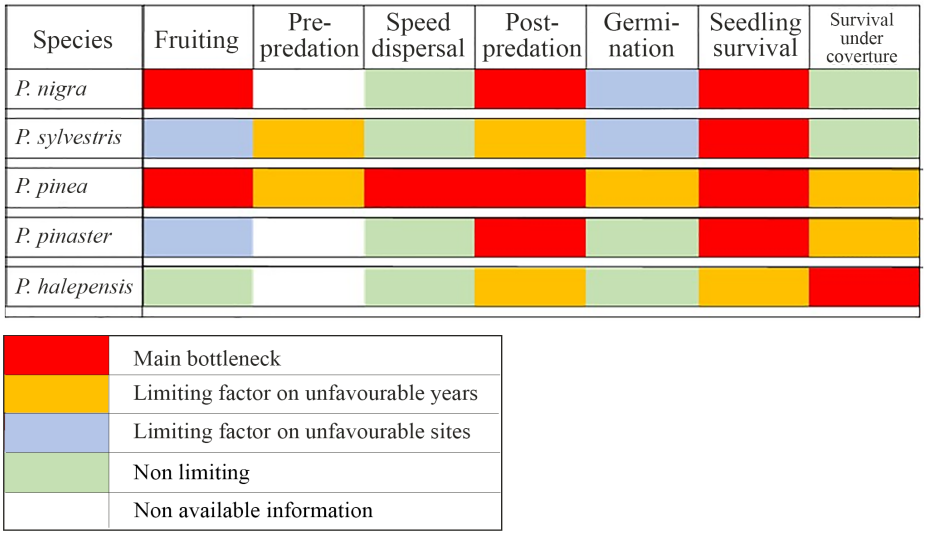


Figure 7. Influence of the different subprocesses on the success of natural regeneration for each pine species.

with densities of young seedlings varying from 0.1 up to 10 seedlings/m^2 (Rodrigo *et al*., 2004). The fact that *P. halepensis* shows similar environmental conditions for both germination and initial seedling establishment, as well as a wide plastic response, confirm the lack of a seed-seedling conflict in this species (Broncano *et al*., 1998). Thus, the lack of natural recruitment in some cases could be associated with the absence of effective dispersal. Interestingly, in contrast with the myriad of studies in Spain that have analysed the regeneration of *P. halepensis* forests after stand-replacing wildfires and that claimed for the high resilience of this species to these disturbance, the regeneration in the absence of fire has been seldom explored (Beltrán *et al*., 2011), and this is a main constrain to predict the dynamics of undisturbed forests (but see Zavala *et al*., 2000, 2011) and their response to global challenges.

Main bottlenecks and threats for natural regeneration in Iberian pines

Findings from the previous section allow us to identify the main bottlenecks for natural regeneration in Iberian pines (Fig. 7), and give insight into the potential threats for the future.

Seed production can be a key limiting factor in non-mast years for masting species such as *P. nigra* and *P. pinea*, especially in the ecological limits of their distribution. For the rest of species, even though some interannual variability in cone and seed production is observed, seed availability seems sufficient except under very limiting environments (*e.g.* at lower altitudinal limits for *P. sylvestris*, or in very dry years). Little is known about the process of non-fire-associated ripening of serotine and non-serotine cones in *P. halepensis*, though the total amount of seeds produced and dispersed even in non-fire events seems sufficient. Given the climate control over masting on pine species, limitation due to seed availability could be a limiting factor for regeneration of pines under future climate scenarios.

Concerning seed dispersal, the only species severely affected by ineffective dispersal seems to be *P. pinea*, which is the unique species showing a main gravity dispersal process. Low current densities of mature *P. pinea* stands-associated with a common silvicultural practice applied in the territory during the 20th century to promote cone production-resulted in large gaps that cannot be occupied by the seeds. The postulated animal mediated seed dispersal in the species seems not to be sufficient to fill these gaps, thus resulting in a patched and clumped distribution of seeds under the crowns of adult trees.

Seed predation is a key limiting factor for the main part of the species, especially on low seed years. In this sense, masting can be considered a regeneration strategy to deal with this, by satiating predator populations on mast years and starving them on non-mast years, according to the postulated predator-satiation theory (Salisbury, 1942; Janzen, 1976). At within-year temporal levels, we detect a delay among the season of seed fall and the maximum activity of predators (mainly rodents), which would allow seeds to escape predation if favourable conditions for germination are attained. On the contrary, complete losses of seed crop can be found on unfavourable years for many of the studied species.

Seed germination and seedling emergence is mediated by both environmental control and soil conditions where seed arrives. Seed germination is mainly regulated by temperature, water availability and light. Freezing temperatures can limit autumn germination in *P. pinea*, as well as germination of *P. sylvestris* and *P. nigra* on their altitudinal limits. Dry years can result in lack of spring germination for all the species. With respect to light, germination is generally favoured under mid-shaded environments, except in *P. halepensis*, whose germinative ability remains high under a wide range of cover conditions. Finally, for the small seeded species, as *P. nigra*, *P. sylvestris* and *P. halepensis*, the presence of a dense herbal layer limiting the access of seeds to mineral soil can prevent seed germination and seedling emergence. In this sense, light exerts a multiple control, since in very open stands the presence of herbs and competitors is enhanced, while soil water content is minimized. On the opposite, in very dense stands the presence of a very thick litter layer together with low light availability could be detrimental to emergence and survival (Sayer, 2006).

Shortage in water during the first summer seasons together with excessive light irradiance seems to be the key factors impairing seedling survival in all the studied pine species, except, once more, in *P. halepensis*, which shows large rates of survival even at high exposures. The rest of species require initial shading for seedling survival, and initial survival is more likely in the close vicinity of parent trees, or even under the presence of shrubs acting as nurse plants. Nevertheless, as seedlings grow, different degrees of tolerance are identified among species. In this sense, and according to their low shade tolerance, *P. halepensis* seedlings require earlier liberation (Scarascia-Mugnozza & Schirone, 1984), followed by *P. pinea* and *P. pinaster* (Ruano *et al*., 2009; Manso *et al*., 2014a). On the opposite side, *P. sylvestris* and *P. nigra* are the species whose seedlings can survive longer periods under the shade of parent trees (Calama *et al*., 2015b; Lucas-Borja *et al*., 2016).

The main bottlenecks identified for all the species in the studied areas are climate-mediated. This means that it is very likely to have unfavorable conditions for one or several of these processes in a given year, thus favorable conditions for the regeneration of the species occur within a lapse of years. Under changing climate scenarios we should expect, in general, more unfavorable conditions for seed production, seed germination and seedling initial survival. On the other hand, processes as autumn-winter germination can be favored by increasing temperatures, which could also affect the population dynamics of predators as rodents. In any case, natural regeneration of the species in the studied areas would surely continue to exhibit an intermittent temporal pattern, which should be aggravated under drier scenarios.

Managing natural regeneration in Iberian pines

Based on the previous findings, new proposal for managing forests in order to attain the natural regeneration have been proposed for the species in the studied areas.

In the case of *P. nigra* it has been proposed (Lucas–Borja *et al*., 2016) an extension of both the rotation and the regeneration periods up to 150 and 30 years, respectively, in order to ensure the occurrence of favorable conditions permitting successful natural regeneration. In addition, less intense and more gradual and continuous regeneration fellings should be applied. These fellings should be programmed following a mast year, and applied in combination with soil treatments (*i.e*. scalping) oriented to prevent soil compaction and to favour soil humus. Shrubs cover might have an important role regarding natural regeneration. In drier years, shrub cover should be promoted since seedling emergence has been enhanced under moderate light (about 25 m^2/ha) and shrubs protection. However, in wetter years, forest managers should promote *P. nigra* regeneration by clearing shrubs after seedling emergence to increase light availability and to avoid shrub competition. Overall, the natural regeneration of *P. nigra* has to go through conflicting situations between conditions suitable for seedling emergence (medium basal area interval, shrub cover) and conditions suitable for seedling survival (outside shrub cover without basal area influence), these effects being modulated by the climate of a given year, seed predation and site quality. These issues make many of these recommendations difficult to be implemented in the field.

Similar, but even more flexible schedules are proposed for *P. sylvestris* in the Central Range (Cabrera & Donés, 2010). Uniform shelterwood system is being now replaced by a more gradual group regeneration system, where the shelterwood fellings are gradually applied on small patches and trees are harvested through several fellings. In this way, natural regeneration establishes progressively under the older trees canopy during a 40 years regeneration period and a 140 years rotation length, with some seed trees still remaining after the last cutting. For example, in Valsaín forest, the aim is to gradually substitute the

old stand by a thicket stand with 250 trees per ha. This initial density will decrease by natural mortality and harvesting operations. Under these proposed practices, *P. sylvestris* stands would naturally turn to semiregular or multi-aged structures, making the stand more vulnerable to fire. It is important to note the adaption of the silviculture to the peculiarities of the different stands, with important restrictions to the harvesting operations in those stands that hold protected species as the European black vulture (*Aegypius monachus* L.).

The main innovative proposal in managing natural regeneration in *P. pinea* (Gordo *et al*., 2012b) is that in order to ensure seed arrival into gaps, thinning schedules should target to densities about 125-150 stems/ha at the beginning of regeneration fellings. This means that less intensive and more gradual thinnings should be applied during the whole cycle. Early thinning operations are also recommended in order to favor initial lateral expansion of the crowns, facilitating seed arrival into the gaps. A second concern is related to the need of initial shading conditions to favor seed germination and seedling survival, especially under more severe climate scenarios. Intense uniform shelterwood system should be replaced by more gradual fellings. An initial single preparatory-seeding felling, reducing stand density up to 80-100 stems/ha, is recommended. With this cutting we aim to remove dominated, co-dominant and dominant trees in a bad state, with inadequate stem form, malformed crown and low cone production. The remaining trees will act as seed trees, also providing initial shelter for the recently emerged seedlings. Simultaneously, it may be necessary to eliminate the understory vegetation and nonviable advanced regeneration. Once a sufficient number of viable seedlings had been already established beneath the crown cover of the seed trees (after 5-10 years), a secondary felling should be applied, aiming to release the most promising regeneration patches. Subsequent removal cuttings should aim to gradually uncover the new cohort of regenerated trees. These removal cuttings should elapse a maximum of 5 years, to prevent the negative effect due to competition or damage from harvested mature trees on the young saplings. At the end of the period, 5-10 extra mature trees per ha are to be retained.

The regulation of light through operational forestry practices influences significantly the germination, survival and growth of the *P. pinaster*. Shelterwood method applied by light interventions (reduction of basal area between 25 and 50 % at maximum) favors the seed germination generating seedlings protected by residual trees. In this way, seedlings will grow to generate stands compatible with the provision of ecosystem services (resin and wood), while obtaining other environmental services. A reduction of 50% of the basal area should be applied when economic conditions restrict operations, thus larger amount of wood must be removed to make feasible the intervention. As for other Mediterranean pines, the role of tree canopy protection will be more important as the climatic conditions become more stressful (especially extreme dry and hot summers). When an adequate amount of viable seedlings is obtained (after regeneration felling or taking advantaging of advance regeneration) a final felling should be applied to avoid damages to new crop trees. In some special cases, a reduced number of trees from the previous cohort can remain in the stand to enhance biodiversity values.

The management proposals for natural regeneration of *P. halepensis* on absence of fire should aim to mimic small perturbations (Prévosto *et al*., 2012). Beltrán *et al*. (2011) propose even-aged structures following shelterwood regeneration system with 80-150 years rotation. The authors suggest the application of shelterwood method in two phases: seeding cutting and final cutting. Moreover, they propose optionally the regeneration by clearcutting with reserves, retaining uniformly spaced ca. 50 trees/ha after the clearcut. In addition, they point out the importance of some treatments to help regeneration: clearing, with the partial or total removal of the understory vegetation (Serrada, 2003) and slash management to facilitate the germination of the seeds and establishment of the saplings. Soil preparation techniques as scarification and even prescribed burning are also recommended to favor the contact of the seeds with the mineral soil and to promote regeneration of *P. halepensis* stands after cutting (Prévosto & Ripert, 2008).

Conclusions

Many different bottlenecks have been identified to limit natural regeneration of the Iberian pine species, except for *P. halepensis*. The main part of the limiting subprocesses are climate-mediated, thus joint occurrence of favourable conditions for natural regeneration occurs on intermittent events. Under changing climate scenarios we expect an increase of the time lapse between two successful regeneration events. Consequently, new silvicultural schemes aimed to promote natural regeneration should rely on taking profit of all the successful regeneration events, favouring advanced regeneration, ensuring mid-shaded optimal conditions for seed germination and seedling survival, preventing the creation of big gaps, and programing fellings in those mast years where abundance of seeds allow predator satiation. Intensive clearcutting and uniform shelterwood systems are mainly substituted by more

flexible schedules, including group shelterwood systems. This would result in stand age structures closer to that of semiregular forest, which mimics the natural dynamics of regeneration of the species, but could be more vulnerable to forest fires, a main risk in Mediterranean forests.

Acknowledgements

Author wish to thank all the persons and institutions involved in the installation, maintenance and monitoring of the different trials, mainly: G. Madrigal, M. Conde, E. Garriga, F. J. Gordo, Ayto. El Portillo and Servicio Territorial de Medio Ambiente de Valladolid (*P. pinea*); A. Bachiller, I. Cañellas, J. Donés and Centro de Montes de Valsaín (*P. sylvestris*); J.A. García Abarca and J. L. Serrano Cuenca (*P. nigra*); Oficina Técnica de Prevención Municipal de Incendios Forestales de la Diputación de Barcelona-OTPMIF (*P. halepensis*); I. Ruano, E. Rodríguez-García, C. Ordóñez, and Servicio Territorial de Medio Ambiente de Segovia (*P. pinaster*).

References

Aizen MA, Patterson WA, 1990. Acorn size and geographical range in the North American oaks (*Quercus* L.). J Biogeog 17: 327-332. https://doi.org/10.2307/2845128

Alejano R, González JM, Serrada R, 2008. Selvicultura de *Pinus nigra* Arn. subsp *salzmannii* (Dunal) Franco. In: Serrada R, Montero G, Reque JA (eds.). Compendio de selvicultura aplicada en España. INIA-FUCOVASA, Madrid. pp: 313-355.

Awada T, Radoglou K, Fotelli MN, Constantinidou HIA, 2003. Ecophysiology of seedlings of three Mediterranean pine species in contrasting light regimes. Tree Physiol 23 (1): 33-41. https://doi.org/10.1093/treephys/23.1.33

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

Barbeito I, Fortin MJ, Montes F, Cañellas I, 2009. Response of pine natural regeneration to small-scale spatial variation in a managed Mediterranean mountain forest. Appl Veg Sci 12: 488-503. https://doi.org/10.1111/j.1654-109X.2009.01043.x

Baskin CC, Baskin JM, 2001. Seeds. Ecology, biogeography, and evolution of dormancy and germination. Acad Press, San Diego, USA.

Beltrán M, Piqué M, Vericat *P.* Cervera T, 2011. Models de gestió per als boscos de pi blanc (*Pinus halepensis*): producció de fusta i prevenció d'incendis forestals. Sèrie: Orientacions de gestió forestal sostenible per a Catalunya (ORGEST). Centre de la Propietat Forestal. Generalitat de Catalunya.

Broncano MJ, Riba M, Retana J, 1998. Seed germination and seedling performance of two Mediterranean tree species, holm oak (*Quercus* ilex L.) and Aleppo pine (*Pinus halepensis* Mill.): a multifactor experimental approach. Plant Ecol 138: 17-26. https://doi.org/10.1023/A:1009784215900

Broncano MJ, Rodrigo A, Retana J, 2008. Post-dispersal seed predation in *Pinus halepensis* and consequences on seedling establishment after fire. Int J Wildl Fire 17: 407-414. https://doi.org/10.1071/WF07095

Burschel *P.* Huss J, 1997. Grundiβ des Waldbaus. Parey Buchverlag, Berlin. 487 pp.

Cabrera M, Donés J, 2010. Proyecto de la 7ª Revisión de la Ordenación del Monte de U. *P.* Nº 2 de la provincia de Segovia «Pinar» de Valsaín, perteneciente al OAPN, sito en el término municipal de San Ildefonso de La Granja. MAPAMA.http://www.mapama.gob.es/es/parques-nacionales-oapn/centros-fincas/valsain/ordenaciones.aspx .

Calama R, Finat L, Gordo FJ, Bachiller A, Ruíz-Peinado R, Montero G, 2005. Estudio comparativo de la producción de madera y piña en masas regulares e irregulares de *Pinus pinea* en la provincia de Valladolid. IV Cong For Esp (SECF). Zaragoza, Sept.

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

Calama R, Mutke S, Pardos M, Morales L, Gordo Fj, Montero G, Finat L, 2012. La producción de piña y piñón de *Pinus pinea* L. en la Meseta Norte; Gordo FJ, *et al*. (eds.): La regeneración natural de los pinares en los arenales de la meseta castellana: 81-98, iuFOR-INIA-JCyL.

Calama R, Manso R, Barbeito I, Madrigal G, Garriga E, Gordo FJ, Montero G, Cañellas I, Pardos M, 2015a. Do inter-specific differences in seed size determine natural regeneration traits in *Pinus pinea* and *Pinus sylvestris*? Appl Ecol Environ Res 13 (2): 387-404.

Calama R, Manso R, Barbeito I, Cañellas I, Pardos M, 2015b. Is natural regeneration a bottleneck in the performance of *Pinus sylvestris* mountain forests? Mountain Forest Management in a Changing World, Smokovce, 6-9 July.

Calama R, Puértolas J, Manso R, Pardos M, 2015c. Defining the optimal regeneration niche for *Pinus pinea* L. through physiology-based models for seedling survival and carbon assimilation. Trees 29 (6): 1761-1771. https://doi.org/10.1007/s00468-015-1257-5

Calama R, Gordo FJ, Madrigal G, Mutke S, Conde M, Montero G, Pardos M, 2016. Enhanced tools for predicting annual stone pine (*Pinus pinea* L.) cone production at tree and forest scale in Inner Spain. Forest Syst 25(3): e079. https://doi.org/10.5424/fs/2016253-09671

Calama R, Fortin M, Pardos M, Manso R, 2017. Modelling spatiotemporal dynamics of *Pinus pinea* cone infestation by Dioryctria mendacella. For Eco Manage 389: 136-148.

Cañellas I, Montes F, del Río M, Pardos M, Montero G, 2004. The effect of different soil substrates in the germination and survival of seed in *Pinus sylvestris* L. regeneration mountain forests. In: Ammer Ch, Weber M, Mosandl R (eds), Conf Proc. Kloster Seeon, Germany, p 83.

Castro J, Gómez JM, García D, Zamora R, Hódar JA, 1999. Seed predation and dispersal in relict Scots pine forests in southern Spain. Plant Ecol 145 (1): 115-123. https://doi.org/10.1023/A:1009865703906

de Las Heras J, Moya D, Vega JA, Daskalakou E, Vallejo R, Grigoriadis N, Tsitsoni T, Baeza J, Valdecantos A, Fernández C, Espelta JM, Fernandes *P.* 2012. Post-fire management of serotinous pine forests. In: Post-Fire Management and Restoration of Southern European Forests, vol 24; Moreira F *et al*. (eds.), pp: 121-150. Springer, Dordrecht, Netherlands. https://doi.org/10.1007/978-94-007-2208-8_6

del Peso C, Bravo F, Ruano I, Pando V, 2012. Patrones de diseminación y nascencia de *Pinus pinaster* en Mesta castellana. In: La regeneración natural de los pinares en los arenales de la Meseta Castellana; Gordo FJ, *et al*. (eds.). pp 161-174. iuFOR-INIA-JCyL.

del Río M, Calama R, Montero G, 2008. Selvicultura de *Pinus halepensis* Mill. In: Compendio de selvicultura aplicada en España; Serrada R, Montero G, Reque JA (eds.), pp: 289-312. INIA-FUCOVASA, Madrid.

Espelta JM, 1996. La regeneración de bosques de encina (*Quercus* ilex L.) y pino carrasco (*Pinus halepensis* Mill.): Estudio experimental de la respuesta de las plántulas a la intensidad de luz y disponibilidad hídrica. Tesis doctoral, UAB, 187 pp.

Espelta JM, Verkaik I, Eugenio M, Lloret F, 2008. Recurrent wildfires constrain long-term reproduction ability in *Pinus halepensis* Mill. Int J Wildl Fire 17: 579-585. https://doi.org/10.1071/WF07078

Espelta JM, Arnan X, Rodrigo A, 2011. Non-fire induced seed release in a weakly serotinous pine: Climatic factors, maintenance costs or both? Oikos 120: 1752-1760. https://doi.org/10.1111/j.1600-0706.2011.19570.x

Eugenio M, Verkaik I, Lloret F, Espelta JM, 2006. Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). For Eco Manage 231: 47-54.

Gordo FJ, 1999. Ordenación y selvicultura de *Pinus pinea* en L. en la provincia de Valladolid. In Ciencias y Técnicas Forestales. 150 años de aportaciones de los ingenieros de montes; Madrigal A (Ed.). pp: 79-100. FUCOVASA. Madrid.

Gordo FJ, Montero G, Gil L, 2012a. La problemática de la regeneración natural de los pinares en los arenales de la Meseta Castellana. In: La regeneración natural de los pinares en los arenales de la Meseta Castellana; Gordo FJ *et al*. (eds.). pp 11-16. iuFOR-INIA-JCyL.

Gordo FJ, Rojo LI, Calama R, Mutke S, Martín R, García M, 2012b. Selvicultura de regeneración natural de *Pinus pinea* L. en montes públicos de la provincia de Valladolid. In: La regeneración natural de los pinares en los arenales de la Meseta Castellana; Gordo FJ *et al*. (eds.). pp: 145-159. iuFOR-INIA-JCyL.

Greene DF, Zasada JC, Sioris L, Kneeshawd, Morin H, Charron I, Simard MJ, 1999. A review of the regeneration of boreal forest trees. Can J For Res 29: 824-839. https://doi.org/10.1139/x98-112

Herrero C, Bravo F, San Martin R, 2004. Modelo de probabilidad de germinación de pino negral (*Pinus pinaster* Aiton) tras incendio. Actas de la Reunión de Modelización Forestal. Cuad Soc Esp Cienc For 18: 57-63.

Hille M, den Ouden J, 2004. Improved recruitment and early growth of Scots pine (*Pinus sylvestris* L.) seedlings after fire and soil scarification. Eur J For Res 123 (3): 213-218. https://doi.org/10.1007/s10342-004-0036-4

Hilli A, Hokkanen T, Hyvonen J, 2008: Long-term variation in Scots pine seed crop size and quality in northern Finland. Scan J For Res 23 (5): 395-403. https://doi.org/10.1080/02827580802334217

Howe HF, Smallwood J, 1982. Ecology of seed dispersal. Annu Rev Ecol Syst 13: 201-228. https://doi.org/10.1146/annurev.es.13.110182.001221

Hulme PE, 1997. Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. Oecologia 111: 91-98. https://doi.org/10.1007/s004420050212

Janzen DH, 1976. Why bamboos wait so long to flower. Ann Rev Ecol Syst 7: 347-391. https://doi.org/10.1146/annurev.es.07.110176.002023

Jordano *P.* 1992. Fruits and frugivory. In: Seeds: the ecology of regeneration in natural plant communities; Fenner M (ed). CAB Int, Wallingford.

Juez L, González-Martínez SC, Nanos N, Lucas AI, Ordoñez C, del Peso C, Bravo F, 2014. Can seed production and restricted dispersal limit recruitment in *Pinus pinaster* Ait from the Spanish Northern Plateau? For Eco Manage 313: 329-339.

Kelly D, 1994. The evolutionary ecology of mast seedling. Trends Ecol Evol 9: 465-470. https://doi.org/10.1016/0169-5347(94)90310-7

Latham RE, 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology 73 (6): 2129-2144. https://doi.org/10.2307/1941461

Lucas-Borja ME, Silva-Santos *P.* Fonseca T, Tíscar PA, López-Serrano FR, Andrés-Abellán M, Martínez-García E, Del Cerro-Barja A, 2010. Modelling Spanish black pine postdispersal seed predation in Central-eastern Spain. For Syst 19: 393-403.

Lucas-Borja ME, Fonseca T, Parresol B, Silva-Santos *P.* García-Morote FA, Tíscar-Oliver PA, 2011. Modelling Spanish black pine seedling emergence: Establishing management strategies for endangered forest areas. For Eco Manage 262: 195-202.

Lucas-Borja ME, Fidalgo-Fonseca T, Lousada JL, Silva-Santos *P.* Martínez-Garcia E, Andrés-Abellán M, 2012. Natural regeneration of Spanish black pine [*Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco] at contrasting altitudes in a Mediterranean mountain area. Ecol Res 27: 913-931. https://doi.org/10.1007/s11284-012-0969-x

Lucas-Borja ME, Candel-Pérez D, García-Morote FA, Onkelinx T, Tíscar PA, Balandier *P.* 2016. *Pinus nigra* Arn. ssp. *salzmannii* seedling recruitment is affected by stand basal area, shrub cover and climate interactions Ann For Sci 73 (3): 649-656. https://doi.org/10.1007/s13595-016-0550-9

Manso R, Pardos M, Keyes CR, Calama R, 2012. Modelling the spatio-temporal pattern of primary dispersal in stone pine (*Pinus pinea* L.) stands in the Northern Plateau (Spain). Ecol Model 226: 11-21. https://doi.org/10.1016/j.ecolmodel.2011.11.028

Manso R, Calama R, Madrigal G, Pardos M, 2013a. A silviculture-oriented spatio-temporal model for germination in *Pinus pinea* L. in the Spanish Northern Plateau based on a direct seeding experiment. Eur J For Res 132 (5): 969-982. https://doi.org/10.1007/s10342-013-0724-z

Manso R, Fortin M, Calama R, Pardos M, 2013b. Modelling seed germination in forest tree species through survival analysis. The *Pinus pinea* L. case study. For Eco Manage 289: 515-524.

Manso R, Pukkala R, Pardos M, Miina J, Calama R, 2014a. Modelling *Pinus pinea* forest management to attain natural regeneration under present and future climatic scenarios. Can J For Res 44 (3): 250-262. https://doi.org/10.1139/cjfr-2013-0179

Manso R, Pardos M, Calama R, 2014b. Climatic factors control rodent seed predation in *Pinus pinea* L. stands in Central Spain. Ann For Sci 71(8): 873-883. https://doi.org/10.1007/s13595-014-0396-y

Martín-Sanz RC, Santos-del-Blanco L, Notivol E, Chambel R, Sanmartín R, Climent J, 2016. Disentangling plasticity of serotiny, a key adaptive traït in a Mediterranean conifer. Am J Bot 103: 1582-1591. https://doi.org/10.3732/ajb.1600199

Masetti C, Mencussini M, 1991. Régénération naturelle du pin pignon (*Pinus pinea* L.) dans la Pineta Granducale di Alberese (Parco Naturalle della Maremma, Toscana, Italie). Ecol Medit 17: 103-188.

Mast JN, Veblen TT, 1999. Tree spatial patterns and stand development along the pine-grassland ecotone in the Colorado Front Range. Can J For Res 29: 575-584. https://doi.org/10.1139/x99-025

Matias L, Jump AS, 2014. Impacts of predicted climate change on recruitment at the geographical limits of Scots pine. J Exp Bot 65 (1): 299-310. https://doi.org/10.1093/jxb/ert376

Matias L, Mendoza I, Zamora R, 2009. Consistent pattern of habitat and species selection by post-dispersal seed predators in a Mediterranean mosaic landscape. Pl Ecol 203 (1): 137-147. https://doi.org/10.1007/s11258-008-9518-7

MacArthur RH, Wilson EO, 1967. The theory of island biogeography (MPB-1). Princeton University, USA.

Meiners SJ, Pickett STA, Handel SN, 2002. Probability of tree seedling establishment changes across a forest-old field edge gradient. Am J Bot 89 (3): 466-471. https://doi.org/10.3732/ajb.89.3.466

Modrý M, Hubený, Rejsêk K, 2004. Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. For Eco Manage 188: 185-195.

Montero G, del Río M, Roig S, Rojo A, 2008a. Selvicultura de *Pinus sylvestris* Mill. In: Compendio de selvicultura aplicada en España; Serrada R, Montero G, Reque JA (eds.). INIA-FUCOVASA, Madrid. pp: 503-534.

Montero G, Calama R, Ruiz-Peinado R, 2008b. Selvicultura de *Pinus pinea* L. In: Compendio de selvicultura aplicada en España; Serrada R, Montero G, Reque JA (eds.). INIA-FUCOVASA, Madrid. pp: 431-470.

Moya D, Espelta JM, Verkaik I, López-Serrano F, de Las Heras J, 2007. Tree density and site quality influence on *Pinus halepensis* Mill. reproductive characteristics after large fires. Ann For Sci 64: 649-656. https://doi.org/10.1051/forest:2007043

Moya D, de las Heras J, López-Serrano FR, Leone V, 2008. Optimal intensity and age of management in young aleppo pine stands for post-fire resilience. For Eco Manage 255: 3270-3280.

Muller-Landau HC, Wright SJ, Calderón O, Hubbell S*P.* Foster RB, 2002. Assessing recruitment limitation: concepts, methods and case-studies from a Tropical Forest. In: Seed dispersal and frugivory: Ecology, evolution and conservation; Levey DJ, *et al*. (eds). CAB Int,, Wallingford, pp: 35-53. https://doi.org/10.1079/9780851995250.0035

Mutke S, Gordo J, Gil L, 2005a. Variability of Mediterranean stone pine cone production: yield loss as response to climatic change. Agric For Met 132: 263-272. https://doi.org/10.1016/j.agrformet.2005.08.002

Mutke S, Calama R, González-Martinez S, Montero G, Gordo J, Bono D, Gil L, 2012. Mediterranean Stone Pine: Botany and Horticulture. Hortic Rev 39: 153-202.

Mutke S, Calama R, Gordo J, Nicolas JL, Herrero N, Roques A, 2015. Pérdida del rendimiento en piñón blanco de *Pinus pinea* en fábrica - Leptoglossus y la seca de la piña. III Reun Cien de San For, SECF. Madrid 7-8 oct.

Myczko L, Benkman CW, 2011. Great spotted woodpeckers Dendrocopos major exert multiple forms of phenotypic selection on Scots pine *Pinus sylvestris*. J Avian Biol 42 (5): 429-433. https://doi.org/10.1111/j.1600-048X.2011.05326.x

Nathan R, Ne'eman G, 2000. Serotiny, seed dispersal and seed predation in *Pinus halepensis*. In Ecology, biogeography and management of *Pinus halepensis* and *Pinus* brutia forest ecosystems in the Mediterranean Basin; Ne'eman G, Trabaud L. (eds). Backhuy Publ, Leiden, pp: 105-118.

Nathan R, Casagrandi R, 2004. A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connel and beyond. J Ecol 92 (5): 733-746. https://doi.org/10.1111/j.0022-0477.2004.00914.x

Ne'eman G, Goubitz S, Nathan R, 2004. Reproductive traits of *Pinus halepensis* in the light of fire - A critical review. Plant Ecol 171: 69-79. https://doi.org/10.1023/B:VEGE.0000029380.04821.99

Núñez MR, Sierra de Grado R, Alía R, Bravo F, 2013. Efecto del estrés hídrico y la oscilación de las temperaturas sobre la germinación de semillas de diversas procedencias de *Pinus pinaster* Ait. VI Congr For Esp, Vitoria, junio.

Nyland R. 2002. Silviculture: Concepts and Applications, 2nd ed. The McGraw-Hill Companies, NY.

Pardos M, Ruiz Del Castillo J, Cañellas I, Montero G, 2005. Ecophysiology of natural regeneration of forest stands in Spain. Invest Agrar: Sist Rec For 14 (3): 434-445. https://doi.org/10.5424/srf/2005143-00939

Pardos M, Montes F, Aranda I, Cañellas I, 2007. Influence of environmental conditions on Scots pine (*Pinus sylvestris* L.) germinant survival and diversity in Central Spain. Eur J For Res 126 (1): 37-47. https://doi.org/10.1007/s10342-005-0090-6

Pardos M, Montes F, Cañellas I, 2008. Spatial dynamics of natural regeneration in two differently managed *Pinus sylvestris* stands before and after silvicultural intervention using replicated spatial point patterns. For Sci 54 (3): 260-272.

Pardos M, Climent J, Almeida H, Calama R, 2014. The role of developmental stage in frost tolerance of *Pinus pinea* L. seedlings and saplings. Ann For Sci 71 (5): 551-562. https://doi.org/10.1007/s13595-014-0361-9

Prévosto B, Ripert C, 2008. Regeneration of *Pinus halepensis* stands after partial cutting in southern France: Impacts of different ground vegetation, soil and logging slash treatments. For Eco Manage 256: 2058-2064.

Prévosto B, Amandier L, Quesney T, de Boisgelin G, Ripert C, 2012. Regenerating mature Aleppo pine stands in fire-free conditions: site preparation treatments matter. For Eco Manage 282: 70-77.

Pukkala T, Kolström T, 1992. A stochastic spatial regeneration model for *Pinus sylvestris*. Scan J For Res 7: 377-385. https://doi.org/10.1080/02827589209382730

Putman RJ, 1996. Ungulates in temperate forest ecosystems: perspectives and recommendations for future research. For Eco Manage 88: 205-214.

Rodrigo A, Retana J, Picó FX, 2004. Direct regeneration is not the only response of Mediterranean Forests to large fires. Ecology 85: 716-729. https://doi.org/10.1890/02-0492

Rodriguez-García E, Gratzer G, Bravo F, 2011. Climatic variability and other site factors influence on natural regeneration *Pinus* pinastre Ait. in Mediterranean forests. Ann For Sci 68: 811-823. https://doi.org/10.1007/s13595-011-0078-y

Rojo A, Montero G, 1996. El pino silvestre en la Sierra de Guadarrama. Ministerio de Agricultura, Pesca y Alimentación, 293 pp.

Ruano I, Pando V, Bravo F, 2009. How do light and water influence *Pinus pinaster* Ait. Germination and early seedling development? For Eco Manage 258: 2647-2653.

Ruano I, del Peso C, Bravo F, 2014. Post-dispersal predation of *P. pinaster* Aiton seeds: key factors and effects on belowground seed bank. Eur J Forest Res 134 (2): 309-318. https://doi.org/10.1007/s10342-014-0853-z

Ruano I, Manso R, Fortin M, Bravo F, 2015. Extreme climate conditions limit seed availability to succesfully attain natural regeneration of *Pinus pinaster* in sandy areas of Central Spain. Can J For Res 45: 1795-1802. https://doi.org/10.1139/cjfr-2015-0257

Ruiz de la Torre J, Ceballos L, 1979. Árboles y arbustos de la España peninsular. UPM, ETS Ingenieros de Montes, Madrid.

Salisbury EJ, 1942. The reproductive capacity of plants. Bell, London.

Saura S, Piqué M, 2006. Forests and forest sector in Catalonia. Agric Agri-food Prod Perspect Profile Sect Catalonia. [cd-rom].

Sayer EJ, 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol Rev Camb Philos Soc 81 (1): 1-31. https://doi.org/10.1017/S1464793105006846

Scarascia-Mugnozza G, Schirone B, 1984. Effetti dell'intesitá luminosa sullo sviluppo dei semnzali di pino d'Aleppo. Ann Acad It Sci For 33: 137-153.

Serrada R, 2003. Apuntes de Selvicultura. EUIT Forestal, Universidad Politécnica de Madrid, Madrid. 490 pp.

Serrada R, Domínguez S, Sánchez MI, Ruiz J, 1994. El problema de la regeneración natural del *Pinus nigra* Arn. Montes 36: 52-57.

Shmida A, Ne'eman G, Goubitz S, Lev-Yadun S, 2000. Sexual allocation and gender segregation in *Pinus*

halepensis. In: Ecology, biogeography, and management of *Pinus halepensis* and *P.* brutia forest ecosystems in the Mediterranean basin; Ne'eman G, Trabaud L. (eds), pp: 91-104. Backhuys Publ, Leiden.

Smith CC, Fretwell SD, 1974. The optimal balance between size and number of offspring. Am Nat 108: 499-506. https://doi.org/10.1086/282929

Smith CS, Hamrick JL, Kramer CL, 1990. The advantage of mast years for wind pollination. Am Natur 136: 154-166. https://doi.org/10.1086/285089

Tapias R, Gil L, Fuentes-Utrilla *P.* Pardos JA, 2001. Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. J Ecol 89: 629-638. https://doi.org/10.1046/j.1365-2745.2001.00575.x

Thanos CA, Daskalakou EN, 2000. Reproduction in *Pinus halepensis* and *P.* brutia. In: Ecology, biogeography, and management of *Pinus halepensis* and *P.* brutia forest ecosystems in the Mediterranean basin; Ne'eman G, Trabaud L. (eds), pp: 79-90. Backhuys Publ, Leiden.

Tíscar PA, 2007. Dinámica de regeneración de *Pinus nigra* subsp. *salzmannii* al sur de su área de distribución: etapas, procesos y factores implicados. Invest Agrar: Sist Rec For 16: 124-135.

Tíscar PA, Lucas-Borja ME, Candel-Pérez D, 2011. Changes in the structure and composition of two *Pinus nigra* subsp. *salzmannii* forests over a century of different silvicultural treatments. For Syst 3: 525-535.

Trabaud L, Campant C, 1991. The difficulty of natural regeneration of Sazmann pine (*Pinus nigra* subsp. *salzmannii*) following fire. Biol Conserv 58 (3): 329-343. https://doi.org/10.1016/0006-3207(91)90099-U

Verkaik I, Espelta JM, 2006. Post-fire regeneration thinning, cone production, serotiny and regeneration age in *Pinus halepensis*. For Eco Manage 231: 155-163.

Westoby M, Jurado E, Leishman M, 1992. Comparative evolutionary ecology of seed size. Trees 7 (11): 368-372. https://doi.org/10.1016/0169-5347(92)90006-w

Worthy FR, Law R, Hulme PE, 2006. Modelling the quantitative effects of pre- and post-dispersal seed predation in *Pinus sylvestris* L. J Ecol 94 (6): 1201-1213. https://doi.org/10.1111/j.1365-2745.2006.01168.x

Zamora R, Gómez JM, Hódar JA, Castro J, García D, 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. For Eco Manage 144: 33-42.

Zavala MA, Espelta JM, Retana J, 2000. Constraints and trade-offs in Mediterranean plant communities: the case of holm oak - Aleppo pine forests. The Bot Rev 66: 119-149. https://doi.org/10.1007/BF02857785

Zavala MA, Espelta JM, Caspersen J, Retana J, 2011. Interspecific differences in sapling performance with respect to light and aridity gradients in Mediterranean pine-oak forests: implications for species coexistence. Can J For Res 41: 1432-1444. https://doi.org/10.1139/x11-050