Seeding pines in the Mediterranean region

Jorge Castro[1]✉, Maria Pérez-García[1], Harrie Lovenstein[2], Simone Pedrini[3]

[1]Department of Ecology, Faculty of Science, University of Granada, Spain
[2]Land Life Company BV, Amsterdam, The Netherlands
[3]School of Molecular and Life Sciences, Curtin University, Bentley, Australia

✉ jorge@ugr.es

ARTICLE INFO

Citation:
Castro J, Pérez-García M, Lovenstein H, Pedrini S (2026) Seeding pines in the Mediterranean region. Reforesta 21: 10-31.
DOI: https://dx.doi.org/10.21750/REFOR.21.02.132

Editors: Gardiner Emile, Stanturf John
Received: 15.11.2025
Accepted: 15.12.2025
Published: 20.01.2026

Note
This paper is a part of a Special issue on International Practices for Regenerating and Restoring Forest Trees by Seeding, edited by Emile S Gardiner and John A Stanturf

Abstract

Extensive disturbance to the ecologically, socially, and economically important pine (*Pinus* spp. L.) forests of the Mediterranean region has created a strong need for forest restoration throughout the region. Seeding could potentially be a viable option for regenerating some of the 10 pine species that occur in the region, especially the fire-adapted serotinous species, but previous seeding efforts have been marked with inconsistent success. From our synthesis of available literature and practical experience, we briefly summarize the history of applied trials and pine seeding research, examine the factors that determine pine seeding success, and discuss what we have learned that can make seeding an ecologically and economically viable approach to pine forest establishment in the Mediterranean region. Future refinement of autonomous drones for seed delivery, selection of favorable sowing microsites, and improvement of seed coating technologies that minimize seed predation and support seedling establishment will support "precision restoration" practices that promise to advance pine seeding to an operational scale in the Mediterranean region.

Keywords

forest restoration, direct seeding, *Pinus* spp., precision restoration, seeding drones, seed coating

Contents

1 Introduction

Pine (*Pinus* spp. L.) forests in the Mediterranean region have experienced extensive disturbance due to human activities, including excessive logging, overgrazing, and fire. There is a need to restore many of these forests, as pines are a major component of Mediterranean region forests and have high ecological, social, and economic relevance (Moreira et al. 2012; Ne'eman and Osem 2021). A heterogeneous set of pine species grow naturally in the Mediterranean region with very different biogeographical origin and ecology. In this chapter, we follow the criteria of Grivet and Olsson (2021), who considered ten species with "a native distribution range extending to the Mediterranean region and which grow under a Mediterranean climate" (Figure 1, Table 1). Overall, in the Mediterranean region these pines are distributed from sea level to ca. 2500 m elevation (Table 1). Some of the species show clear Mediterranean-type characteristics, such as adaptation to fire (e.g., serotinous cones) or high drought resistance (e.g., *P. halepensis* Mill. and *P. brutia* Ten.) relative to other pines, while others show typical boreo-alpine traits such as high cold resistance and low drought resistance (e.g., *P. sylvestris* L. and *P. mugo* Turra) (Table 1). Seed mass of the different species varies by 80 times, from ca. 7.5 mg in *P. sylvestris* and *P. mugo* to 600 mg in *P. pinea* L. Finally, there are striking differences between species in morphological and functional traits including root/shoot ratio, control of stomatal aperture, water potential, or photochemical efficiency. These traits, which determine seedling size, water uptake, and growth rate, underlie species adaptation to environmental conditions and are key for seeding success under drought stress (Matías et al. 2017; Salazar-Tortosa et al. 2018a,b; Salazar-Tortosa et al. 2020), and, subsequently, the regeneration capacity of the various species that inhabit the region.

Table 1. Pines that inhabit the Mediterranean region and some of their characteristics relevant to revegetation through seeding. Data on seed mass are the average of the entries listed in the Supplementary Information of Salazar-Tortosa et al. 2020, which were extracted from available databases or published articles and reports except for *P. uncinata* Ramond ex D.C.; for *P. uncinata*, seed mass was obtained from Notivol et al. 2012. Information about serotiny is extracted from Salazar-Tortosa et al. 2020 (Supplementary Information Table S2). Drought tolerance and frost resistance are broadly defined in relative terms across the species. Elevational ranges sourced from Boydak 2004 (‡), San-Miguel-Ayanz et al. 2016 (†), AEMA 2008 (*), and Franco 1986 (**).

Species	Main distribution; species silvics; and habitat characteristics	Elevational range (m)	Seed mass (mg)	Serotiny
P. brutia **Ten. (Turkish pine)**	Mediterranean; Drought tolerant and fast growing; Low elevation and coastal areas	0–1500‡	45.7	Yes
P. canariensis **C.Sm. ex D.C. (Canary island pine)**	Canary Islands (endemic); Resprouts after fire from epicormic buds; Volcanic slopes between 700 and 1200 m.a.s.l.	1200–1800*	102.4	Yes
P. halepensis **Mill. (Aleppo pine)**	Mediterranean; Drought tolerant and fast growing; Low elevation to intermediate elevation, very common in coastal areas	0–2000†	25.7	Yes
P. heldreichii **H.Christ (Bosnian pine)**	Mediterranean, small distribution in southern Italy and the Balkan peninsula; From intermediate elevation to high Mediterranean mountain areas, where it can reach the tree line	900–1800*	22.5	No
P. mugo **Turra (dwarf mountain pine)**	Frost resistant, drought intolerant, and slow growing; Alpine, high mountain habitats, pine that reaches the highest elevation in the Mediterranean region	200–2700†	7.6	No

P. nigra **J.F.Arnold (black pine)**	Mediterranean; Drought intolerant and fast growing; Moderate elevation to high Mediterranean mountain areas where it can form part of the timberline	800–1500†	19.8	No
P. pinaster **Aiton (maritime pine)**	Mediterranean; Drought resistant and fast growing; Temperate to warm locations, inhabiting from coastal areas to moderate elevation	0–2000†	55.6	Yes
P. pinea **L. (stone pine)**	Mediterranean; Drought resistant and cold sensitive, wingless seed; Mostly in coastal areas, very common in sandy soils and on dunes	0–1000**	600.4	No
P. sylvestris **L. (Scots pine)**	Frost resistant, drought intolerant, and slow growing; Boreo-alpine, high Mediterranean mountains where it forms part of the timberline.	0–2600†	7.6	No
P. uncinata **(mountain pine) Ramond ex D.C.**	Frost resistant, drought intolerant, and slow growing; High European mountains where it forms the timberline.	600–2400†	9	No

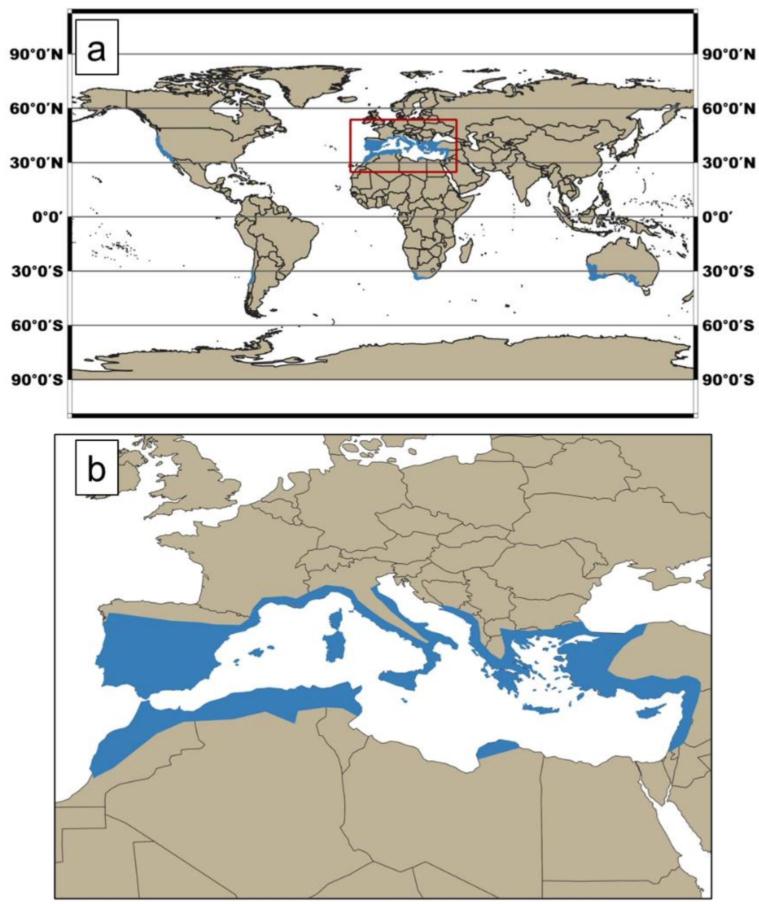

Figure 1. (a) Regions of the world with Mediterranean-type ecosystems (in blue); and (b) distribution of Mediterranean-type ecosystems in the Mediterranean basin. The climate of the Mediterranean region is characterized by low to moderate rainfall but with a hot and dry summer that imposes strong drought conditions on plants. Redrawn from Rundel et al. (2016).

Pine regeneration via seeding should be feasible at least for some species. This is substantiated by many examples of high natural pine recruitment from seed after wildfire. In the case of serotinous pines, seedling densities can often approach several thousand ha^{-1} after wildfire (e.g., Calvo et al. 2013; Hibsher et al. 2013). Moreover, pine seeding has been done with great success in some cases, particularly in dunes and other sandy areas, as relayed through oral communications, local reports, or journals by personnel of local forest districts—though often difficult to access, these sources provide information of high ecological and forestry value (e.g., Cueto 2001) (Figure 2). The challenge to make sowing seeds an efficient method for restoration of pine forests in the Mediterranean basin is, therefore, to understand the bottlenecks for seedling recruitment for the various species and to apply the most appropriate practices and technologies to overcome these barriers. In this sense, practices exist today to protect seed from biotic and abiotic stresses and to select the most suitable microsites for improving sowing efficiency. In the following sections, we describe the success of pine seeding relative to seedling recruitment in the Mediterranean region, the main environmental factors that determine this success, and suggest several ways to improve the feasibility of seeding as a reforestation method for pine forest restoration in this region.

Figure 2. Seeding of stone pine (*P. pinea* L.) in sand dune reforestation in Doñana National and Natural Park, southern Spain (year 2022). The central plant was planted as a 1-year-old. The plants at each side of the central seedling resulted from sowing one seed at each spot at the same time as seedling planting. Pine reforestation via direct seeding, sowing the seed in soil, has been successful in many cases, particularly in sand dunes, although there are scant academic reports (Photo credits: Óscar Pérula, Plant-for-the-Planet foundation).

2 Low success rate reported in the literature

As a starting point we need to define what is regarded as success in pine seeding for reforestation or forest restoration. The most basic measure of success is determined by the proportion of seedlings or saplings established from a given number of seeds (hereafter recruitment success). Many other ecological, economic, or social considerations should also be considered, such as the development of ecosystem structure and function, resilience, biodiversity, ecosystem services, or various socio-ecological aspects including the emotional engagement by the local population to the restored forest and the economic benefits it may bring to them. Nonetheless, to set the issue to the most basic definition, we only consider recruitment success in this chapter. In this sense, pine seeding success is evaluated as a seedling recruitment percentage that reduces the economic and ecological costs (this can be monetized in a single index) of planting nursery raised seedlings (hereafter seedling outplanting), which currently is the most used reforestation technique (Lázaro-González et al. 2023). Furthermore, success may differ from one site to another depending on expectations. For example, we might set a higher expectation for recruitment success in environments or biomes with mild summer stress than in others with strong summer stress, as observed across the Mediterranean region. In addition, an even distribution of recruited seedlings would be more important for establishing production forests than for restoring forests holding a conservation objective.

We frame recruitment success for this chapter with a goal of establishing resilient forests with a structure that will promote natural succession. Under this criterion, we consider recruitment success of 2.5% at the sapling stage an acceptable baseline, i.e., a minimum of 250 saplings from seeding 10,000 seed ha^{-1}. This may not be considered a success for other biomes or objectives, e.g., regeneration of productive stands, but it can be in the context of restoring functional forests with a main aim of the provision of ecosystem services and biodiversity conservation.

A maximum of 10,000 seed ha^{-1} is also critical to our assessment. The amount of seed used in seeding operations today is extremely high (often above 100,000 ha^{-1}) as it is expected that many seeds or seedlings will be lost to seed predation, failure to germinate, mortality during seedling emergence, or mortality during establishment. High sowing rates are a clear disadvantage as compared to planting nursery-grown seedlings, because of the size and vigor of planting stock. Seed collection and preparation is often the costliest part of a pine seeding operation (see section on Making Seeding a Viable Approach), and therefore, measures to reduce seeding density ha^{-1} will positively impact seeding efficiency. Additionally, procuring large quantities of seed can be problematical if local seed availability is low—this can move seed provisioning to non-local sources that consequently can threaten indigenous genetic diversity and local adaptation of populations (Mohan et al. 2021; Castro et al. 2024). Thus, it is imperative to reduce sowing rates for seeding to be a scalable alternative to other afforestation or reforestation practices.

Under these criteria, we can state that the overall success of seeding to regenerate pine forests in Mediterranean ecosystems is low (Table 2). For example, Ordoñez et al. (2004) sowed *P. nigra* J.F. Arnold seed over the soil surface at 111,111 seed ha^{-1} and obtained 0% regeneration in open habitats and shrublands. Espelta et al. (2003), who broadcasted 25,000 *P. nigra* seed ha^{-1}, observed between 0 to 200 seedlings ha^{-1} after two years (recruitment success of 0.8% in the best case). J. Castro (unpublished data) conducted an experimental sowing of *P. sylvestris* in relict forests in southern Spain by broadcasting 100,000 seed ha^{-1}, and seedling recruitment after the first growing season was 0% (climatic conditions were very adverse because of drought). The company DroneCoria (Spain) conducted aerial drone seeding (10,000 seed ha^{-1}) of *P. halepensis* across several hectares in a semi-arid region of SE Spain (Supplementary Material in Castro et al. 2024). Again, recruitment success was 0% after one year, even though *P. halepensis* grows naturally in the area and very often regenerates abundantly after fire (climatic conditions were also particularly dry in this case).

Some positive results are also reported, but mostly from reports of various forest districts or other administrations, not peer-reviewed journals. Despite the value of these reports, this information is difficult to track. Moreover, these reports should be considered with caution because they are often not supported by an experimental design that would allow one to draw unequivocal conclusions about establishment success, as very often neither seeding density nor seedling density are properly controlled. Still, some academic studies report good or acceptable recruitment success from seeding, with recruitment values around 5% after several years and sometimes considerably higher (Table 2). However, most of these works are designed to disentangle factors that determine seedling establishment, not necessarily results that can be applied at large spatial scales. For example, it is common for seeds to be buried about 1 cm deep in these studies, a measure that reduces seed predation and improves germination (see section on Factors that Determine Pine Seeding Success). Additionally, it is common in these studies to protect sown seeds from predators with measures such as wire cages (Table 2). This is done to ensure seedlings will be present to study in subsequent phases of the research. Such control of environmental factors is usually infeasible for large-scale forest restoration, but this knowledge provides direction for improving pine seeding success.

Table 2. Compilation of studies showing data of pine seedling establishment across different environmental conditions, including habitats, microhabitats, sowing method, soil conditions, or experimental manipulation such as predator exclusion or irrigation. The inclusion of studies does not follow a systematic search; rather, it seeks to include a wide representation of different conditions. Ys = years of study. Emrg. = Seedling emergence. Seed was sown at ≈ 1 cm below the soil surface in all cases where seed was buried. Succ. = seedling survival at the end of the study; survival refers either to the percentage of seedlings that survived from those registered as emerged (*), or the percentage of seedlings recruited from sown seed (†), depending on the data available in each study; the values for recruitment have been calculated in some cases if they were expressed in other terms, e.g., seedlings ha^{-1} divided by seed sown ha^{-1}. The data refers to the time expressed in column Ys. For data extraction from figures, we used WebPlotDigitizer 4.7. Precip. = annual precipitation. Pred. = predators.

Ref.	Ys	Species	Location and environmental conditions	Seeding details (when buried, at ≈ 1 cm in all cases)	Emrg. (%)	Succ. (%)	Highlighted comments
Bladé and Vallejo 2008	2	*P. halepensis* Mill.	Spain, burnt pine forest. Semiarid. Precip. ≈ 640 mm	Buried, intact soil. Pred. excluded. Data are average values for all the experimental plots and families (maternal trees)	71.7	48.6*	A clear example of *P. halepensis* regeneration success with seeding, but pred. excluded, and seeds buried.
Castro et al. 2002a	3	*P. sylvestris* L.	Spain, mountain meadows. Precip. ≈ 830 mm	Buried with 3 soil treatments: intact (meadow), clipped vegetation, and scarified soil. Pred. not excluded	≈25	1.2*	Ca. 1.2% survival in all the treatments. Seedling emergence is possible without pred. exclusion if seeds are buried
Castro et al. 2002a	<1	*P. sylvestris* L.	Spain, mountain meadows. Precip. ≈ 830 mm	Surface, pred. not excluded, the same treatments indicated above Surface, intact soil (meadow) + pred. excluded Surface, clipped veg. (meadow) + pred. excluded Surface, scarified soil + pred. excluded	0–0.8 6.4 17.2 55.5		Pred. block regeneration if seeds are on the surface. Soil scarification boost emergence. (Survival not monitored in this study).
Castro et al. 2004	4	*P. sylvestris* L.	Spain, native forests.	Buried, intact soil in bare ground + pred. excluded	49.2 50.8	2.4* 8.2*	*Juniperus communis* acts as a nurse plant for seedling recruitment

			Precip. ≈ 830 mm	Buried, intact soil under *Juniperus* + pred. excluded			
Castro et al. 2004	3	*P. sylvestris* L.	Spain, shrublands. Precip. ≈ 830 mm	Buried, intact soil in bare ground. Pred. not excluded	28.7	0*	*Salvia* acts as a nurse plant for seedling recruitment. Emergence is possible without pred. exclusion if seeds are buried
				Buried, intact soil under *Salvia*. Pred. not excluded	41.7	4.2*	
Castro et al. 2005	2	*P. sylvestris* L.	Spain, native forests. Precip. ≈ 830 mm	Buried, intact soil in bare ground. Pred. excluded	25.4	8.9†	Shrubs act as nurse plants for seedling recruitment. Summer drought reduction with irrigation boost seedling establishment
				Buried, intact soil under shrubs. Pred. excluded	60.8	9.7†	
				Buried, intact soil in bare ground. Pred. excluded + irrigation	24.9	12.7†	
				Buried, intact soil under shrubs. Pred. excluded + irrig.	67.8	32.2†	
Espelta et al. 2003	2	*P. nigra* J.F.Arnold	Spain, burnt areas. Precip. ≈ 600 mm.	Spot seeding. Not indicated if buried or surface. Two soil treatments: grazed and prescribed burning. Chemical repellent for insects and birds.		0.6† in all cases	Recalculated from original data. Not successful
García-Morote et al. 2017	2	*P. halepensis* Mill.	Spain, burnt areas. Semiarid. Precip. ≈ 332 mm	Buried in scarified soil. Pred. not excluded	5.8	0.2†	A cover of wood chips increased soil moisture and seedling recruitment. Aspect (N or S-facing) had no effect
				Buried in scarified soil + wood chips cover. Pred. not excluded	18.2	4.6†	
Martínez-García et al. 2018	5	*P. nigra* J.F.Arnold	Spain, burnt areas. Precip. ≈ 647 mm	Buried, 2 soil treatments: intact soil and scarified soil. Pred. not excluded. South facing slopes	45.8	0*	Seedling emergence is possible without pred. exclusion if seeds are buried. Seedling survival in locations with reduced water stress (north-facing slopes). Woodchips had little effect (not included in these data).
				Buried, 2 soil treatments: intact soil and scarified soil. Pred. not excluded. North facing slopes	44.2	7.5*	
Nackhoul et al. 2020	0.5	*P. pinea* L.	Lebanon, mature pine stand. Precip. ≈ 964 mm	Buried slightly. Intact soil (with pine litter)	48	Ca. 0	The exclusion of pred. had no effect in this study.
				Buried slightly, scarified soil, Pred. excluded	64	Ca. 0	
Tíscar et al. 2017	3	*P. pinaster* Aiton *P. nigra* J.F.Arnold *P. sylvestris* L.	Spain, different elevations; data for the lowest value of basal area. Precip. ≈ 765mm	Buried, intact soil (but litter removed). Pred. excluded Buried, intact soil (but litter removed) + water addition (similar to Castro et al. 2005). Pred. excluded.	70–90	0–40*	Seedling emergence very high when litter is removed and seed are buried. Drought reduction boost seedling establishment (ca. 3 times higher in irrigated plots).
Espelta et al. 2003	2	*P.nigra* J.F.Arnold	Spain, burnt areas. Precip. ≈ 600 mm	Broadcast (manual) 25,000 seeds ha^{-1} in different treatments, including intact soil. Pred. not excluded	–	<0.8†	Recalculated from original data. Not successful
Fernandes et al. 2017	<1	*P. pinaster* Aiton	Portugal, two sites of the Atlantic coast: Precip. ≈ 944 mm (wetter and cooler) and Precip. ≈ 735 mm (drier and hotter)	Broadcast in 1 x 1 m experimental plots at a density of 600,000 seeds ha^{-1}. Scarified soil, pred. not excluded. • Wetter site: • Drier site:	≈12 ≈10	≈26* ≈5*	Summer drought reduction boost seedling establishment. Data reported are the average of different treatments in shrubland habitats (recalculated from original).

Ordóñez et al. 2004	<1	*P. nigra* J.F.Arnold	Spain, different habitats. Precip. ≈ 725 mm	Broadcast in 3 x 3 m experimental plots at a density of 111,111 seeds ha^{-1}. Habitats: bare soil, short grasses and shrublands. Pred. not excluded.	0	–	Seedling establishment happened below the canopy of the pine forest, but this habitat does not need restoration.
Taboada et al. 2017	3	*P. pinaster* Aiton	Spain, burnt areas. Precip. up to 900 mm	Broadcast in contour lines with a portable shoulder spreader at ≈ 25000 seeds ha^{-1}. Pred. not excluded.	–	24†	6000 seedlings ha^{-1}. However, the effect of previous seed bank not controlled. A resampling 5 y after controlling seed bank offers no effect.

3 Factors that determine pine seeding success in the Mediterranean region

In general, pine regeneration via seeding in the Mediterranean region is constrained by four fundamental factors: seed predation, drought stress (mostly summer drought), non-contact with mineral soil, and weed competition.

3.1 Seed predation

Seeds of the Mediterranean pines are consumed by birds, mammals, and insects, e.g., ants (Family Formicidae) and beetles (Order Coleoptera) (Castro et al. 1999; Espelta et al. 2003) (Figure 3), with rates that can reach almost 100% of seed availability (Castro et al. 1999; Lucas-Borja et al. 2010; Ziffer-Berger et al. 2017; and references therein). Therefore, measures that reduce seed predation will be advantageous for pine seeding. Seed burial clearly reduces loss to predators (Castro et al. 2002a; Martínez-García et al. 2018) (Table 2), which is a general fact across species. Seed burial also boosts germination, and thus, it is a method with cumulative advantages for seeding. However, it is difficult to implement seed burial with broadcast techniques and especially with aerial seeding, so seed burial is largely restricted to ground-based operations. In cases where seed remains exposed on the surface, alternatives are to coat seed with substances that either repel predators or camouflage their appearance, smell, or both (Figure 3; also see section on Seed Coating to Improve Pine Recruitment Success). Ongoing research on these technologies holds promise for advancing seeding as a useful and scalable restoration method (Pedrini et al. 2020).

Methods to reduce predation may be combined to increase their efficiency. For example, capsaicin (the spicy molecule in chili pepper (*Capsicum* spp. L.) deters mammals but is ineffective against birds. Thus, we may treat seed with capsaicin if they are to be spot seeded under shrub nurse plants (see below for information concerning nurse plants). This is because rodent (Order Rodentia) activity increases under shrubs, where they find protection from their own predators. Some avian seed predators may not venture below shrubs, presumably because their movements would be restricted and their probability of escaping predation compromised (this is, in any case, a supposition to be tested). Thus, predation by two seed predator guilds may be reduced by seeding capsaicin-treated seed under nurse shrubs. Similarly, the timing of seeding can be critical to the level of seed predation sustained. For example, the high seedling density that often occurs after fires for species bearing serotinous cones may be due to the combined effects of the ashes camouflaging seed and the reduced density of predators such as rodents and insects (many seed predators will die or be displaced during the fire and the site will not be recolonized for several months (Retana et al. 2012)). Post-fire restoration via sowing seed should be conducted shortly (within months) after the fire to reduce the effect of seed predators, and ideally during a period of rain.

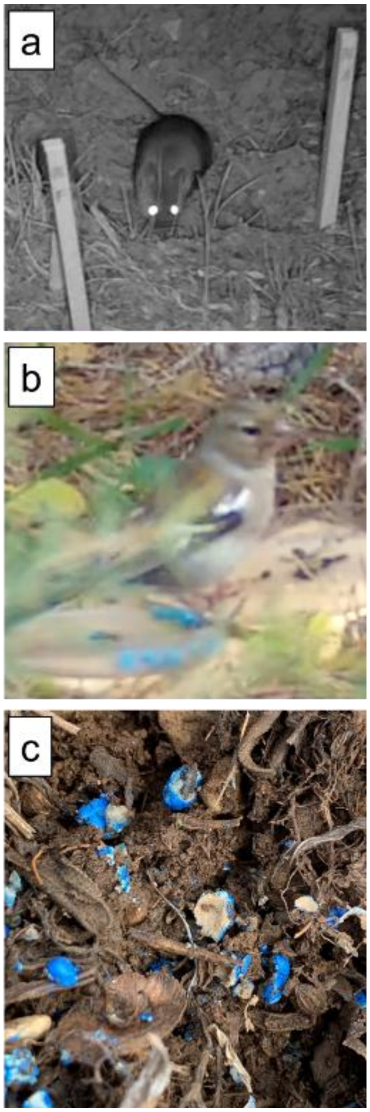

Figure 3. Rodents and birds are the main predators of pine seeds in the Mediterranean region. (a) A wood mouse (*Apodemus sylvaticus*) feeding on Scots pine (*P. sylvestris* L.) seed in Sierra Nevada National Park (Granada, Spain); seed coated with 4 different deterrent substances were scattered onto the soil surface. (b) A common chaffinch (*Fringilla coelebs*) is offered seed of Aleppo pine (*P. halepensis* Mill.) in the mountainous area close to the seashore in Granada (Spain). The control (non-coated) seed (petri dish on right) were predated unlike the seed coated with Bitrex (bitter substance) dissolved in a blue dye (petri dish on left). It is postulated that the color blue is not noticed by some birds. (c) A blue coating and Bitrex did not prevent seed predation by the wood mouse in Sierra Nevada National Park. Presented data are preliminary (Castro et al. unpublished) (Photo credits: Jorge Castro).

3.2 Drought stress

Pine seedling mortality from drought, in particular summer drought, can be very high in the Mediterranean region. The stress of drought may be considered the main factor of seedling mortality with values that usually range between 70–95% depending on the species, often reaching 100% after the first year (Espelta et al. 2003; Castro et al. 2004; Nackhoul et al. 2020). The situation may get even worse under current climate change scenarios, which is an increase in aridity that may impact regeneration capacity and distribution of pine species in the region (Salazar-Tortosa et al. 2024). Accordingly, any measure to reduce summer drought stress could help seedling establishment resulting from seeding operations. For example, mitigation of summer drought with irrigation that simulates a mild summer is a measure that has consistently resulted in positive effects on regeneration for various species, multiplying recruitment success by a factor of 2 to 3 (Castro et al. 2005 and Tíscar et al. 2017 in Table 2; see also Ruano et al. 2009; Mendoza et al. 2009; Matías et al. 2012 for similar results). However, irrigating seedlings will not be feasible in most restoration cases, especially in remote areas. Nonetheless, the risk of summer drought stress can be reduced in other ways. For example, we may consider the landscape (macro) when prioritizing seeding efforts—Martínez-García et al. (2018) obtained 7.5% seedling survival for *P. nigra* on north-facing slopes in contrast to 0% on south-facing slopes (Table 2).

Site selection for pine seeding in the Mediterranean region should also consider a smaller spatial scale, i.e., the microhabitat. Several studies have consistently reported the beneficial effect of nurse plants on regeneration of many tree species, particularly pines in the Mediterranean region (Castro et al. 2004; Boulant et al. 2008; Petrou and Milios 2012) (Table 2). As a result, it is common to observe a clear association of pine seedlings and saplings with successional shrubby species (Figure 4). Shrubs reduce radiation, evaporation, and thus heat stress (Castro et al. 2002b). They also enhance water availability by directing stem flow from rain intercepted by branches and foliage to soil, by hydraulic lifting, or by reducing surface runoff (Tromble 1988; Muller et al. 2018) that facilitates water infiltration in microhabitats. The latter aspect is further enhanced by soil porosity which is improved by the root system of the shrub. Soil moisture availability is further retained by leaf litter from the shrub, reducing evaporative losses. Both leaf litter and (decaying) roots also contribute to soil organic matter which positively impacts soil water retention and soil nutrient status.

Biological legacies such as burnt logs or branches remaining after fires can be important microhabitat. These biological legacies can provide nurse structures that reduce drought and heat stress, trap water runoff, and provide nutrients and organic matter, all together improving pine seedling recruitment (Castro 2021). Also, shrubs and biological legacies may protect seedlings from large herbivores (Figure 4) thereby facilitating pine recruitment (Castro 2021). The use of shrubs as nurse plants or biological legacies as nurse structures is likely the most necessary measure for increasing success of pine seeding in Mediterranean environments. Some benefits provided by shrubs may be replicated by mulching with woodchips, i.e., layered mulch on top of the sown seed. For example, García-Morote et al. (2017) found that recruitment success increased from 0.2% to 4.4% when seeds of *P. halepensis* were covered with a layer of woodchips, in accordance with a common positive effect of mulching on seedling establishment across many species due to increased moisture, reduced weed competition, temperature buffering, and nutrient supply (Jonas et al.

2019; Lucas-Borja et al. 2020). Additionally, seed can be coated with a hydrogel to further improve moisture retention after sowing (Section 4).

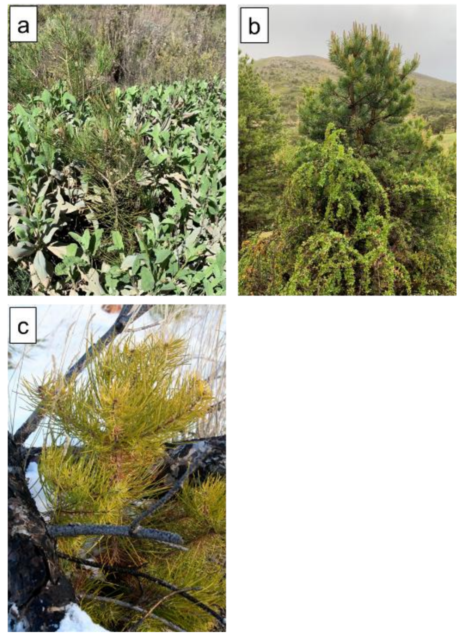

Figure 4. A common situation in Mediterranean ecosystems is the recruitment of tree species facilitated by nurse shrubs that improve microclimatic conditions, particularly by reducing drought stress during the summer. Because they are vulnerable to drought, pine seedling mortality can be substantial in summer. (a) Two individual Aleppo pine (*P. halepensis* Mill.) trees recruiting within the canopy of a salvia plant (*Salvia oxyodon* Webb & Heldr.) in a semiarid environment (Albacete, southeastern Spain). (b) Scots pine (*P. sylvestris* L.) sapling growing within a spiny shrub (*Berberis hispanica* Boiss. & Reut.) in Sierra de Baza, southern Spain. (c) A seedling of maritime pine (*P. pinaster* Aiton) recruiting in a burnt area: biological relics, dead branches after the fire, serve as nurse structures providing favorable microclimatic conditions (moderating irradiation and desiccating winds) without competing for water (Sierra Nevada National Park, southern Spain) (Photo credits: Jorge Castro).

Favorable microhabitats may also include small depressions or simple soil pits where surface runoff accumulates after a rain event (Evenari et al. 1971). This concept is mimicked by soil scarification prior to seeding, which breaks soil crusts that restrict rainwater infiltration. For drought prone areas, customized seed drills are integrated with V-shaped scalping blades or discs that create a weed-free strip and collect surface runoff in the seeded line (Whyte 2003). Seeded lines should preferably follow contour lines of the site to trap surface runoff without inducing gully erosion. The seeding implement is drawn behind a four-wheel drive vehicle or tractor, so it is restricted to flat or undulating terrain without too many rocks.

Finally, we may select the most appropriate sowing times for seed germination and plant establishment, for example, during periods of expected rainfall (as far as these periods fall within the period of seed germination), reducing the residence time of seeds during which they are vulnerable to seed predation. In summary, there is a suite of practices to alleviate drought stress; these focus on soil moisture conservation by reducing evaporational losses and increasing water availability next to seeds. Their effectiveness can be further improved in combination with other interventions. For example, seed coated with hydrogel can be sown under nurse shrubs and buried in the ground.

3.3 Seed contact with mineral soil and weed competition

Seed contact with mineral soil is essential. If the seed remains on a layer of organic matter, such as leaf litter or a layer of herbaceous plants, germination is still possible. However, the radicle will likely desiccate before reaching mineral soil and the seedling will die prematurely (Castro et al. 2002a) (see summary in Table 2). This differs in respect to pine seeding in other biomes where soil moisture is higher during the germination period. In drier regions, direct seeding (burying or pressing seeds in the ground) is particularly expected to be more successful than broadcasting seed. Germination of broadcasted seed may be improved by scarifying the soil surface, e.g., using disc or tine harrows, prior to seeding to facilitate seed burial or contact with mineral soil (Nackhoul et al. 2020; Rautio et al. 2023), especially in the presence of a soil crust or weed cover. Overall, site preparation such as soil scarification or scalping will increase the probability of seeding success due to higher water infiltration, reduced competition with herbaceous vegetation, or increased contact of the radicle with mineral soil (e.g., Castro et al. 2002a; Nakhoul et al. 2020). These measures can be effective even if applied at a small spatial scale, localized where the seed will be sown, which will minimize negative impacts of soil disturbance across the entire site.

The impact of the surface organic layer will also depend on seed mass. We may expect that the larger the seed, and thus, the more nutrients and energy it contains, the more likely the radicle will reach mineral soil. This is supported by Nackhoul et al. (2020), who found seedling emergence by *P. pinea*, the species with the largest seed mass in the Mediterranean region, was reduced if seed were sown on unscarified soil, but these seed still reached a relatively high (48%) emergence percentage (Table 2). These observations contrast markedly with those for small-seeded species like *P. sylvestris* (Castro et al. 2002a) (Table 2), suggesting that establishment of small-seeded species will particularly benefit from soil scarification, scalping, or seed burial (to aid contact of the seed with mineral soil).

Competition from weeds, especially dense herbaceous vegetation, also reduces pine seedling recruitment and growth (Castro et al. 2002a; Castro and Leverkus 2019). It is thus advisable to scalp soil or simply avoid areas where herbaceous vegetation has become too dense. Alternatively, as noted earlier, nurse shrubs can reduce herbaceous weed competition, providing a suitable microhabitat for seeding.

4 Seed coating to promote pine recruitment success

Because seed predation and seedling mortality caused by summer drought are the main limitations to pine seeding success in the Mediterranean region, any measure to alleviate the negative effects of these factors will increase the probability of success. As stated above, a common practice for achieving this objective is seed coating.

Seed coating consists of applying layers of beneficial materials through an accretion process to the seed coat. Coating seed modifies the physical traits (size, weight) of the seed and delivers substances that help the seed endure environmental stress or avoid predation. Coatings that provide protection against predators or pathogens, or promote germination and establishment are most common (Pedrini et al. 2017; Pearson et al. 2019). Coating pine seed is particularly feasible and easy given their size, shape, and lack of external appendices (except the wing, which is easily removed) (Benkman 1995). Coating seed is especially beneficial to mechanical seeding, either terrestrial broadcasting or aerial seeding, because they can be transformed into a spherical structure of desired diameter to facilitate spreading (Figure 5). Also, seed coating could be particularly useful for aerial seeding with drones (see below). This is because coating can be used to improve the ballistic properties of seeds, allowing them to fall to the ground with more predictable trajectories that are less influenced by wind and turbulent air currents (Domaradzki et. al. 2012).

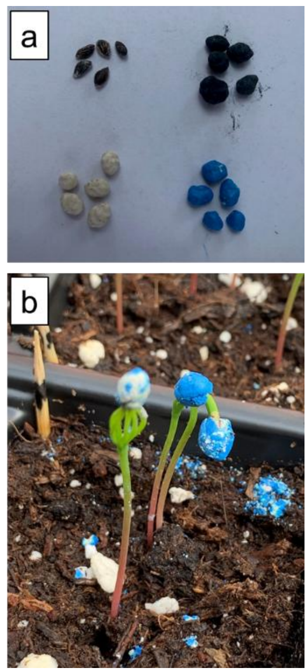

Figure 5. (a) Coating Aleppo pine (*P. halepensis* Mill.) seed. Natural seed (upper left), seed coated with active carbon (upper right), coated with neem oil (bottom left), and coated with bitrex plus a blue dye (bottom right). (b) A greenhouse experiment to test the effect of coatings on seed germination and seedling emergence (Photo credits: Jorge Castro).

A key feature of seed coating is the ability to load the artificial coating with substances designed to deter seed predation. For example, coloring the external surface of the seed coat blue was enough to limit predation by some bird species (Pawlina et al. 1996) (Figure 5). While this practice can work on predators that rely on vision, it may not work on rodents that rely heavily on taste and smell (Figure 3c). A primary problem with deterring substances is that their effect is often not consistent across sites. The extent of protection given by repellents may depend on factors such as the nutritional quality of seed, the species depredating the seed, or the availability of alternative foods (Nolte and Barnett 2000). As a result, some repellents show positive effects in some cases but no effect in others. For example, Bitrex (denatonium benzoate), an extremely bitter chemical compound, has sometimes reduced seed predation by rodents. However, in an ongoing experiment conducted by the authors, preliminary results indicate that Bitrex did not provide protection against predation by the wood mouse (*Apodemus sylvaticus*) (Figure 3c). Another approach reported to be effective is to mask the smell of seed with material such as activated carbon (Taylor et al. 2020). However, in the above-mentioned experiments, activated carbon did not seem to protect *P. sylvestris* seed from predation by the wood mouse (Castro et al. unpublished data).

Seed coating can also be used to promote seed germination and seedling survival. For example, we can add super-absorbent hydrogels that attract and retain water to the proximity of the seed and provide extra water during periods of drought (Amirkhani et al. 2023). Surfactants (or wetting agents) have also been used on hydrophobic soils to allow water to infiltrate soil right under the seed. This seed treatment can be particularly relevant in improving germination and emergence in post-wildfire reforestation. Coating seed with nutrients has also been evaluated but the delivery of macronutrients (NPK) often proved detrimental because of damage to the extending radicle (Scott 1989). Application of trace elements has proven effective in supplementing missing micro-nutrients. Other coating additives have been tested to promote seed germination, such as gibberellic acid to overcome dormancy (Larson et al. 2023), activated carbon to provide protection from herbicides (Davies et al. 2024), and salicylic acid to improve survival under stress conditions (Pedrini et al. 2021), though these have not yet been tested on pine seeds. Clearly, more research is needed to find effective seed coating practices that improve protection and promote pine establishment and recruitment in restoration settings.

5 Making seeding a viable approach for pine forest restoration in the Mediterranean basin

Seeding success is determined by three main, inter-related factors: (1) increase the recruitment probability associated with each seed, (2) reduce sowing density, and (3) reduce cost of seeding while limiting impact to the ecosystem (Castro et al. 2024). An action that meets any of these conditions will make seeding more competitive with planting seedlings and more viable as a restoration approach. We propose several options that meet these conditions. All strategies may use coated seed as described in Section 4, as this contributes to restoration success and facilitates the use of mechanical devices.

Direct seeding or spot seeding, burying seeds in the ground, is probably the best option to increase recruitment success while reducing the amount of seed needed (e.g., Table 2). Sowing can be done manually, including hand-operated seeders, allowing seeds to be easily inserted at the desired depth. Manual seeding also facilitates precision placement of seed at selected microsites, for example underneath shrubs. Because of early seedling mortality, it can be prudent to sow multiple seed per spot. Seed could be dispensed separately at the same spot or within a single pellet containing several seeds (agglomerate).

Direct seeding could also be done with terrestrial seeding robots that are currently being developed by companies like Land Life (Amsterdam, The Netherlands; Figure 6a). Terrestrial seeding robots can integrate spot-wise site preparation and sowing by scalping to remove weeds, exposing the mineral soil before burying seeds or seed pellets and creating a small depression to trap rainwater (Figure 6b). Considering their limited weight and spot-level operation, seeding robots are environmentally less intrusive than conventional terrestrial seeding methods that use heavy machinery to scarify soil or pull seeding lines. Seeding robots may operate in fleets covering large parcels of land, including moderately inclined, rugged, and rocky terrain, cumbersome for operation of conventional seeding machinery. The fully controlled seeding process addresses variation in microhabitat conditions regarding natural shelter, soil conditions including aspect and rainwater entrapment, and can enable precision seeding near nurse shrubs.

In the absence of nurse shrubs, microsite conditions can be improved artificially by using biopolymer based mini-protectors, i.e., shuttles (©Land Life, 2024) (Figure 7a). Shuttles are partly pushed into the soil to provide above- and belowground protection against seed predation and to provide shelter against high irradiation and desiccating winds. In the driest environments, an additional disc-shaped structure, composed of biodegradable pulp fiber, can be affixed onto the soil surface around the shuttle (Figure 7b). This device reduces evaporation from soil and suppresses weed competition, while water captured from rain events is channeled to the seed. Additional cardboard-based sleeves can be fixed on above-ground spike structures to further reduce light and drought stress, while providing extra protection against seed predation and browsing (Figure 7c). Considering the additional investment, shuttles should preferably protect multiple seeds to realize cost effective recruitment (Figure 7d).

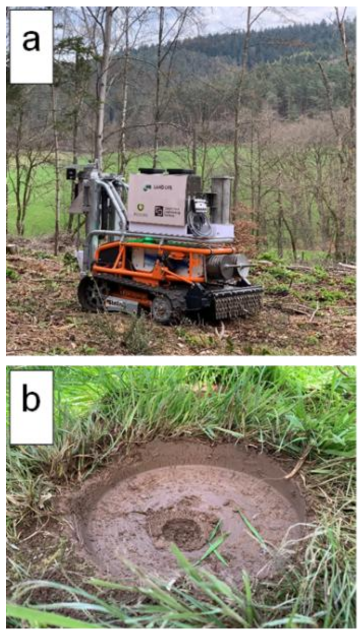

Figure 6. Terrestrial seeding robot developed by Land Life Company BV (Amsterdam, The Netherlands). (a) Prototype of a seeding unit mounted onto an electrically powered mobile platform enabling spot seeding particularly under rugged terrain conditions. (b) Detail of scarified soil spot prior to seeding: exposing mineral soil by eliminating weed cover, while its conical shape traps rainwater favoring soil moisture retention (Photo credits: Land Life Company BV).

Aerial seeding using conventional methods like airplanes or helicopters appears ineffective in the Mediterranean region. Even if coated seed are used to reduce seed predation, conventional aerial seeding places most seeds on microsites unsuitable for germination (e.g., dense weed cover, hard soil crust). Because pine recruitment success in the Mediterranean region relies enormously on favorable microhabitat selection, aerial seeding based on current drone technology should be considered. Drones can place seed in preferred microhabitats with favorable moisture and aspect conditions and can methodically avoid areas with dense herbaceous cover at small spatial scales. Also, drones may place seed in preselected microsites at sub-meter scale, for example, under nurse shrubs—an application termed "precision drone seeding" (Castro et al. 2024) (Figure 8). This method can markedly reduce the number of seed required and, hence, the operational cost can be reduced up to 6–7 times in respect to traditional seedling planting (Castro et al. 2024). Drone seeding could, therefore, be useful and competitive if the paradigm were changed from broadcast seeding the entire site to be restored to precision drone seeding that delivered seed to the most suitable microsites for establishment (Castro et al. 2024). This procedure could be further automated with the use of artificial intelligence that incorporates high resolution remote-sensing imagery and algorithms that recognize the best microsites for seed deployment at the sub-meter scale, e.g., specific nurse shrubs (Castro et al. 2024). Unlike terrestrial seeding, drone seeding can be deployed on particularly steep terrain with poor access where large areas can be seeded in a short period of time, broadening the scalability of reforestation. However, soil preparation and seed burial, two factors that clearly increase seeding success, cannot be addressed by seeding with drones.

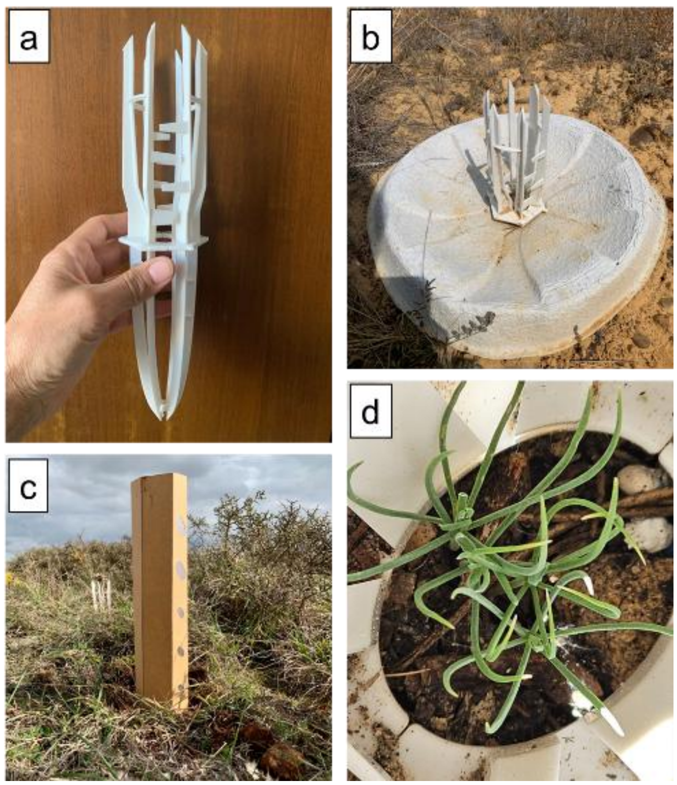

Figure 7. Shuttle technology developed for seeding or planting by Land Life Company BV (Amsterdam, The Netherlands). (a) The shuttle is inserted in the ground to the middle flange, the device provides above- and belowground protection against birds, browsers, and rodents, while the upper part improves microclimatic conditions by providing shelter against high irradiation and desiccating winds. Under more challenging drought conditions shuttles may be combined with a rainwater harvesting disc (b), which also controls weeds, and a top sleeve (c) providing more shelter to support germination and early seedling establishment. Several seeds can be sown per shuttle to ensure recruitment success (d); in the picture, four Scots pine (*P. sylvestris* L.) seedlings plus two non-germinated, coated seeds (Photo credits: Land Life Company BV).

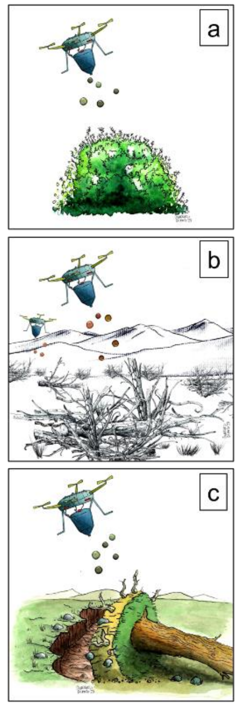

Figure 8. Examples of potential uses of drone seeding at the sub-meter scale. (a) Nurse shrubs provide favorable microclimatic conditions for seedling establishment and protection against herbivory. (b) Biological legacies such as piles of branches left after post-fire management can act as nurse structures. (c) Microtopographic features such as pits and mounds left by fallen trees after windstorms create favorable ecological niches where seedling establishment could have greater success. Drones can drop seed in these particular microsites using a precision-seeding approach. The process can be automated with the use of high-resolution remote sensing imagery and artificial intelligence. Reproduced from Castro et al. 2024.

6 Conclusions

Pine seeding is an afforestation and reforestation method that has generally showed low success in the harsh environmental conditions of the Mediterranean region. Results for seeding are typically much more unpredictable than planting in terms of reforestation success. Additionally, successful cases of pine reforestation with seeding usually employed a large amount of seed per hectare, which could create problems of seed supply and scalability. These are the most likely reasons that seeding has been used much less commonly than seedling outplanting. Nonetheless, seeding has been demonstrated to be a feasible and successful method of forest restoration in some cases for the Mediterranean region.

Building on past successes, pine seeding may become more successful and increasingly efficient as a restoration approach through incorporation of new technologies with traditional methods and ecological knowledge under the paradigm of "precision restoration" (Castro et al. 2021). In this respect, development of effective and efficient seed coating technologies to deter seed predators and increase seedling establishment are needed. We also must become more proficient in selecting the best locations to sow seed, even at sub-meter scale (microhabitats), and factoring potential hazards that the seedlings will face through recruitment, e.g., herbivory. Seed should ideally be sown in the ground. This increases the cost of the operation but can substantially increase establishment success, particularly if seed is placed below nurse shrubs. Aerial seeding with drones and terrestrial seeding robots may help to scale pine seeding beyond what can be achieved with conventional technologies and should be a main focus for future research.

7 Acknowledgements

This study was supported by project AIDroneSeeding (Ref. PID2023.147483OB.I00) funded by Ministerio de Ciencia, Innovación y Universidades from the Spanish Government and the European Union FEDER Program Andalucía 2021–2027, project C-EXP-130-UGR23 funded by the Consejería of University, Research and Innovation and by the European Union under the FEDER Program Andalusia 2021–2027, project SmartForRest (Ref. TED2021-129690B-I00) funded by MCIN/AEI/10.13039/501100011033 and by the European Union NextGenerationEU/ PRTR, and by the "Aula de Restauración Ecológica" from the University of Granada. The article is an activity within the work of IUFRO Task Force "Transforming Forest Landscapes for Future Climates and Human Well-Being." We thank the editors and two anonymous reviewers for helpful suggestions.

Disclaimer

The use of trade or firm names in this publication is for reader information and does not imply endorsement by the authors or their respective institutions of any product or service.

8 References

AEMA (2008) Agencia Europea de Medio Ambiente. Tipología de bosques europeos. https://www.miteco.gob.es/content/dam/miteco/es/calidad-y-evaluacion-ambiental/publicaciones/TipologiaBosquesEuropeos_tcm30-185660.pdf (last accessed 23 November 2024).

Amirkhani M, Mayton H, Loos M, Taylor A (2023) Development of superabsorbent polymer (SAP) seed coating technology to enhance germination and stand establishment in red clover cover crop. Agronomy 13(2):438. https://doi.org/10.3390/agronomy13020438

Benkman CW (1995) Wind dispersal capacity of pine seeds and the evolution of different seed dispersal modes in pines. Oikos 73:221–224. https://doi.org/10.2307/3545911

Bladé C, Vallejo R (2008) Seed mass effects on performance of *Pinus halepensis* Mill. seedlings sown after fire. For Ecol Manag 255:2362–2372. https://doi.org/10.1016/j.foreco.2007.12.039

Boulant N, Navas ML, Corcket E, Lepart J (2008) Habitat amelioration and associational defence as main facilitative mechanisms in Mediterranean grasslands grazed by domestic livestock. Écoscience 15:407–415. https://doi.org/10.2980/15-3-3126

Boydak, M (2004) Silvicultural characteristics and natural regeneration of *Pinus brutia* Ten.—a review. Plant Ecol 171:153–163.

Calvo L, Torres O, Valbuena L, Luis-Calabuig E (2013) Recruitment and early growth of *Pinus pinaster* seedlings over five years after a wildfire in NW Spain. For Syst 22(3):582–586. http://dx.doi.org/10.5424/fs/2013223-04623

Castro J (2021) Chapter 25 - Post-fire restoration of Mediterranean pine forests. In: Ne'eman G, Osem Y (eds) Pines and their mixed forest ecosystems in the Mediterranean Basin. Springer Nature Switzerland AG, Cham, Switzerland, pp 537–565. https://doi.org/10.1007/978-3-030-63625-8

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 145:115–123. https://doi.org/10.1023/A:1009865703906

Castro J, Zamora R, Hódar J (2002a) Mechanisms blocking *Pinus sylvestris* colonization of Mediterranean mountains meadows. J Veg Sci 13:725–731. https://doi.org/10.1111/j.1654-1103.2002.tb02100.x

Castro J, Zamora R, Hódar JA, Gómez JM (2002b) Use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. Restor Ecol 10:297–305. https://doi.org/10.1046/j.1526-100X.2002.01022.x

Castro J, Zamora R, Hódar J A, Gómez J M (2004) Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. J Ecol 92(2):266–277. https://doi.org/10.1111/j.0022-0477.2004.00870.x

Castro J, Zamora R, Hódar J A, Gómez J M (2005) Alleviation of summer drought boosts establishment success of *Pinus sylvestris* in a Mediterranean mountain: An experimental approach. Plant Ecol 181:191–202. https://doi.org/10.1007/s11258-005-6626-5

Castro J, Leverkus AB (2019) Effect of herbaceous layer interference on the post-fire regeneration of a serotinous pine (*Pinus pinaster* Aiton) across two seedling ages. Forests 10:74. https://doi.org/10.3390/f10010074

Castro J, Morales-Rueda F, Navarro FB, Löf M, Vacchiano G, Alcaraz-Segura D (2021) Precision restoration: a necessary approach to foster forest recovery in the 21st century. Restor Ecol 29(7):e13421. https://doi.org/10.1111/rec.13421

Castro J, Alcaraz-Segura D, Baltzer JL, Amorós L, Morales-Rueda F, Tabik S (2024) Automated precise seeding with drones and artificial intelligence: a workflow. Restor Ecol 32(5):e14164. https://doi.org/10.1111/rec.14164

Cueto M (2001) Ordenaciones de pinares de pino piñonero en la provincia de Cádiz. Cuadernos de la Sociedad Española de Ciencias Forestales 11:125–134.

Davies KW, Clenet DR, Madsen MD, Brown VS, Ritchie AL, Svejcar LN (2024) Activated carbon seed technologies: Innovative solutions to assist in the restoration and revegetation of invaded drylands. J Environ Manag 371:123281. https://doi.org/10.1016/j.jenvman.2024.123281

Domaradzki M, Kaniewska J, Weiner W (2012) The application of agglomerative granulation for seeds. Part 2. Pelleting of organic seeds. Chemik 66:473–478.

Espelta JM, Retana J, Habrouk A (2003) An economic and ecological multi-criteria evaluation of reforestation methods to recover burned *Pinus nigra* forests in NE Spain. For Ecol Manag 180:185–198. https://doi.org/10.1016/S0378-1127(02)00599-6

Evenari M, Shanan L, Tadmor N (1971) The Negev, the Challenge of a Desert. Harvard University Press, Cambridge, MA, USA.

Fernandes P, Máguas C, Correia O (2017) Combined effects of climate, habitat, and disturbance on seedling establishment of *Pinus pinaster* and *Eucalyptus globulus*. Plant Ecol 218(5):501–515. https://doi.org/10.1007/s11258-017-0706-1

Franco JDA (1986) *Pinus*. In: Castroviejo S, Laínz M, López-González G, Montserrat P, Muñoz-Garmendia F, Paiva J, Villar L (eds) Flora Ibérica, vol. I. Real Jardín Botánico, CSIC, Madrid, Spain, pp 168–174.

García-Morote FA, Martínez-García E, Andrés-Abellán M, Caballero ER, Miettinen H, López-Serrano FR (2017) Direct seeding of *Pinus halepensis* Mill*.* for recovery of burned semi-arid forests: Implications for post-fire management for improving natural regeneration. Forests 8(9):353. https://doi.org/10.3390/f8090353

Grivet D, Olsson S (2021) Chapter 1 - Phylogenies and evolution of Mediterranean pines. In: Ne'eman G, Osem Y (eds) Pines and their mixed forest ecosystems in the Mediterranean Basin. Springer Nature Switzerland AG, Cham, Switzerland, pp 3–17. https://doi.org/10.1007/978-3-030-63625-8

Hibsher N, Moshe Y, Bney-Moshe E, Ben-Moshe E, Zangi E, Zuck A, Osem Y (2013) Post-fire regeneration in Mediterranean reforested sites as affected by mechanical site preparation—lessons for restoration. Appl Veg Sci 16:629–639. https://doi.org/10.1111/avsc.12030

Jonas JL, Berryman E, Wolk B, Morgan P, Robichaud PR (2019) Post-fire wood mulch for reducing erosion potential increases tree seedlings with few impacts on understory plants and soil nitrogen. For Ecol Manag 453:117567. https://doi.org/10.1016/j.foreco.2019.117567

Larson AJS, Cartwright MM, Jones WD, Luce K, Chen M-Y, Petersen K, Nelson SV, Michaelis DJ, Madsen MD (2023) Slow release of GA_3 hormone from polymer coating overcomes seed dormancy and improves germination. Plants 12(24):4139. https://doi.org/10.3390/plants12244139

Lázaro-González A, Andivia E, Hampe A, Hasegawa S, Marzano R, Santos AMC, Castro J, Leverkus AB (2023) Revegetation through seeding or planting: A worldwide systematic map. J Environ Manag 337:117713. https://doi.org/10.1016/j.jenvman.2023.117713

Lucas-Borja ME, Silva-Santos P, Fonseca TF, Tíscar-Oliver 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(3):393–403.

Lucas-Borja ME, Plaza-Álvarez PA, González-Romero J, Miralles I, Sagra J, Molina-Peña E, Mora D, de las Heras J, Fernández C (2020) Post-wildfire straw mulching and salvage logging affects initial pine seedling density and growth in two Mediterranean contrasting climatic areas in Spain. For Ecol Manag 474:118363. https://doi.org/10.1016/j.foreco.2020.118363

Martínez-García E, Miettinen H, Rubio E, García-Morote FA, Andrés-Abellán M, López-Serrano FR (2018) Effects of post-fire management practices and slope-aspect on medium-term Spanish black pine regeneration: implications of using a direct seeding strategy in burnt areas. European J For Res 137(4):527–540. https://doi.org/10.1007/s10342-018-1121-4

Matías L, Castro J, Villar-Salvador P, Quero JL, Jump AS (2017) Differential impact of hotter drought on seedling performance of five ecologically distinct pine species. Plant Ecol 218:201–212. https://doi.org/10.1007/s11258-016-0677-7

Matías L, Zamora R, Castro J (2012) Sporadic rainy events are more critical than increasing of drought intensity for woody species recruitment in a Mediterranean community. Oecologia 169:833–844. https://doi.org/10.1007/s00442-011-2234-3

Mendoza I, Zamora R, Castro J (2009) A seeding experiment for testing tree-community recruitment under variable environments: implications for forest regeneration and conservation in Mediterranean habitats. Biol Conserv 149:1491–1499. https://doi.org/10.1016/j.biocon.2009.02.018

Mohan M, Richardson G, Gopan G, Aghai MM, Bajaj S, Galgamuwa GA, Vastaranta M, Arachchige PSP, Amorós L, Corte APD, de-Miguel S, Leite RV, Kganyago M, Broadbent EN, Doaemo W, Shorab MAB, Cardil A (2021) UAV-supported forest regeneration: current trends, challenges and implications. Remote Sens 13(13):2596. https://doi.org/10.3390/rs13132596

Moreira F, Arianoutsou M, Corona P, De las Heras J (eds) (2012) Post-fire management and restoration of southern European forests. Springer, Dordrecht, The Netherlands.

Muler AL, van Etten EJB, Stock WD, Howard K, Froend RH (2018) Can hydraulically redistributed water assist surrounding seedlings during summer drought? Oecologia 187:625–641. https://doi.org/10.1007/s00442-018-4158-7

Nakhoul J, Santonja M, Fernandez C, Greff S, Bousquet-Mélou A, Dupouyet S, Nemer N, Kattar S, Abboud J, Prévosto B (2020) Soil scarification favors natural regeneration of *Pinus pinea* in Lebanon forests: Evidences from field and laboratory experiments. For Ecol Manag 459:117840. https://doi.org/10.1016/j.foreco.2019.117840

Ne’eman G, Osem Y (eds) (2021) Pines and their mixed forest ecosystems in the Mediterranean Basin. Springer Nature Switzerland AG, Cham, Switzerland.

Nolte DL, Barnett JP (2000) A repellent to reduce mouse damage to longleaf pine seed. Int Biodeterior Biodegrad 45:169–174. https://doi.org/10.1016/S0964-8305(00)00060-3

Notivol E, Oliet JA, Serrada R (2012) *Pinus uncinata* Ram. In: Pemán JG, Navarro RM, Nicolás JL, Prada MA, Serrada R (eds), Producción y Manejo de Semillas y Plantas Forestales. Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, Spain, pp 1003–1018.

Ordóñez JL, Franco S, Retana J (2004) Limitation of the recruitment of *Pinus nigra* in a gradient of post-fire environmental conditions. Écoscience 11:296–304. https://doi.org/10.1080/11956860.2004.11682836

Pawlina IM, Proulx G (1996) Study of house sparrow (*Passer domesticus*) feeding preference to natural color and guard coat blue coated seeds. Crop Prot 15:143–146. https://doi.org/10.1016/0261-2194(95)00087-9

Pearson DE, Valliant M, Carlson C, Thelen GC, Ortega YK, Orrock JL, Madsen MD (2019) Spicing up restoration: can chili peppers improve restoration seeding by reducing seed predation? Restor Ecol 27:254–260. https://doi.org/10.1111/rec.12862

Pedrini S, Merritt DJ, Stevens J, Dixon K (2017) Seed coating: Science or marketing spin? Trends Plant Sci 22:106–116. https://doi.org/10.1016/j.tplants.2016.11.002

Pedrini S, Balestrazzi A, Madsen MD, Bhalsing K, Hardegree SP, Dixon KW, Kildisheva OA (2020) Seed enhancement: getting seeds restoration-ready. Restor Ecol 28(S3):266–275. https://doi.org/10.1111/rec.13184

Pedrini S, Stevens JC, Dixon KW (2021) Seed encrusting with salicylic acid: A novel approach to improve establishment of grass species in ecological restoration. PLOS ONE 16:e0242035. https://doi.org/10.1371/journal.pone.0242035

Petrou P, Milios E (2012) Establishment and survival of *Pinus brutia* Ten*.* seedlings over the first growing season in abandoned fields in central Cyprus. Plant Biosyst 146:522–533. https://doi.org/10.1080/11263504.2011.633574

Rautio P, Hallikainen V, Valkonen S, Karjalainen J, Puttonen P, Bergsten U, Winsa H, Hyppönen M (2023) Manipulating overstory density and mineral soil exposure for optimal natural regeneration of Scots pine. For Ecol Manag 539:120996. https://doi.org/10.1016/j.foreco.2023.120996

Retana J, Arnan X, Arianoutsou M, Barbati A, Kazanis D, Rodrigo A (2012) Chapter 7 - Post-fire management of non-serotinous pine forests. In: Moreira F, Arianoutsou M, Corona P, De las Heras J (eds) Post-fire management and restoration of southern European forests. Springer, Dordrecht, The Netherlands, pp 151–170.

Ruano I, Pando V, Bravo F (2009) How do light and water influence *Pinus pinaster* Ait*.* germination and early development*?* For Ecol Manag 258:2647–2653. https://doi.org/10.1016/j.foreco.2009.09.027

Rundel PW, Arroyo MT, Cowling RM, Keeley JE, Lamont BB, Vargas P (2016) Mediterranean biomes: Evolution of their vegetation, floras, and climate. Annu Rev Ecol Evol Syst 47(1):383–407. https://doi.org/10.1146/annurev-ecolsys-121415-032330

Salazar-Tortosa D, Castro J, de Casas RR, Viñegla B, Sánchez-Cañete EP, Villar-Salvador P (2018a) Gas exchange at whole plant level shows that a less conservative water use is linked to a higher performance in three ecologically distinct pine species. Environ Res Lett 13:045004. https://doi.org/10.1088/1748-9326/aab18f

Salazar-Tortosa D, Castro J, Villar-Salvador P, Viñegla B, Matías L, Michelsen A, de Casas RR, Querejeta I (2018b) The "isohydric trap": a proposed feed-back between water shortage, stomatal regulation and nutrient acquisition drives differential growth and survival of European pines under climatic dryness. Glob Chang Biol 24:4069–4083. https://doi.org/10.1111/gcb.14311

Salazar-Tortosa D, Castro J, Saladin B, Zimmermann NE, Rubio de Casas R (2020) Arid environments select for larger seeds in pines (*Pinus* spp). Evol Ecol 34:11–26. https://doi.org/10.1007/s10682-019-10016-1

Salazar-Tortosa D, Saladin B, Castro J, Rubio de Casas R (2024) Climate change is predicted to impact the global distribution and richness of pines (genus *Pinus*) by 2070. Divers Distrib 30(7):e13849. https://doi.org/10.1111/ddi.13849

San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (Eds) (2016) European atlas of forest tree species. Publication Office of the European Union, Luxembourg. https://doi.org/10.2788/038466

Scott JM (1989) Seed coatings and treatments and their effects on plant establishment. Adv Agron 42:43–83. https://doi.org/10.1016/S0065-2113(08)60523-4

Taboada A, Tárrega R, Marcos E, Valbuena L, Suárez-Seoane S, Calvo L (2017) Fire recurrence and emergency post-fire management influence seedling recruitment and growth by altering plant interactions in fire-prone ecosystems. For Ecol Manag 402:63–75. https://doi.org/10.1016/j.foreco.2017.07.029

Taylor JB, Cass KL, Armond DN, Madsen MD, Pearson DE, St Clair SB (2020) Deterring rodent seed-predation using seed-coating technologies. Restor Ecol 28:927–936. https://doi.org/10.1111/rec.13158

Tíscar PA, Candel-Pérez D, Estrany J, Balandier P, Gómez R, Lucas-Borja ME (2017) Regeneration of three pine species in a Mediterranean forest: A study to test predictions from species distribution models under changing climates. Sci Total Environ 584–585:78–87. https://doi.org/10.1016/j.scitotenv.2017.01.150

Tromble JM (1987) Water interception by two arid land shrubs. J Arid Environ 15:65–70. https://doi.org/10.1016/S0140-1963(18)31005-X

Whyte S (2003) Revegetation techniques - a guide for establishing native vegetation in Victoria. Greening Australia Victoria, Victoria, Australia.

Ziffer-Berger J, Weisberg PJ, Cablk ME, Moshe Y, Osem Y (2017) Shrubs facilitate pine colonization by controlling seed predation in dry Mediterranean dwarf shrublands. J Arid Environ 147:34–39. https://doi.org/10.1016/j.jaridenv.2017.07.012