

## Mechanisms blocking *Pinus sylvestris* colonization of Mediterranean mountain meadows

Castro, Jorge<sup>1,2\*</sup>; Zamora, Regino<sup>1</sup> & Hódar, José A.<sup>1</sup>

<sup>1</sup>Grupo de Ecología Terrestre, Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain;

\*Corresponding author: Fax: +34 958 243238; E-mail: jorge@ugr.es

<sup>2</sup>Botanical Institute, University of Copenhagen, Øster Farimagsgade 2D, DK-1353, Copenhagen K, Denmark

**Abstract.** In southern Mediterranean *Pinus sylvestris* forests there are grassy meadows that resist invasion of trees despite the proximity to seed sources. In this study, we investigate the mechanisms blocking colonization by *Pinus sylvestris* of the meadows. Two experiments were conducted in which seeds were sown either at 1 cm depth or on the surface to simulate dispersal, and three treatments of vegetation removal were applied: Disturbed (where the herbaceous layer was eliminated, exposing the mineral soil), Clipped (vegetation cut at ground level) and Control (no disturbance of the herbaceous layer). In addition, the effect of seed predators was controlled by using wire cages in the case of the surface sown experiment.

When seeds were sown at 1 cm depth, seedling emergence was not reduced by the herbaceous layer. In contrast, when seeds were surface sown and predators were excluded, the rate of emergence was low in the Control treatment, intermediate in Clipped and high in Disturbed. Seedling emergence was, however, minimal when predators were not excluded, irrespective of the disturbance level. Seedling survival and growth after three years of study were similar among treatments. The results show that the seed predation and the physical barrier created by the herbaceous layer are the two mechanisms blocking the encroachment of *Pinus sylvestris* onto these Mediterranean mountain meadows, limiting the regeneration and potential expansion of the forest.

**Keywords:** Disturbance; Herbaceous competition; Interference; Invasion; Seed predation; Seedling encroachment; Scots pine; Sierra Nevada; Spain; Tree establishment.

**Nomenclature:** Tutin et al. (1964-1980).

### Introduction

Seedling establishment is often the critical step for the persistence of plant populations and can thus influence species distribution and abundance (Harper 1977; Silvertown & Lovett-Doust 1993; Grime 2001). Even trees, long-lived organisms with low adult mortality rates, may be quite vulnerable as seedlings to various

mortality factors and their distribution relies mostly on seed germination and seedling survival during the early phases of establishment. The recruitment of seedlings of woody species is therefore a decisive phase for the succession from grassy areas to woodlands (Gill & Marks 1991; Magee & Antos 1992; Scholes & Archer 1997).

The interference exerted by a herbaceous layer may limit the establishment of seedlings of woody species, which in its turn may change the successional dynamics, limiting forest regeneration within stands and precluding expansion to adjacent areas (Archer 1994; Risser 1995). The factors and mechanisms involved in this limitation have been related mainly to resource competition (Nambiar & Sands 1993; Scholes & Archer 1997; Davis et al. 1999; Gordon & Rice 2000; Löf 2000; Peltzer & Köchy 2001), but other mechanisms such as seed predation (Gill & Marks 1991; Davidson 1993; Reader 1997), herbivory (McPherson 1993; Ostfeld & Canham 1993) or toxic effects of the herbaceous layer (Jarvis 1964) have also been reported. Consequently, the recruitment of woody species in dense herbaceous stands frequently relies on the availability of small gaps (e.g. Hill et al. 1995) which may be created by vertebrates through trampling, digging or grazing (e.g. DeSimone & Zedler 1999).

In the Sierra Nevada, southern Spain, *Pinus sylvestris* reaches its southernmost distribution limit (Boratynski 1991) forming relict forests isolated in Mediterranean high mountains. These populations currently have a constrained regeneration capacity, and huge losses of propagules result mostly from high rates of seed predation and seedling mortality (Castro et al. 1999; Castro 2000). Within the forests, there are grassy meadows that are usually surrounded by adult trees. The herbaceous layer in the meadows covers almost 100%, with small gaps of bare soil created mainly by ungulate trampling and wild boar grubbing. *Pinus* seeds enter the meadows from nearby trees (Castro et al. 1999). However, saplings are absent, even though planted juveniles develop normally (Castro 2000). In the present study we seek to

identify the mechanisms underlying the lack of *Pinus* colonization of Mediterranean mountain meadows. We used a combination of different sowing depths, vegetation-removal intensity, and control of seed predators in order to address the following questions: 1) What is the probability of emergence for seeds located in the meadows? 2) What are the requirements for seedling emergence? and, 3) Once a seedling has emerged, what is the effect exerted by the herb layer, in relation to open gaps, upon seedling survival, growth and causes of mortality?

## Material and Methods

### Study area

The study area is located at 1800 m a.s.l. in the National Park of Sierra Nevada (Trevenque area, southern Spain, 37°5' N, 3°28' W), a mountain range where *Pinus sylvestris* (Scots pine) grows between 1600 and 2100 m a.s.l. on calcareous soils. The climate is mediterranean continental with hot, dry summers and cold winters. Mean annual rainfall is 830 mm, mean temperature of the coldest month (January) is 3.5 °C and mean temperature of the hottest month (August) is 21.6 °C (data from 1990 to 2000).

*Pinus* forms a canopy of ca. 30% cover, whereas the understorey is a mosaic of shrub patches, open areas and grassy meadows (Castro et al. 1999). The meadows range from 300 to ca. 5000 m<sup>2</sup>. They are dominated mostly by grasses (e.g. *Bromus tectorum* and *Festuca nevadensis*), together with some forbs, (e.g. *Arenaria grandiflora*, *Crucianella angustifolia* and *Helianthemum apenninum*). The herbaceous layer is ca. 8–15 cm high. Seed dispersal of *Pinus* lasts from January to March (Castro et al. 1999). Seeds have a germination rate of ca. 95%, are not dormant and germinate when it is sufficiently warm and moist (Castro 1999) which occurs in late April (Castro 2000). Seedlings emerge in May and June.

### Experimental design

Two experiments involving control of the herbaceous layer, sowing depth and seed predation were conducted in a meadow of ca. 3000 m<sup>2</sup>, which was inside a fenced area. The seeds used in the two experiments were from the current year, i.e. were collected just before cone opening (early January) and stored at room conditions until the start of the experiments.

#### 1. Seedling recruitment and growth from sown seeds (Experiment 1)

This experiment was designed to test the impact of herbaceous competition on seedling emergence, sur-

vival and growth. Seeds were sown at 1 cm depth in order to avoid seed predation and to provide the best conditions to ensure recruited seedlings. We randomly established 100 sampling points in the meadow with three plots of 15 cm × 15 cm, one for each of the treatments.

1. **Disturbed:** vegetation cut at ca. 3 cm below-ground with a hoe, minimizing regrowth. This simulated vertebrate trampling, which removes the vegetation and exposes the mineral soil. The plots remained bare for two growing seasons and were partially recolonized at the end of the third growing season.

2. **Clipped:** vegetation cut at ground level, leaving only basal parts. A further clipping was applied just before tree seedling emergence. This simulated ungulate grazing. The plots remained without vegetation during the first growing season and got covered by vegetation at the end of the second growing season.

3. **Control:** a 15 cm × 15 cm area left intact and thus covered by grasses.

The three plots at each sampling point were separated by ca. 50 cm to ensure independence. In each plot, we sowed four viable seeds in the corners of a quadrat (6 cm × 6 cm) in the centre of the plot, totalling 1200 seeds (100 plots × 3 treatments × 4 seeds). Sowing date was 19 April 1997.

The treatments were censused weekly until seedling emergence stopped. The seedlings were marked individually, and their survival, growth and cause of mortality were monitored until 10 July 2000 – for more than three years after sowing and well into the fourth growing season. Survival was monitored 5 × during the first growing season and thereafter at the end of summers and winters (except winter 1999). Mortality causes were:

- (1) summer drought (seedlings drying during the summer);
- (2) pathogens (seedlings dying shortly after emergence, when the soil was wet enough to prevent desiccation; often with root-collar necrosis);
- (3) hail storms (seedlings broken by hailstones);
- (4) herbivory (cut seedlings, without distinction between invertebrates or microvertebrates);
- (5) vole tunnels (seedling roots disturbed);
- (6) frost heave.

Seedling growth was estimated by non-destructive measurements at the end of the first and second growing seasons (end of summer 1997 and 1998, respectively). These included length of the stem (from cotyledon insertion), number of leaves produced in each year and

the length of the largest leaf produced in the current year. Seedlings remaining by 10 July 2000 (well into the fourth growing season) were uprooted and the total shoot length and shoot dry weight (both from cotyledon insertion) were measured.

In 1998 we performed a second trial of the same experiment, with seeds sown on 24 March. Sampling stations were again randomly assigned following the same schedule (i.e. 100 replicates per treatment). In this case, we monitored survival and cause of mortality after the first growing season (i.e. after summer 1998), again in May 1999 and at the end of the experiment on 10 July 2000 (well into the third growing season).

## 2. Seedling emergence from surface sown seeds (Experiment 2)

This experiment was designed to test both the effect of post dispersal seed predators and the interference of the herbaceous layer on seedling emergence after simulating natural dispersal, for which the seeds were surface-sown. We used 20 replicates ('plots') per treatment (Disturbed, Clipped and Control; created in the same way as previously described) which were randomly located in the meadow. Because we were only studying emergence we sowed 25 seeds per plot to obtain a reliable proportion for analysis (see below). The seed density used was 400 seeds.m<sup>-2</sup>, which is comparable to peak production in a mast year (Koski 1991) and the area of the plots was 25 cm × 25 cm. In addition, the experimental design was replicated with and without exclusion of seed predators, resulting in a total of 3000 seeds (20 plots × 3 perturbation levels × 2 predation levels × 25 seeds). Predators were excluded by covering the plot with a wire cage of 1.3 cm mesh and 25 cm side × 10 cm high. This prevents the access of rodents and birds, which are the post dispersal seed predators of *Pinus sylvestris* in these forests (Castro et al. 1999). The seeds were previously de-winged to prevent losses due to secondary movements by wind or other abiotic factors, sowing date was 24 March 1998. We monitored seedling emergence weekly, considering a seedling to have emerged when its root had at least partially penetrated the ground. Germinated seeds that expanded their radicle across the soil surface but did not root, drying out some days after germination and before forming an erect seedling, were not considered as emerged.

## Data analysis

Seedling emergence in Experiment 1 was compared among treatments, and for each year separately, by a contingency analysis in which seed emergence was considered a nominal variable with four levels (0, 1, 2, or > 2 seedlings emerged; plots with 3 and 4 emerged

seedlings were grouped into one category due to low values of observed frequencies; Zar 1996). Seedling emergence in Experiment 2 was analysed using ANOVA. Five replicates of the Disturbed + Predator excluded treatment were eliminated from the analysis because wood mice got into the enclosures.

The survival of seedlings from seeds planted in 1997 in Experiment 1 was analysed with a failure-time approach, which measures the time to failure (death) of each individual (Fox 1993). We used the SAS LIFEREG procedure, which produces estimates of parametric regression models with censored survival data using the method of maximum likelihood. A Weibull distribution was used because it gave the highest likelihood value and the best graphic inspection (Fox 1993; Allison 1995). For seedlings that emerged from seeds planted in 1998 in Experiment 1 we censored survival on three occasions, which was too seldom to use the failure-time analysis. For this data set, we analysed survival at the end of the first growing season with a  $\chi^2$ -test. Very low values of observed frequencies hampered the analysis of survival at the end of the experiment. Growth parameters were analysed with ANOVA, considering every seedling as a replicate. Causes of mortality were compared using a  $\chi^2$ -test.

The failure-time analysis was performed using SAS 6.12, the rest of the analyses were made with JMP 3.2.6. For ANOVAs, data were log transformed for growth parameters and arcsine transformed for proportions (Zar 1996). Throughout the paper, values are means ± 1 s.e.

## Results

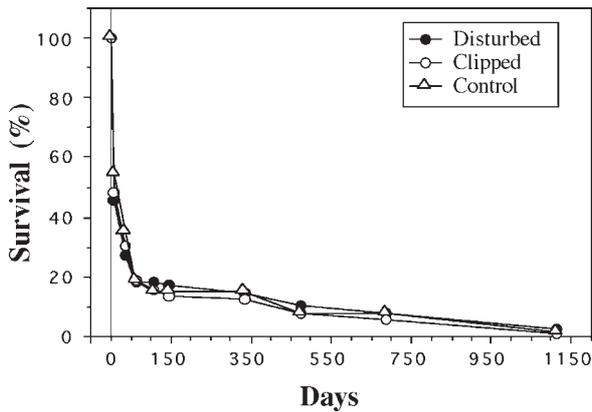
### Experiment 1

Seedling emergence did not differ among treatments for seeds planted in 1997 (Disturbed = 28.5%, Clipped = 22.2%, Control = 29.2%;  $\chi^2 = 9.28$ ,  $df = 6$ ,  $p = 0.1584$ ). In 1998, statistically significant differences appeared among treatments ( $\chi^2 = 13.90$ ,  $df = 6$ ,  $p = 0.0308$ ), with

**Table 1.** Results from the failure-time analysis (LIFEREG procedure) for seedling survival after three years (Experiment 1, seeds sown in 1997). Treatments are Disturbed, Clipped and Control.

Variable	df	Estimate	s.e.	$\chi^2$	P
Intercept	1	4.37	0.26	285.40	0.0001
Treatment	1	-0.00	0.12	0.00	0.9994
Scale	1	1.78	0.07		

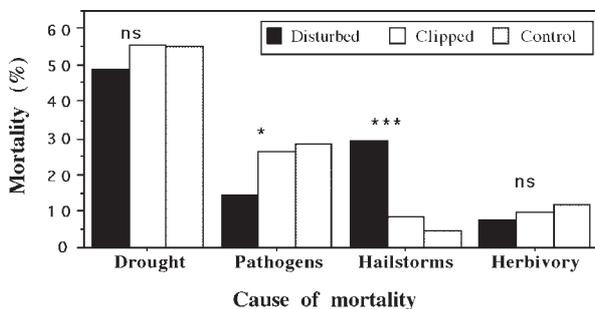
Log likelihood = - 656.77



**Fig. 1.** Percentage of seedling survival after three years for seeds planted at 1 cm depth in 1997 (Experiment 1).

the highest value in the Control (23.8%) followed by Clipped (19.8%) and Disturbed (16.2%) treatments.

The survival of seedlings from seeds planted in 1997 did not differ among treatments after 3 years (Table 1). The highest mortality was recorded during the first growing season (84.4%; see Fig. 1). After the second growing season the cumulative mortality reached 93.0% of the seedlings and 98.1% at the end of the experiment. Overall, we identified the cause of mortality for 95.9% of the seedlings, the main cause being summer drought (51.8%; Fig. 2), followed by pathogens (22.6%), hailstorms (13.9%) and herbivory (9.6%), with significant differences among causes ( $\chi^2 = 133.04$ ;  $df = 3$ ;  $p < 0.0001$ ; minor causes such as vole tunnels and frost heave were not considered in the analysis). Summer drought and herbivory had similar effects on all three treatments, whereas pathogens and hailstorms caused significant



**Fig. 2.** Causes of mortality after 3 yr for seedlings emerged in 1997 (Experiment 1). Comparisons among treatments were performed independently for any of the causes by using  $\chi^2$  (from 1.04 to 29.30,  $df = 2$ ; ns = non-significant; \* =  $p < 0.05$ ; \*\*\* =  $p < 0.001$ ). Herbivory corresponds to invertebrate and microvertebrate herbivory.

differences in mortality among the treatments (Fig. 2). For seeds planted in 1998, the mortality after the first growing season reached 94.1%, with no differences among treatments ( $\chi^2 = 2.15$ ;  $df = 2$ ;  $p = 0.3412$ ). At the end of the experiment, only three seedlings still survived (98.8% mortality), one per treatment. Overall, the cause of mortality was identified for 65.3% of the seedlings and, as for the 1997 trial, summer drought was the main cause, reaching 95.8%.

Growth parameters of seedlings did not differ among treatments after one or two growing seasons (i.e. stem length, leaf number and length of the largest leave for seedlings emerged in 1997;  $df = 2$ ; 47 for 1997 sampling;  $df = 2$ ; 26 for 1998 sampling;  $p > 0.05$  in all cases). Growth after 3 yr was not analysed due to the low number of surviving seedlings (six). Mean shoot length of these seedlings, pooled over all treatments, was  $28.3 \pm 7.0$  mm and mean dry shoot weight was  $0.11 \pm 0.04$  g.

### Experiment 2

Only five seedlings emerged in the uncaged plots (Table 2), which were omitted from further analysis; we found remains of seeds depredated by rodents and birds (separated seed coats or bitten seeds) in all plots. For the caged plots, significant differences appeared among treatments for seedling emergence ( $F = 35.68$ ;  $df = 2$ ; 52  $p < 0.0001$ ; one-way ANOVA). The highest value was recorded in the Disturbed treatment (55.5%), where the seeds were in direct contact with the mineral soil (Table 2). In Control and Clipped treatments many seeds had germinated and expanded the radicle over the ground for some days, but the majority desiccated and died before rooting.

## Discussion

### Seedling emergence

The results show that the probability of *Pinus sylvestris* seedling emergence in the meadows is extremely low under natural conditions. Values were below 1% in all treatments for surface-sown seeds (simulating natural dispersal), despite the fact that the seed rain assigned mimicked a mast year (Koski 1991). These low values can be explained in two ways. First, post-dispersal seed predators consumed most of the surface-sown seeds and consequently the emergence of seedlings was almost nil in uncaged plots. This implies that predation was a main factor constraining the encroachment of *Pinus*, which is in agreement with previous studies showing that rodents and birds consumed most of the dispersed *Pinus* seeds in the forests (Castro et al. 1999). Second, the herbaceous layer hampered seedling emergence for seeds protected

**Table 2.** Percentage emergence for surface-sown seeds in Experiment 2.

Treatment	Seedling emergence (%)	
	With predation	Predators excluded
Disturbed	0.0 ± 0.0	55.5 ± 3.2
Clipped	0.2 ± 0.2	17.2 ± 4.6
Control	0.8 ± 0.5	6.4 ± 1.8

against predators, decreasing emergence from 55.5% on exposed soil to 6.4% with an intact herbaceous layer.

The effect of the herbaceous layer, however, vanished when seeds were sown 1 cm deep; in that case emergence values were similar for all treatments. This, together with the pattern of emergence for surface-sown seeds, strongly suggests that the herbaceous layer constitutes a physical barrier against recruitment, which may result from two non-exclusive processes related to seed-soil contact. First, seed germination in the surface of the herbaceous layer may be hampered because hydraulic conductivity is lower than in the mineral soil (Hadas 1982). In fact, under non-saturated conditions (which prevail in Mediterranean mountain meadows), a layer of organic matter hampers the germination of *Pinus* seeds compared with rates on a mineral soil, whereas a slight burial that improves seed-soil contact increases the germination rate (Oleskog et al. 2000; see also Dolling 1996). Second, once a seed has germinated, the herbaceous layer may also block the radicle from reaching the mineral soil, resulting in seedling death by drying or depletion of reserves before reaching water and nutrients from the soil (e.g. Borchert et al. 1989). Many seeds that germinated in the Control and Clipped treatments in the surface-sown experiment expanded their radicle through the surface but died after a few days and before rooting, indicating that they were suspended too far above the soil. The formation of such a physical barrier, which is created by growing plants plus decomposed litter, might be particularly relevant for grassy areas located in environments characterized by a dry growing season and low winter temperatures. This decreases the rate of litter decomposition (Gallardo 2001), reinforcing the formation of a carpet of herbaceous vegetation and dry litter that hampers seed imbibition and seed-soil contact (Xiong & Nilsson 1999). The results indicate, therefore, that the contact of the seed with the mineral soil is a critical requirement for the establishment of *Pinus sylvestris* on Mediterranean mountain meadows (cf. Magee & Antos 1992; Prach et al. 1996).

### *Seedling survival and growth*

Seedling survival and growth were similar among treatments, i.e., gaps and the herb layer had a similar effect, suggesting that competition with the herbaceous vegetation may not be regarded as the reason of the lack of Scots pine encroachment on meadows. This could be related to an amelioration of microclimatic conditions provided by the herbaceous layer that counteract the negative effect of a possible interference (e.g. De Steven 1991; Ryser 1993; O'Connor 1995; Brown et al. 1998; Brown & Archer 1999), and in fact the herb layer provided protection against some mortality factors such as hailstorms (Fig. 2). On the other hand, seedling survival, although low, was comparable to the values obtained in these forests for seedlings located in sites other than meadows (Castro 2000) and, moreover, mortality rates above 95% are not rare for coniferous species growing in the Mediterranean mountain (Arista 1993; García 2001). The causes of mortality were also similar to those affecting seedlings in these mountains, with summer drought being the most important (Hódar et al. 1998; Castro 2000; Castro et al. 2002). Similarly, the growth after three growing seasons was comparable to the growth achieved by seedlings located in placements where they are able to recruit (basically under the canopy of nurse shrubs; Castro 2000). All this indicates that meadows do not particularly hamper seedling survival and performance. Lack of recruitment on these Mediterranean mountain meadows is therefore attributable to factors blocking recruitment before the seedling establishment stage.

### *Consequences for regeneration*

The recruitment of *Pinus sylvestris* seedlings in grassy meadows of these mountains is a process seriously constrained by a series of successive filters. First, seed dispersal is concentrated mostly around the parental trees (Castro et al. 1999) and meadows receive a low number of seeds. Second, seeds rarely escape predation (see also Castro et al. 1999). Third, seedling emergence requires gaps created by animal trampling, and these gaps are scarce and scattered throughout the meadows. Finally, seedlings suffer very high rates of mortality (Hódar et al. 1998; Castro 2000). Thus, seedling recruitment in the meadows relies on a high number of available seedlings. As a consequence, the combined effect of seed predation and physical impedance of the herbaceous layer reducing seedling emergence must be considered as the two main mechanisms limiting the colonization of meadows, thus limiting regeneration in these forests.

### Final considerations

This work reports that the herb layer mechanically impedes the establishment of a woody species in herbaceous stands, rather than acting through biotic interactions such as competition. Many studies have reported a similar physical barrier when considering the effect of the litter layer, both on woody and non-woody species (Pierson & Mack 1990; Facelli & Pickett 1991; Eriksson 1995; Herr et al. 1999; Vellend et al. 2000). However, a mechanical impediment has rarely been discussed in detail when the barrier is formed by herbaceous cover and particularly against woody species. This mechanism implies that (1) the recruitment limitation is not mediated by plant-plant interactions, but rather by a previous, physical process (Xiong & Nilsson 1999) and (2) that the limiting process occurs between seed dispersal and seedling emergence, a phase that has been scarcely considered in demographic studies. The scarcity of reports concerning a physical barrier created by a herbaceous layer could, in part, be due to the *a priori* assumption that the herbaceous carpet represents competition against seedling recruitment, a cue that might have detracted attention from other possible mechanisms. The barrier mechanism examined here may, therefore, be more common than generally believed, particularly in environments where, as in mediterranean areas, the herbaceous carpet loses most of its moisture before seedling emergence is achieved.

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