

Reproduction of postfire *Pinus halepensis* Mill. stands six years after silvicultural treatments

Jorge DE LAS HERAS^{a*}, Daniel MOYA^a, Francisco LÓPEZ-SERRANO^a, Sonia CONDÉS^b

^a Escuela Técnica Superior de Ingenieros Agrónomos de Albacete, Universidad de Castilla-La Mancha, Campus Universitario s/n, 02071, Albacete, Spain

^b Escuela Técnica Superior de Ingenieros de Montes, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, 28040, Madrid, Spain

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Abstract – In Spain, wildfires have increased during the last decades with *Pinus halepensis* forests being the most affected. Cone differentiation and the early flowering of this species in comparison to other native Spanish species, are traits considered as adaptations to postfire regeneration. The high recurrence of fires promotes a high increase in young and immature pine stands with low capability of regeneration. In this study, silvicultural treatments such as thinning and pruning were carried out 5 years after fire in eleven years old *P. halepensis* stands located in dry and semi-arid sites in SE Spain. The formation of male and female strobili, production of serotinous grey, mature brown and new green cones were recorded six years after treatments. Seed production and germination percentage were also tested. Results showed acceleration in cone and viable seed production in thinned plots, with some differences between sites being recorded. Serotinous cone production also increased as a result of this treatment.

Pinus halepensis / thinning / pruning / postfire / reproduction

Résumé – Reproduction de pinèdes de *Pinus halepensis* Mill. six ans après incendies et traitements sylvicoles. Les incendies forestiers sont en train d'augmenter ces dernières décennies en Espagne, et les forêts de *Pinus halepensis* sont les plus atteintes. Le fait qu'elles portent plusieurs types de cônes et la floraison précoce de cette espèce, par rapport aux autres espèces espagnoles, sont considérés comme des adaptations aux conditions post-incendie. La récurrence élevée d'incendies favorise un nombre croissant de jeunes pinèdes à faible potentiel de régénération. Des traitements sylvicoles tels que l'éclaircie et l'élagage ont été effectués sur deux peuplements de *P. halepensis* régénérés cinq ans après l'incendie (onze ans d'âge), situés dans une localité sèche et dans une autre semi-aride du sud-est de l'Espagne. La formation de strobiles masculins et féminins, la production de cônes sérolineux mûrs et récents furent enregistrées six ans après les traitements. La production de semences et le pourcentage de germination ont aussi été testés. Les résultats ont démontré une accélération de la production de cônes et de semences viables dans les clairières, bien que certaines différences aient été constatées entre les localités. La production de cônes sérolineux a augmenté à la suite de ce traitement.

Pinus halepensis / éclaircie / élague / post-incendie / reproduction

1. INTRODUCTION

Fire is considered as one of the major ecological factors that helped shape Mediterranean landscapes into the present mosaic-like regeneration and disturbance patterns [23, 36] as occurs in other climate regions with different coniferous forests [37]. In this sense, [20] discussed the dynamics of the landscape in a Mediterranean fire-prone area in Corsica: Forests expansion was more rapid in unburnt sites than in other areas affected by recurrent fires.

Fire is linked to some specific characteristics of the Mediterranean climate e.g. water stress, which influence the growth, survival and distribution of pine forest species [2]. It is widely accepted that the postfire recovery in Mediterranean plant communities is carried out by direct regeneration, i.e., the fast recovery of a plant community with the same species pool that it had immediately prior to disturbance even though

this theory has been reconsidered by [30] in several cases when results did not entirely support the direct regeneration model. After a great fire, the high pH conditions caused by ash inhibit the germination of many plants, thus helping to insure the establishment of sparse pine seedlings under the dead tree canopies, followed by rapid development without interference from other plants [8, 24]. Seed age is an important factor to consider in this process [28, 29].

Three main strategies are predominant in fire-prone environments: seedling, adult tolerance and resprouting [17]. In this sense, it is well known that Aleppo pine (*Pinus halepensis* Mill.) is a compulsory seeder [34] noted for its ability to grow in difficult environmental conditions. In the Mediterranean environment, Aleppo pine's marked drought resistance is especially important while provenances from less xeric sites displayed the strategy typical of drought tolerant species. *Pinus halepensis*, is a wind-dispersed Mediterranean serotinous tree, with xeriscence (seed release induced primarily by

* Corresponding author: jorge.heras@uclm.es

drying conditions not generated by fire) bearing intrinsic adaptive values, independent of those of pyriscence (fire-induced seed release [21, 22]). Thus, postfire *P. halepensis* strategies are based on sexual reproduction and seed development and are related to seed storage in long-closed cones within the plant canopy (serotiny [19, 32]) with postfire regeneration depending totally upon its canopy-stored seed bank [26]. These cones remain closed until exposed to high temperatures which melt their resin [32], so seed release usually occurs after a fire. Other cones are xeriscent and open after a variable drought period [21]. The scales of xeriscent seed-bearing pine cones move in response to changes in relative humidity, and the scales gape open when dry-releasing the cone seeds by means of a passive mechanism based on the structure of the scale [9]. Serotiny levels vary among and within pine populations, mainly depending on age and fire regime [33]. Frequent fires which kill all adult trees will favour serotiny [16, 19] especially if they affect large areas and there is little dispersal from adjacent unburnt areas [33]. The increase of forest fires during the last decades in Spain has increased the distribution area of *P. halepensis*, especially in the East part of the country, a phenomenon which also occurred in other areas of the Mediterranean Basin affected by fire [20]. The non-self pruning of branches and the high resin content increase the probability of canopy fires and consequent death of *P. halepensis* trees.

Both the natural and artificial expansion of *P. halepensis* stands along with the increase in the number of fires and burnt surface in Spain, has made appropriate forest management necessary during the early stages of the pine regeneration, since this regeneration is weak when a new fire occurs on forests covered by immature trees as occurs with other pine species in NE Spain such as *P. sylvestris* L. [11].

As noted in [13], stands should be thinned prior to the onset of severe between-tree competition if timber production is a high priority. From a cost benefit perspective, thinning during post-fire regeneration of *P. halepensis* is usually carried out from 4 to 6 years after fire in Spain due to the small size of saplings at this time. Thinning can be performed with a clearing saw (portable swinging arm scythe) since the more expensive use of the chain-saw is still not needed. Although effects of silvicultural treatments on pine growth [13] and on the accompanying vegetation [6] two years after treatments have been studied, effects of silvicultural treatments on the first stage of cone and seed production are currently not well known. In this sense [13] points out that silvicultural treatments including thinning improved the probability of cone production by a factor of 2.07 in relation to the control 22 months after treatment. However, no results have been given concerning effects on serotiny and seed viability. Some effects of pest attacks during the first year after treatments on these pine stands have been also studied [12].

In order to provide adequate information for foresters, this study has examined the effects of silvicultural treatments (carried out five years after fire and studied six years later) on pine stands reproduction.

2. MATERIALS AND METHODS

Two large fires occurred in mature *P. halepensis* forests in August 1994 in SE Spain. Total surface area burnt was about 44 000 ha in two different provinces (Albacete and Murcia). In each burnt zone a site with high regeneration density was selected: Yeste (2° 20' W 38° 22' S, elevation 1 010 m, Province of Albacete) and Calasparra (1° 38' W 38° 16' S, elevation 325 m, Province of Murcia). Average annual rainfall and temperature for the last thirty years were respectively: 530 mm and 33.01 °C in Yeste compared to 290 mm and 16.5 °C in Calasparra.

After fire, natural regeneration took place in both localities, reaching a very high seedling density: 5 116 trees/ha with a medium height of 105 cm in Yeste, and 46 000 trees/ha with a medium height of 51 cm in Calasparra five years after fire. In July 1999, experimental plots were laid out in each study site in order to conduct different silvicultural treatments (t: thinning to a density of 800 trees/ha; T: thinning up to 1 600 trees/ha; P: pruning up to half of the tree size; TP: a combination of pruning plus thinning up to 1 600 trees/ha). The selected final densities were selected due to those are commonly used by foresters in older pine forests of SE Spain. Each plot was 10 × 15 m² and, in order to avoid a border effect, a 6 m distance was kept between plots. In Yeste a total of 27 plots were installed in which 4 different treatments (t, T, P and TP) were conducted (5 replicates of every treatment). Initially a new treatment was also considered (scrubbing) although it was discarded from the present study due to its non significant effect on pine stand development [13]. Seven more plots were left untreated as control plots (C). In Calasparra, 21 plots were set out with three of the mentioned treatments (T, P and TP) and 5 replicates were considered in each case. Thinning up to 800 trees/ha (t) was not carried out in Calasparra due to the extreme dry conditions. Six more untreated plots were designed as controls (C). Silvicultural treatments were randomly assigned and carried out in plots.

Once silvicultural treatments were carried out, a total of 25 trees per plot (i.e. 1 600 trees/ha, the usual density in artificial regeneration) in T, P, TP and C were selected and tagged. In the t plots, 15 trees per plot were selected due to their lower density. In order to determine the early effects of the treatments on cone production, all the selected trees (1 170 saplings) were previously measured in 1999 and 2001, and the number of male and female cones (strobili) were also counted [13]. Male and female cones of the selected trees were all counted in February–March 2005 and fertilized cones from each of the selected trees were counted and grouped into three types: (N) new: cones not yet two years old with a small size and coloured in green; (M) mature brown: closed mature cones between two and three years old and coloured in brown. To estimate biometric characteristics of the cones, seed production and seed viability, three cones per type and plot were randomly selected; (S) serotinous: closed grey cones over three years old. Length and diameter of the cones, total number of seeds in each cone and the seed weight data were obtained. For opening the collected cones, there were arranged on a baking sheet and placed for 2 min in a conventional oven that has been pre-heated to 180 °C to break the resin bonds. After heating, the cones were kept at room temperature for 3–4 days until scales were fully open. Immediately after collection, seeds were sown in Petri dishes filled with sterilized humid-soil, placed in a greenhouse and kept at 21 ± 1 °C and 14-h photoperiod. Petri dishes were moistened with de-ionized water every 2 days. Germination was checked daily, with germinated seeds being removed. The germination test ended 35 days after sowing, when the germination rate was null. Empty seeds were

Table I. Average number of young cones for each treatment in both sites (Ye: Yeste and Ca: Calasparra). NMC: number of male cones; NMC/T: number of male cones per tree; NFC: number of female cones; NFC/T: number of female cones per tree. Small letters mean significant differences among treatments at $p < 0.05$.

| Site | Treat. | NMC | NMC/T | NFC | NFC/T |
|------|--------|------------------|----------------|-----------------|--------------|
| Ye | C | 453.3 ± 262.80a | 23.05 ± 14.60a | 92.33 ± 50.35a | 4.69 ± 2.70a |
| Ye | P | 689.33 ± 145.54b | 27.57 ± 5.80b | 63.33 ± 13.86c | 2.53 ± 0.55b |
| Ye | TP | 429.16 ± 376.10a | 22.58 ± 24.41a | 61.16 ± 31.99c | 3.21 ± 1.91b |
| Ye | t | 936.33 ± 375.88c | 72.0 ± 28.91c | 94.33 ± 32.0a | 7.25 ± 2.46a |
| Ye | T | 655.16 ± 369.51b | 26.20 ± 14.78b | 135.33 ± 69.72b | 5.41 ± 2.77a |
| Ca | C | 147.0 ± 171.52b | 5.80 ± 6.80b | 11.83 ± 4.79b | 0.47 ± 0.19b |
| Ca | P | 53.66 ± 48.56c | 3.15 ± 3.92c | 23.33 ± 18.58a | 1.57 ± 1.56a |
| Ca | TP | 159.33 ± 242.53b | 8.38 ± 18.99b | 14.33 ± 14.85b | 0.87 ± 1.20a |
| Ca | T | 305.50 ± 331.34a | 12.28 ± 13.53a | 39.50 ± 26.79a | 1.77 ± 1.10a |

Table II. Cone production for each treatment (mean percentage of trees with cones and cones/ha) and for each cone type (cones/ha; N: new; M: mature-brown and S: serotinous cones) in both sites (Ye: Yeste and Ca: Calasparra). Small letters mean significant differences among treatments at $p < 0.05$.

| Site | Treat. | % trees with cones | Total cones/ha | N | M | S |
|------|--------|--------------------|----------------|-------------|-------------|--------------|
| Ye | C | 38 ± 26a | 1355 ± 1210a | 178 ± 183a | 422 ± 564a | 755 ± 700a |
| Ye | P | 38 ± 15a | 1577 ± 934a | 422 ± 435a | 376 ± 234a | 777 ± 468a |
| Ye | TP | 38 ± 24a | 1888 ± 1916a | 355 ± 234a | 711 ± 621a | 822 ± 987a |
| Ye | t | 76 ± 7b | 5911 ± 2286c | 1200 ± 865c | 2178 ± 657b | 2533 ± 1289b |
| Ye | T | 52 ± 14b | 3455 ± 1783b | 622 ± 456b | 123 ± 34b | 1600 ± 1234b |
| Ca | C | 21 ± 12a | 666 ± 495a | 122 ± 112a | 388 ± 365a | 156 ± 86a |
| Ca | P | 33 ± 21a | 622 ± 504a | 200 ± 165a | 266 ± 654a | 156 ± 234a |
| Ca | TP | 25 ± 19a | 722 ± 621a | 145 ± 256a | 311 ± 546a | 267 ± 367a |
| Ca | T | 26 ± 18a | 944 ± 424b | 200 ± 78a | 355 ± 156a | 386 ± 567b |

determined by cutting and ungerminated but not empty seeds were submitted to the tetrazolium test (TZ) in order to determine the viability of those seeds. In the case of the TZ test, only those seeds that showed a significant respiratory activity (dark red) were considered as viable.

For all statistical tests, data were transformed using the log or $\sqrt{\text{arcsine}}$ transformation to meet the assumptions of normality and homoscedasticity. Tables and figures present untransformed data and standard error of the mean (\pm SE). A One-Way ANOVA was used to test differences. Fisher's Least Significant Difference (LSD) procedure was used to compare mean values. All statistical analyses were conducted using a critical p -value ≤ 0.05 .

3. RESULTS

3.1. Effects on young cones

In Yeste, the average number of male strobili showed significant differences among silvicultural treatments (Tab. I). The highest average number of male cones was obtained in the t treatment (936.33 ± 375.88) and the average number of male cones per tree was 72 ± 28.91 for this treatment. In the case of female cones, the highest average number was 135.33 ± 69.72

in T treatment and significant differences were also recorded for the average number of female cones per tree, with trees in the t plots having the highest value (7.25 ± 2.46). The lowest values of female cones number were obtained in P and TP plots.

In Calasparra, significant differences in the average number of cones were also obtained (Tab. I). The highest average numbers of male and female cones were obtained in T (305.5 ± 331.34 and 39.5 ± 26.79 respectively). Furthermore, the lowest values of male and female cones were recorded in P.

3.2. Effects on cones

In Yeste, number of cones/ha presented significant differences among thinning and the rest of treatments (Tab. II). In both cases (T and t treatments), the number of cones/ha and the number of cones per tree presented the highest values. These differences were also recorded for different cone types: the highest average values of S, N and M cones were obtained in T and t and in the case of mature cones (M) TP values were higher than those obtained in T.

In Calasparra, there were no such differences in the cone production (Tab. II), even though the highest number of

Table III. Average diameter (D, cm) and total length (L, cm) of the different cone types (N: New; M: Mature-brown and S: Serotinous cones) in both sites (Ye: Yeste and Ca: Calasparra). First small letter means significant differences among cone types at $p < 0.05$ and second letter means significant differences among treatments at $p < 0.05$.

| Site | Treat. | N | | M | | S | |
|------|--------|---------------|---------------|---------------|---------------|---------------|---------------|
| | | D | L | D | L | D | L |
| Ye | C | 3.06 ± 0.53aa | 5.81 ± 1.06ab | 3.45 ± 1.09ba | 5.91 ± 1.04ab | 2.88 ± 0.33aa | 5.75 ± 1.23aa |
| Ye | P | 2.84 ± 0.25ab | 5.19 ± 0.19ab | 3.17 ± 0.78ab | 5.55 ± 1.09ab | 3.05 ± 0.76ab | 5.25 ± 1.18ab |
| Ye | TP | 3.19 ± 0.41ba | 6.31 ± 1.04ba | 3.2 ± 0.79ba | 5.87 ± 1.38bb | 2.72 ± 0.37aa | 5.38 ± 1.36ab |
| Ye | t | 3.04 ± 0.34aa | 6.26 ± 1.14aa | 3.33 ± 0.77ba | 6.24 ± 1.03aa | 2.98 ± 0.42aa | 5.98 ± 1.19aa |
| Ye | T | 3.16 ± 0.38ba | 6.43 ± 1.27ba | 3.32 ± 0.93ba | 6.02 ± 1.08aa | 2.91 ± 0.37aa | 5.83 ± 0.97aa |
| Ca | C | 2.72 ± 0.37aa | 5.66 ± 1.34aa | 2.71 ± 0.74aa | 5.45 ± 1.42aa | 2.21 ± 0.38aa | 4.16 ± 1.24aa |
| Ca | P | 2.53 ± 0.80aa | 4.04 ± 1.72aa | 2.72 ± 0.53aa | 5.55 ± 1.55aa | 2.43 ± 0.55aa | 4.63 ± 1.09aa |
| Ca | TP | 3.13 ± 0.46bb | 7.20 ± 1.11bb | 2.17 ± 0.80ab | 4.22 ± 1.47ab | 2.67 ± 0.46ab | 5.58 ± 1.18ab |
| Ca | T | 2.90 ± 0.33ab | 6.33 ± 1.27ab | 2.84 ± 0.46aa | 5.92 ± 1.08aa | 2.35 ± 0.42aa | 4.50 ± 1.31aa |

Table IV. Mean number of seeds/cone and mean seed weight in each treatment and each site (Ye: Yeste and Ca: Calasparra). Small letters mean significant differences among treatments at $p < 0.05$.

| Site | Treat. | N | | M | | S | |
|------|--------|----------------|----------------|----------------|----------------|----------------|----------------|
| | | Number | Weight | Number | Weight | Number | Weight |
| Ye | C | 74.31 ± 17.04a | 0.011 ± 0.040a | 72.53 ± 21.04a | 0.01 ± 0.001a | 67.61 ± 24.45a | 0.013 ± 0.002a |
| Ye | P | 80.55 ± 6.85a | 0.012 ± 0.003a | 70.05 ± 23.0a | 0.013 ± 0.002a | 64.8 ± 13.1a | 0.014 ± 0.002a |
| Ye | TP | 90.33 ± 11.63a | 0.015 ± 0.005a | 73.60 ± 23.21a | 0.013 ± 0.004a | 61.50 ± 19.78a | 0.011 ± 0.003a |
| Ye | t | 63.00 ± 21.11a | 0.011 ± 0.003a | 81.77 ± 22.26a | 0.015 ± 0.001b | 90.30 ± 36.12b | 0.017 ± 0.005b |
| Ye | T | 72.75 ± 29.55a | 0.013 ± 0.002a | 70.30 ± 24.54a | 0.012 ± 0.001a | 61.30 ± 19.52a | 0.01 ± 0.003a |
| Ca | C | 62.05 ± 24.66b | 0.013 ± 0.02a | 54.35 ± 29.62a | 0.008 ± 0.002a | 63.76 ± 20.9b | 0.008 ± 0.001a |
| Ca | P | 55.88 ± 23.70a | 0.010 ± 0.001a | 41.71 ± 27.95a | 0.004 ± 0.03a | 48.0 ± 21.50a | 0.009 ± 0.003a |
| Ca | TP | 62.0 ± 23.1a | 0.012 ± 0.003a | 37.33 ± 15.57a | 0.008 ± 0.004a | 43.53 ± 19.11a | 0.008 ± 0.001a |
| Ca | T | 69.23 ± 22.40a | 0.013 ± 0.002a | 63.23 ± 18.50b | 0.014 ± 0.011b | 42.87 ± 22.52a | 0.012 ± 0.001b |

total cones/ha was obtained in T. When different cone types were considered, only significant differences were shown for S cones in T ($386 \pm 567/\text{ha}$).

As for cone size (diameter \times length), significant differences were obtained for cone diameter in P plots in comparison to those recorded in the other treatments, in Yeste (Tab. III). In the case of S cones, the highest average size was obtained in t plots ($2.98 \pm 0.42 \text{ cm} \times 5.98 \pm 1.19 \text{ cm}$), in the case of N cones, the highest size was obtained in T ($3.16 \pm 0.38 \text{ cm} \times 6.43 \pm 1.27 \text{ cm}$) and in the case of M cones, this was obtained in t ($3.33 \pm 0.77 \text{ cm} \times 6.24 \pm 1.03 \text{ cm}$).

In Calasparra (Tab. III), the biggest cones were recorded in TP ($2.67 \pm 0.46 \text{ cm} \times 5.58 \pm 1.18 \text{ cm}$) for S cones, TP ($3.13 \pm 0.46 \text{ cm} \times 7.2 \pm 1.11 \text{ cm}$) for N cones and T ($2.48 \pm 0.46 \text{ cm} \times 5.92 \pm 1.08 \text{ cm}$) for M cones.

3.3. Effects on seeds

The number of seeds collected in the cones varied significantly with treatments. Thus, in Yeste (Tab. IV) the average number of seeds in the S and M cones was significantly higher

in t (90.3 ± 36.12 and 81.77 ± 22.26 respectively) whereas in the N cones, the highest value was recorded in TP plots. In Yeste, significant differences were noted in relation to seed weight in S and M cones from t plots in relation to the other treatments.

In Calasparra (Tab. IV), the highest average seed number in S and N cones were recorded in C plots (63.76 ± 20.9 and 62.05 ± 24.66), whereas in the M cones, significant differences were noted in the average number of seeds per cone in T plots (63.23 ± 18.5). Average seed weight was significant higher in S and M cones from T plots in relation to the other treatments.

Seed germination reached high percentage levels in Yeste, especially in C, P, TP and T (Fig. 1), and in the three cone types. However, in t treatment seed germination of both N and M cones, showed significant lower percentage values ($65.32 \pm 16.4\%$ and $50.45 \pm 15.34\%$ respectively). Ungerminated seeds showed significant differences with respect to viability in this locality (Fig. 2). Viable ungerminated seeds were significantly abundant in O cones for most treatments.

In general, seed germination reached lower values in Calasparra than in Yeste, primarily in the case of N cone seeds (Fig. 3) and no significant differences were recorded among

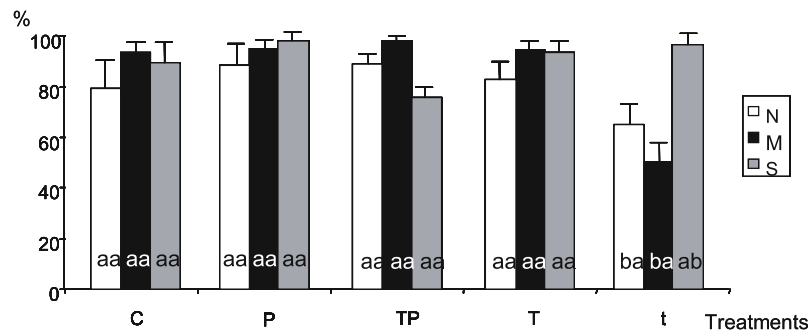


Figure 1. Final germination percentage of seeds from different cone types (N: new; M: mature-brown; S: serotinous) for each silvicultural treatment in Yeste. First letter means significant differences among treatments at $p < 0.05$. Second letter means significant differences among cone types at $p < 0.05$.

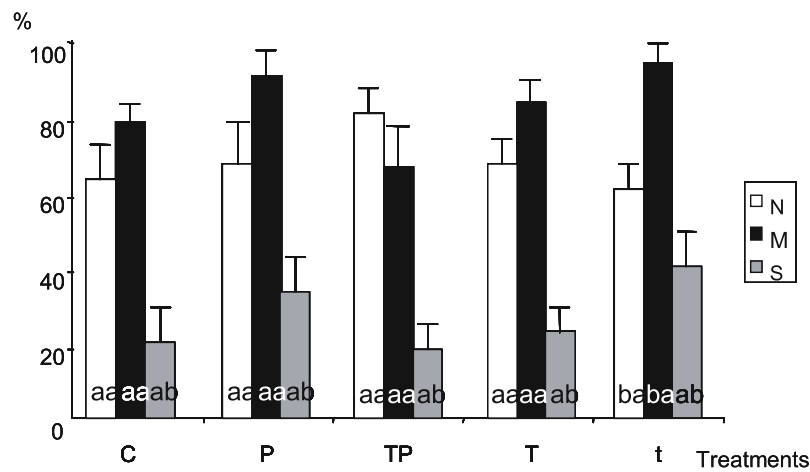


Figure 2. Tetrazolium test (% viable seeds) at the end of the germination test for seeds from Yeste. First letter means significant differences among treatments at $p < 0.05$. Second letter means significant differences among cone types at $p < 0.05$.

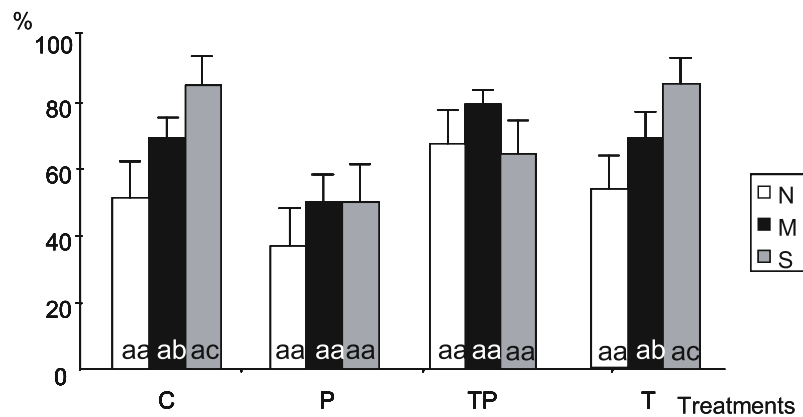


Figure 3. Germination percentage of the different cone types (N: new; M: mature-brown; S: serotinous) for each silvicultural treatment in Calasparra. First letter means significant differences among treatments at $p < 0.05$. Second letter means differences among cone types at $p < 0.05$.

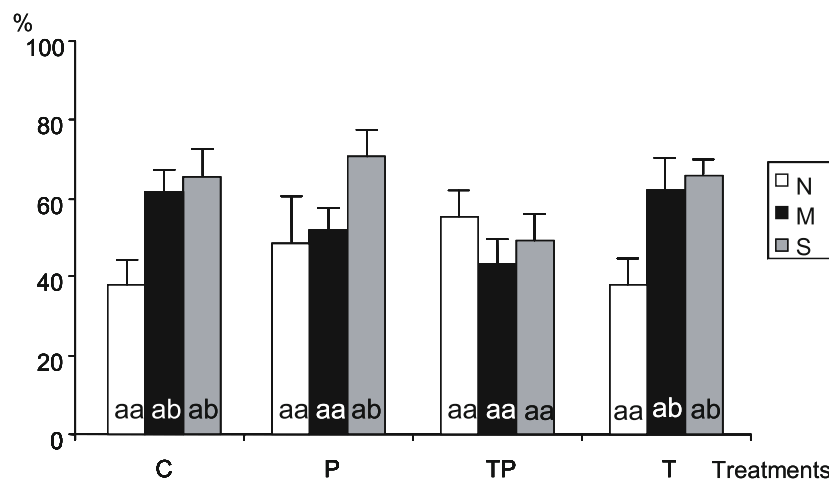


Figure 4. Tetrazolium test (% viable seeds) at the end of the germination test for seeds from Yeste. First letter means significant differences among treatments at $p < 0.05$. Second letter means differences among cone types at $p < 0.05$.

treatments. Ungerminated seed viability did not present significant differences among treatments in Calasparra and showed lower percentage values than in Yeste (Fig. 4).

4. DISCUSSION

As it is well known, age to first reproduction in Aleppo pine trees depends on several factors such as density and site quality [31]. Early flowering is an important adaptation to fire: the sooner cone production starts, the sooner a large canopy seed bank is formed [32]. In general, small trees start as females and later become monoecious (at the age of 13 years, [31]). In the plots studied, at the age of 5–7 years, all cones presented were female [13] but no significant differences among treatments were recorded due to the short period which lapsed after the treatments. However, in the present study P, T and t plots showed significant differences in the average number of male cones in comparison to those obtained in the untreated (C) plots, in Yeste. In general, flowering in crowded trees occurs later than in isolated ones [25] and thinning promote a significant increase in cones. Furthermore, the majority of male strobili are located in the lower part of the trees [10] and early pruning could produce a selective elimination of these strobili, even though the average number of male strobili and the number of cones per tree were significantly higher in P plots in comparison to C, in Yeste. In the case of the semi-arid locality, effects of treatments were not so significant and thinning promoted a great increase in male and female strobili. In this site, pruning affected negatively the production of male cones.

The preliminary study on cone production by [13] showed that two years after treatments there were no differences between sites. However, both the percentage of trees bearing cones and the number of cones/ha were higher in Yeste than in Calasparra. In both sites, the highest values of cones/ha were recorded in thinned plots (t and T). These results mean that a decrease in tree density in the early stands promotes a higher cone production. When the different cone types are compared,

trees in the thinned plots bore the highest number of serotinous cones in both sites. Cone production is influenced by crown development and tree class or canopy position [1,5] and the level of serotiny decreases as tree height increases [16]. The high level of serotiny in short trees could be explained by selection to increase chances of regeneration after burning at a pre-mature age. In thinned plots, the increase in tree height during the two first years after fire [13] is linked to a high production of serotinous cones in dry and semi-arid sites. The cone size also varied depending on treatments and site. In general, a reduction in density promoted bigger cones. This is important because small cones abortion use to be higher than that of well developed cones [14]. The number of seeds per cone increased in serotinous (S) and mature brown cones (M) in thinned plots in Yeste. However, in Calasparra C plots reached the highest values for S and N cones. The development of fertilized strobili may have been delayed until the trees could produce sufficient pollen themselves, especially in great fires with high vegetation mortality [32]. However, with early silvicultural treatments such as thinning, fertilized cones and seed production can be accelerated. In relation to seed weight, larger seeds could have a higher chance of surviving wildfires and producing more vigorous seedlings with a lower death rate [7]. In this study, it has been shown that thinning promoted the highest weight values of seeds of serotinous and mature brown cones in both sites.

The high production of mature and serotinous cones and viable seeds will promote high values of seedling density and survival during the second postfire year and ensure the future constitution of a very dense forest [4, 5]. Furthermore, when seed dispersion occurs after a great fire, the combined effect of heat exposure and ash cover reduces the germination [18, 27]. For these reasons it is very important to know if the cone crop is linked to a high production of viable seeds. In Yeste, the lowest percentage of germination was registered in seeds from N and M cones in the t plots, whereas in the other treatments and cone types, the germination percentage was high (> 75%) and similar. As the cone response to opening is linked

to the germination response of *P. halepensis* seeds with those from serotinous cones being more tolerant to fire related factors [15], the high germination average of serotinous cones in all treatments will ensure a great amount of seedlings during the second year after a new fire, although the timing of emergence and establishment of *P. halepensis* seedlings is correlated with the prevailing meteorological conditions [3, 4]. In the semi-arid site (Calasparra), the average percentage of germination was in general not so high but the serotinous cones bore seeds with the highest germination percentage in T plots (similar to that of the control). If we take into account the significantly higher seed production in thinned plots, ecological results will be similar to those mentioned above for Yeste, in the case of a new fire. Finally, the viability (TZ test) of non germinated seeds from serotinous cones was significantly low in Yeste. The majority of the seeds produced in these cones will disseminate and germinate in a very short time period (a few weeks after a new fire), whereas the remaining seed dissemination will occur over a longer time period.

In conclusion, silvicultural treatments could be an adequate tool for the management of early postfire *P. halepensis* stands. A decrease in pine stand density five years after fire, promoted a very early flowering of female strobili that produced a high number of cones with a large amount of viable seeds, 11 years after fire. The proportion of serotinous cones also increased with thinning both in dry and semi-arid conditions, and the pine forest could regenerate after a new fire when 7–8 years have lapsed since the previous one.

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REFERENCES

- [1] Brender E.V., McNab W.H., Loblolly pine seed production in the lower Piedmont under various harvesting methods, *J. For.* 70 (1972) 345–347.
- [2] Calamassi R., Della Rocca G., Falusi M., Paoletti E., Strati S., Resistance to water stress in seedlings of eight European provenances of *Pinus halepensis* Mill., *Ann. For. Sci.* 58 (2001) 663–672.
- [3] Daskalakou E.N., Thanos C.A., Aleppo pine (*Pinus halepensis*) postfire regeneration: the role of canopy and soil seed banks, *Int. J. Wildland Fire* 6 (1996) 59–66.
- [4] Daskalakou E.N., Thanos C.A., Postfire regeneration of Aleppo pine. The temporal pattern of seedling recruitment, *Plant Ecol.* 171 (2004) 81–89.
- [5] Daniel P.W., Helms U.E., Baker F.S., Principles of silviculture, McGraw-Hill, New York, 1979, 500 p.
- [6] De las Heras J., González-Ochoa A.I., López-Serrano F., Simarro M.E., Effects of silvicultural treatments on vegetation after fire in *Pinus halepensis* Mill. woodlands (SE Spain), *Ann. For. Sci.* 61 (2004) 661–667.
- [7] Escudero A., Núñez Y., Pérez-García F., Is fire a selective force of seed size in pine species? *Acta Oecol.* 21(2000) 245–256.
- [8] Eshel A., Henig-Sever N., Ne'eman G., Spatial variation of seedling distribution in an east Mediterranean pine woodland at the beginning of post-fire succession, *Plant Ecol.* 148 (2000) 175–182.
- [9] Evershed R.P., van Bergen P.F., Peakman T.M., Leigh E.C., Horton M.C., Edwards D., Biddle M., Kjølbye-Biddle B., Rowley-Conwy P.A., How pine cones open, *Nature* 390 (1997) 668.
- [10] Gil L., Aránzazu M., Los pinos como especies básicas de la restauración forestal en el medio mediterráneo, *Ecología* 7 (1993) 113–125.
- [11] González J.R., Pukkala T., Palahí M., Optimising the management of *Pinus sylvestris* L. stand under risk of fire in Catalonia (north-east of Spain), *Ann. For. Sci.* 62 (2005) 493–501.
- [12] González-Ochoa A.I., de las Heras J., Effects of post-fire silvicultural practices on *Pachyrhinus squamosus* defoliation levels and *Pinus halepensis* Mill. growth, *For. Ecol. Manage.* 167 (2002) 185–194.
- [13] González-Ochoa A.I., López-Serrano F.R., de las Heras J., Does post-fire forest management increase tree growth and cone production in *Pinus halepensis*? *For. Ecol. Manage.* 188 (2004) 235–247.
- [14] Goubitz S., Werger M., Shmida A., Ne'eman G., Cone abortion in *Pinus halepensis*: the role of pollen quantity, tree size and cone location, *Oikos* 97 (2002) 125–133.
- [15] Goubitz S., Werger M., Ne'eman G., Germination response to fire-related factors of seeds from non-serotinous and serotinous cones, *Plant Ecol.* 169 (2003) 195–204.
- [16] Goubitz S., Nathan R., Roitemberg R., Shmida A., Ne'eman G., Canopy seed bank structure in relation to: fire, tree size and density, *Plant Ecol.* 173 (2004) 191–201.
- [17] Keeley J.E., Zedler P.H., Evolution of life histories in *Pinus*, in: Richardson D.M. (Ed.), *Ecology and Biogeography of Pinus*, Cambridge University Press, Cambridge, 1998, pp. 219–251.
- [18] Izhaki I., Henig-Sever N., Ne'eman G., Soil seed banks in Mediterranean Aleppo pine forests: the effect of heat, cover and ash on seedling emergence, *J. Ecol.* 88 (2000) 667–675.
- [19] McMaster G.S., Zedler P.H., Delayed seed dispersal in *Pinus torreyana* (Torrey pine), *Oecologia* 51 (1981) 62–66.
- [20] Mouillot F., Ratte J.P., Joffre R., Mouillot D., Rambal S., Long-term forest dynamic after land abandonment in a fire prone Mediterranean landscape (central Corsica, France), *Landsc. Ecol.* 20 (2005) 101–112.
- [21] Nathan R., Safriel U., Noy-Meir I., Schiller G., Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree, *J. Ecol.* 87 (1999) 659–669.
- [22] Nathan R., Ne'eman G., Spatiotemporal dynamics of recruitment in Aleppo pine (*Pinus halepensis* Mill.), *Plant Ecol.* 171 (2004) 123–137.
- [23] Naveh Z., The role of fire and its management in the conservation of Mediterranean ecosystems and landscapes, in: Moreno J.M., Oechel W.C. (Eds.), *The role of fire in Mediterranean type ecosystems*, Springer-Verlag, New York, 1994, pp. 163–186.
- [24] Ne'eman G., Lahav H., Izhaki I., Spatial pattern of seedlings 1 year after fire in a Mediterranean pine forest, *Oecologia* 91 (1992) 365–370.
- [25] Ne'eman G., Regeneration of natural pine forest-review of work done after the 1989 fire in Mount Carmel, Israel, *Int. J. Wildland Fire* 7 (1997) 295–306.

- [26] Ne'eman G., Goubitz S., Nathan R., Reproductive traits of *Pinus halepensis* in the light of fire. A critical review, *Plant Ecol.* 171 (2004) 69–79.
- [27] Núñez M.R., Calvo L., Effect of high temperatures on seed germination of *Pinus sylvestris* and *Pinus halepensis*, *For. Ecol. Manage.* 131 (2000) 183–190.
- [28] Reyes O., Casal M., The influence of seed age on germinative response to the effects of fire in *Pinus pinaster*, *Pinus radiata* and *Eucalyptus globulus*, *Ann. For. Sci.* 58 (2001) 439–447.
- [29] Reyes O., Casal M., Seed germination of *Quercus robur*, *Q. pyrenaica* and *Q. ilex* and the effects of smoke, heat, ash and charcoal, *Ann. For. Sci.* 63 (2006) 205–212.
- [30] Rodrigo A., Retana J., Pico F.X., Direct regeneration is not the only response of Mediterranean forests to large fires, *Ecology* 85 (2004) 716–729.
- [31] Shmida A., Lev Yadun S., Goubitz S., Ne'eman G., Sexual allocation and gender segregation in *Pinus halepensis*, *P. brutia*, and *P. pinea*, in: Ne'eman G., Trabaud L. (Eds.), *Ecology, biogeography and management of Pinus halepensis and P. brutia forest ecosystems in the Mediterranean Basin*, Backhuys Publishers, Leiden, 2000, pp. 91–104.
- [32] Tapias R., Gil L., Fuentes-Utrilla P., Pardos J.A., 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 (2001) 629–638.
- [33] Tapias R., Climent J., Pardos J.A., Gil L., Life histories of Mediterranean pines, *Plant Ecol.* 171 (2004) 53–68.
- [34] Trabaud L., Grosman J., Walter T., Recovery of burnt *Pinus halepensis* Mill. forest. I. Understorey and litter phytomass development after wildfire, *For. Ecol. Manage.* 12 (1985) 269–277.
- [35] Trabaud L., Michels C., Grossman J., The recovery of burned *Pinus halepensis* Mill. forests. II. Pine reconstitution after wild-fire, *For. Ecol. Manage.* 13 (1985) 167–179.
- [36] Trabaud L., Christensen N., Gill A.M., Historical biogeography of fire in temperate and Mediterranean ecosystems, in: Crutzen P., Goldammer J.C. (Eds.), *Fire in the environment: The ecological, atmospheric and climatic importance of vegetation fires*, John Wiley, New York, 1993, pp. 277–295.
- [37] Urretavizcaya M.F., Defossé G.E., Gonda H., Short-term effects of fire on plant cover and soil conditions in two *Austroriparian chilensis* (cypress) forests in Patagonia, Argentina, *Ann. For. Sci.* 63 (2006) 63–71.