New Forests (2014) 45:53–70
DOI 10.1007/s11056-013-9391-7

Predicting time-windows for full recovery of postfire regenerating *Pinus halepensis* Mill. forests after a future wildfire

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Received: 24 January 2013 / Accepted: 3 October 2013 / Published online: 13 October 2013

Abstract A regeneration predictor (RP) has been elaborated to forecast the minimal inter-fire period, required for full recovery (assumed at 1,000 mature stems ha^{-1}, a typical value for a dense pine forest) of an even-aged, postfire regenerating *Pinus halepensis* population after a subsequent wildfire, in the future. The study has been conducted in three Aleppo pine forests of northern Euboea Island, Greece. Postfire field surveys of sapling growth, sapling density and reproductive dynamics (cone-bearing population fraction, annual cone and seed production per sapling, canopy seed bank build-up) were carried out for three, consecutive growing seasons (years). Additional postfire parameters, with values estimated from literature data, have been also included in order to devise the RP. In the cases of the three populations studied, the application of this RP provides time-windows for full recovery after a recurrent fire, as short as 10–15, 8–11 and 7–11 years, respectively (values corresponding to best and worst scenarios). It is suggested that in even-aged, postfire regenerating Aleppo pine populations, the minimal inter-fire period required for full recovery can be predicted by monitoring a few selected variables, namely (a) sapling density, (b) vegetative to reproductive shift dynamics, and (c) cones/sapling and germinable seeds/cone, for at least 2 years (either consecutive or 2–3 years apart) at a postfire age of 7–12 years.

Keywords Postfire regeneration · Sapling density · Reproductive shift · Cone and seed production

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Introduction

Fire is generally acknowledged as a major ecological factor that shaped the Mediterranean landscape, on the one hand, and affected the genus of pines during its evolution, on the other (Keeley and Zedler 1998; Tapias et al. 2004). Afforestation with *Pinus brutia* Ten., *P. halepensis* Mill., *P. pinaster* Ait. and *P. pinea* L. as well, in addition to human changes in land-use practices, notably those affecting fire regime, have greatly influenced the distribution of pine forests in the Mediterranean Basin (Richardson et al. 2007).

Aleppo pine is an obligate reseeder, usually killed by typical wildfires, and has thus evolved several adaptive, regeneration mechanisms in response to the 'catastrophic' fire events (e.g. Daskalakou and Thanos 1996; Thanos and Daskalakou 2000). Species survival depends on a powerful regenerative capacity through seedling recruitment, based on both the annual production of prolific seed crops and the safeguarding of a fraction of them in the canopy seed bank, within bradychorous (serotinous) cones (Daskalakou and Thanos 1996; Goubitz et al. 2003). Thus, the canopy seed bank is of paramount importance for the postfire regeneration, while soil seed banks are both transient and fully destroyed by fire (Daskalakou and Thanos 1996).

An important parameter of the overall postfire regeneration capacity of a pine population, especially at relatively high fire frequencies, is the duration of the juvenile stage. The Mediterranean pines, *P. pinea* (Francini 1958), *P. halepensis* and *P. brutia* (Panetsos 1981) require almost three calendar years to complete their reproduction cycle. In *P. halepensis*, the initiation of female conelets was reported to take place during summer or early fall (Francini 1958). Pollination takes place next spring, from March to April, whereas fertilization occurs only in the spring of the following year, and by the end of that growth season, the green-coloured cones have almost attained their full size. Seeds ripen during the third spring and cones mature and turn brown by the end of season. Cone opening and subsequent seed dispersal may start, depending on weather conditions, namely high temperature and low humidity, late in spring and usually early in summer. Seed release is induced either by fire or by drying atmospheric conditions, and in both cases most seeds travel short distance, less than 30 m; however, the latter may be associated with strong winds, thus long-distance dispersal is more likely to occur in the absence of fire (Nathan and Ne'eman 2004). After seed dispersal, germination is restricted to late autumn-early winter, resulting in postfire seedling recruitment early in the rainy season of the Mediterranean climate; the timing of emergence and establishment of Aleppo pine seedlings was found to be correlated with the prevailing meteorological conditions—mainly rainfall and to a lesser degree temperature (Daskalakou and Thanos 2004).

The juvenile stage of an even-aged Aleppo pine population may end at an age of 3–6 years for a small fraction of the population (Thanos et al. 1998) while and is estimated that the entire population has turned reproductively mature after 12–20 years (Thanos and Daskalakou 2000). In even-aged populations, larger individuals begin their reproduction earlier than smaller ones when a height of 1–1.5 m is attained (Ne'eman et al. 2004). Furthermore, a 15-year old postfire *P. halepensis* population in SE Spain had already developed a large canopy seed bank ($3 - 100 \times 10^4$ seeds ha^{-1}) while cone bearing has been reported to start quite early, at 5 (Tapias et al. 2001) or 7 years (Eugenio et al. 2006) of age, and the vast majority of them, ca. 86 %, were maintained closed. A dramatically high degree of serotiny, ca. 95 % has been already reported elsewhere (Thanos and Daskalakou 2000) and constitutes a noteworthy, adaptive feature of the early reproducing pines. Fire recurrence at intervals shorter than 17 years resulted in resilience loss for *P. halepensis* (Eugenio 2006); therefore, thinning in fire regenerated forests has been proposed for younger stands (10 years old), as it shortens the juvenile, non-reproductive period and greatly increases the number of cones produced per pine in completely serotinous individuals (Verkaik and Espelta 2006).

The aim of this study is the development of a predictive tool for full postfire recovery of an Aleppo pine population by combining actual monitoring of reproductive dynamics in three young, postfire, even-aged (7–12 years old) Aleppo pine populations in northern Euboea Island, Greece as well as a number of parameters and estimators obtained by previous bibliographic results and observations. Thus, this tool, named the regeneration predictor (RP), is compiled by the actually measured (or mathematically extrapolated) reproductive potential, i.e. available seeds per surface unit area after a recurrent fire, and a regeneration factor (RF) that includes the estimators mentioned above. The overall goal is to estimate the time window of the minimal interfire period required for full recovery after a second wildfire, on the basis of a density value of stems per hectare for the mature forest resulting after the future fire. In the present study, that value is set at 1,000 stems ha^{-1}; however, different density values may be applied to the tool. From the applied point of view, this tool may prove useful for both forest ecologists and forest managers. It is well known that a second wildfire at an immature, regenerating stage results in a more or less severe forest degradation. Therefore, the application of the RP may provide the managers with a prioritization tool which could discriminate between immature Aleppo pine populations, in need of strict protection against a second fire event and young forests that have already attained a natural regeneration capacity, satisfactory for full postfire recovery.

Materials and methods

Pinus halepensis Mill. (Aleppo pine) is the dominant, low-altitude Mediterranean, pine tree of Greece and its forests cover a significant fraction, i.e. 26 % of the Greek coniferous forests. Forest fire statistics for Greek forests show an increasing tendency of the total burnt area that accounts for 28,363 burned ha year^{-1} for the period 1996–2005. The above total burnt area mostly includes pine forests, a situation aggravated by recent (e.g. 2007) catastrophic wildfires. Alternatively, the mean reforested area is diachronically reduced to 1,737 ha year^{-1} for the same period (Hellenic Ministry of Environment and Climate Change 2010). Certain rehabilitation processes, e.g. snag removal, log dam creation against soil erosion, reforestation and strict protection measures against grazing and land use changes are selectively applied, taking into consideration, several perspectives for dryland restoration, proposed under the predicted climate change scenarios (Vallejo et al. 2012). Nevertheless, an intensive early thinning of postfire naturally regenerated, young Aleppo pine stands has been recommended, aiming at carbon storage, growth improvement, seed production and biodiversity (De Las Heras et al. 2013). Therefore, natural regeneration is by far the most important process for the restorative management of the frequently burnt Aleppo pine forests, although a cost-benefit output analysis of postfire management operations and particularly salvage logging evaluation (Leverkus et al. 2012) is further needed.

Study site

The research was carried out in the northern part of Euboea Island (Fig. 1), at three different sites close to the villages of Gouves, Rovies and Pili, burnt in 1994, 1996 and 1997, respectively (Table 1). Euboea is the second largest island of Greece; it hosts a rich flora (Trigas et al. 2008) and extensive forests (53.4 % of total surface). Almost one-fifth of these forests correspond to mature Aleppo pine forests, with a remarkable distribution of 44,277 ha in the northern part of the island (Hellenic Ministry of Agriculture 1992).

Experimental plots

Initially, the national wildfire database was searched and evaluated, aiming at the discovery of the severe last decade's Aleppo pine fires, expanded in northern Euboea Island. Consequently, several burned areas, always larger than 50 ha, were investigated and then confirmed by the Local Forest Department. As regards naturalness, i.e. forests in considerable distances from residential areas, and burned forest size as well, Gouves, Rovies and Pili were selected, accounting for 922, 71.7 and 1,689.6 burned ha, respectively. During summer of 2004, the most representative, young and naturally regenerated *P. halepensis* populations were selected (Table 1), taking into consideration soil parent material (Soil Map of Greece 1984), aspect, altitude and predicted minor human land-use changes. Plot coordinates were taken using global positioning system (GPS).

Four permanent experimental plots (I–IV), 1 ha each, were established at randomly selected sites in each of the three burnt Aleppo pine forests. Extensive field measurements of individual growth (height, canopy size) and reproductive capacity ($n = 500$ randomly selected saplings in each burnt forest, data not presented in this study) were obtained twice yearly (May and October) for three successive growing seasons (2004–2006). For more reliable estimations, 50 pine saplings in each of the plots I and III, i.e. a total of 300 for the three forests, were randomly selected and tagged for long-term monitoring, along a transect 50 m long by 1 m wide. Tagged saplings were also classified into reproductive, i.e. already bearing cones and non-reproductive, namely the juvenile ones, without cones on their canopy.

Postfire sapling density was recorded in two transects per plot, each 25 m long and 1 m wide, laid out along the slope contour (as in Eugenio et al. 2006); thus, sapling density was estimated from a total area of 200 m^2 for each population. Measurements were taken only once, in 2005, as no pine sapling mortality was ever observed throughout the 3-year-long study period.

Due to the absence of meteorological stations in the vicinity of the areas studied, air temperature and relative air humidity were monitored every 10 min with HOBO Pro RH/Temp H08-032-08 data loggers (Onset Computer Corporation, USA) for the entire 3-year-long study period. Data loggers, one for each forest, were mounted on the central stem of a representative pine sapling, at a height about 1.3 m where they were partly shaded by the sapling canopy. Daily values were computed from raw data (144 values/day). For the entire period 2004–2006, the overall mean of the recorded temperature and relative air humidity values were 15.5, 16.8 and 15.9 °C and 75.6, 70.3 and 74.0 % in Gouves, Rovies and Pili, respectively. The meteorological stations closest to the study plots are Agriovotano M.S., Aidipsos M.S. and Kimi M.S., respectively. The long-term annual values obtained from these stations are: rainfall 675, 574 and 1,032 mm and mean air temperature 15.8, 18.0 and 16.0 °C, respectively (Trigas 2003). Therefore, the recorded temperatures in these areas are remarkably similar to those recorded in the nearest meteorological stations. Moreover, in all three forests, a typical Mediterranean climate prevailed during the period July 2004–June 2006, with dry and hot summers and mild and wet winters.

Regeneration potential measurements

The reproductive dynamics, i.e. cones produced by young saplings, was measured in all three postfire Aleppo pine populations, aiming at the quantitative and qualitative

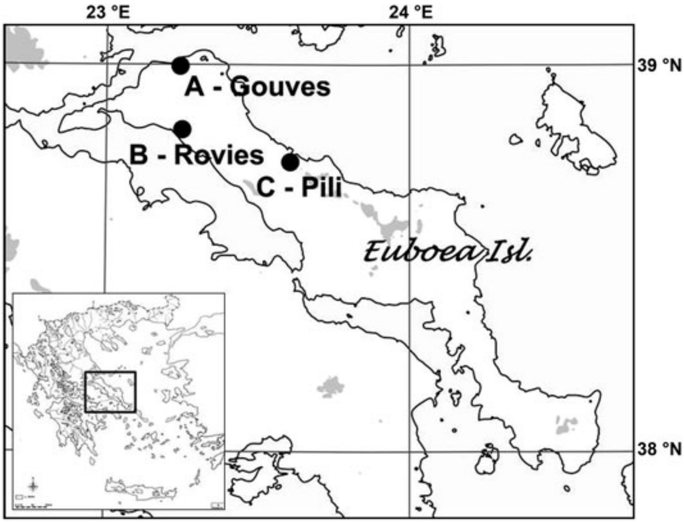


Fig. 1 Map of Euboea Island showing the locations of the 3 sites investigated. *Inset* in the *left bottom* corner: a map of Greece

Table 1 Plot characteristics

Forest—year burned (surface)	Site	Coordinates		Aspect	Altitude (m asl)
		Latitude	Longitude		
A Gouves—1994 (922 ha) Terrestrial deposits, mainly limestone, none erosion, moderate slope, N & S aspects	I	N39°00.065′	E23°15.443′	N	142
	II	N39°00.019′	E23°15.496′	S–SE	122
	III	N38°59.948′	E23°15.658′	E–SE	110
	IV	N39°00.000′	E23°16.147′	W–SW	142
B Rovies—1996 (72 ha) Terrestrial deposits, mainly limestone, none and moderate erosion, gentle slopes, N & S aspects	I	N38°47.403′	E23°15.636′	N	61
	II	N38°47.410′	E23°15.781′	N–NW	69
	III	N38°47.647′	E23°15.687′	E–SE	141
	IV	N38°47.709′	E23°15.594′	W–SW	138
C Pili—1997 (1,690 ha) Igneous rocks, mainly serpentinite and ophiolite, moderate erosion, moderate and steep slopes, various aspects	I	N38°44.917′	E23°34.794′	N	172
	II	N38°44.525′	E23°34.371′	N–NW	181
	III	N38°43.952′	E23°33.491′	W–SW	282
	IV	N38°43.781′	E23°33.872′	S–SE	174

estimation of *P. halepensis* seed production, in regard to estimating the potential natural regeneration after a future fire. Mature, brown coloured, closed cones were collected during summer, from randomly selected, each year, saplings in all three populations, and for three consecutive study years; their morphometric characteristics, namely mass, length and width were quantified in the laboratory (Table 2). Cone opening and seed extraction were achieved by a mild thermal treatment of cones, in an oven, at 48 °C for 2 days. After cone opening, the morphologically sound seeds per cone were counted, weighed and separated from the aborted or abnormally developed seeds (Fig. 4). The extracted sound seeds were used in germination tests.

Table 2 Cone and seed biometrics

Cone collection—postfire year	Cone mass (g)	Cone width (cm)	Cone length (cm)	Number of seeds/cone	Mean seed mass (mg)
A—Gouves					
10	21.8 ± 0.6	3.0 ± 0.0	6.4 ± 0.1	1–84	14.7
11	25.4 ± 0.2	3.1 ± 0.0	6.9 ± 0.0	7–110	14.0
12	33.0 ± 1.9	3.3 ± 0.1	7.4 ± 0.1	17–82	16.5
B—Rovies					
8	15.6 ± 0.3	2.7 ± 0.0	6.0 ± 0.0	8–109	14.8
9	21.5 ± 0.2	2.9 ± 0.0	6.6 ± 0.0	33–141	12.6
10	27.7 ± 1.3	3.3 ± 0.0	7.0 ± 0.1	36–80	20.2
C—Pili					
7	18.5 ± 0.3	2.9 ± 0.0	6.1 ± 0.1	10–83	14.2
8	25.9 ± 0.3	3.1 ± 0.0	6.5 ± 0.0	15–109	16.3
9	36.6 ± 1.4	3.6 ± 0.1	7.6 ± 0.1	34–110	22.1

Freshly matured cones were collected in summer (collection size shown in Fig. 4)

To assess seed germinability all extracted seeds were used: 1531–5548–414, 2117–7580–589, 1971–2580–673 for 2004–2005–2006 from Gouves, Rovies and Pili, respectively. Initially, all undeveloped or damaged, i.e. insect infested seeds were removed. Germination conditions applied to apparently sound seeds were the optimal ones for *P. halepensis*: either 20 °C in alternating light and dark (12 h:12 h) or under simulated autumn (October–November) conditions (Skordilis and Thanos 1995). At the end of the experiments, all non germinated seeds were cut and classified as either dead or empty (Fig. 4).

The estimation of the regeneration potential (seeds m^{-2}) in the three postfire populations is used for the prediction of tree density (trees ha^{-1}). For this purpose, *P. halepensis* resilience was parameterized (Table 3) using (a) a number of actually measured variables (shown in bold in Table 3): sapling density, mature cones/tree, sound seeds/cone, germinable seeds/cone and (b) a number of estimators: non-opened cones (typically more than 95 %, monitored in the field; Thanos and Daskalakou 2000), non-aborted conelets (usually more than 95 %, monitored in the field as well), seed viability within cones (90–100 %, increasing with time for cones up to 3 years old; Daskalakou and Thanos 1996), seeds surviving fire (85–100 %; Thanos et al. unpublished data), seed surviving post-dispersal (20–40 %, a varying fraction with fire season; Nathan et al. 2000), successful germination in the field (estimated to a fraction of 60–80 %), seedling survival to sapling stage (estimated to 1–4 %; Thanos et al. 1996; Ordoñez et al. 2006) and sapling development to mature trees (estimated to 40–80 %; Trabaud 1988; Thanos et al. 1996; Thanos and Doussi 2000). This latter parameter belongs to a rather neglected topic, i.e. the transition of a well established sapling into a mature tree, which should be investigated more intensively in the near future.

Subsequently, the regeneration prediction values, i.e. stem density of the hypothesised newly established, postfire forest, were drawn as a function of the age-at-a-second-wildfire for each of the three Aleppo pine populations (Fig. 5). The predicted densities presented as highest and lowest values (Fig. 5a) and linear regressions (Fig. 5b) of predictions extend over the 4 last years (excluding the first one of Fig. 5a). Horizontal bars show the time

Table 3 Variables and estimators used for the parameterization of *P. halepensis* predictive resilience to fire

Variables			Min	Max	References
Tree (sapling) density	ha^{-1}	Virtually stable	**D**		Measured for each site
Cones/tree	Number	Varying yearly	$\mathbf{C_n}$		Measured for each site (5 annual cohorts)
Non-aborted conelets	Fraction	Varying yearly	0.95	0.95	Applied only to conelets measured; Thanos and Daskalakou (2000); data of this study <5 %
Sound seeds/cone	Number	Varying yearly	$\mathbf{S_n}$		Measured for each site (3 freshly matured annual cohorts)
Non-opened cones	Fraction	Varying yearly	0.95	0.95	Thanos and Daskalakou (2000), Tapias et al. (2001)
Seed viability within cones	Fraction	Increasing with time	0.9	1	Daskalakou and Thanos (1996)
Seeds surviving fire	Fraction	Variable	0.85	1	Unpublished data (Thanos et al.)
Seed surviving post-dispersal	Fraction	Varying with fire season	0.2	0.4	Nathan et al. (2000)
Germinable seeds/cone	Fraction	Variable	$\mathbf{G_n}$		Percentage of germination for each of the corresponding yearly cohort; for cones of future maturation, the average value of the last 2 years is used
Successful germination in the field	Fraction	Estimator	0.6	0.8	Unpublished data (Thanos et al.)
Seedling survival to sapling stage	Fraction	Estimator	0.01	0.04	Thanos et al. (1996), Nathan et al. (2000), Ordoñez et al. (2006)
Sapling survival to mature tree	Fraction	Estimator	0.4	0.8	Trabaud (1988), Thanos et al. 1996, Thanos and Doussi (2000)
Regeneration factor			**0.00033**	**0.00924**	
Germinable seeds required (m^{-2})			**301.8**	**10.8**	

Variables shown in bold represent actual measurements. The regeneration factor (RF) is the product of all non-measured variables. Required seeds refer to a mature forest with a density of 1,000 trees ha^{-1} after a recurrent wildfire (=0.1/RF seeds m^{-2}). The index n refers to the postfire year of a particular measurement windows (early and late durations, according to the regressions of Fig. 5b) for successful regeneration of at least 1,000 established mature stems ha^{-1}, in the case of a second fire, for each of the three postfire populations.

Statistical analysis

The independent samples *t* test was performed with the use of SPSS 21 software, in order to determine whether the mean height of the reproductive saplings differs from the height of the non-reproductive ones. Also, we tested whether the mean length, width and mass of cones changed significantly during the examined period (*P* given in results). Curve fitting was performed by linear regression analysis (Zar 1974).

In addition, due to the possibility of autocorrelation effects, the analysis of sapling heights was made by repeated measures ANOVA (Nemec 1996; Johnson and Wichern 1998) with the use of the SPSS 21 software, using heights per year as the within subjects variable and postfire population provenance and reproductive state as between subjects variables. Post hoc tests for the differences between postfire populations and reproductive states were made by the Tukey LSD.

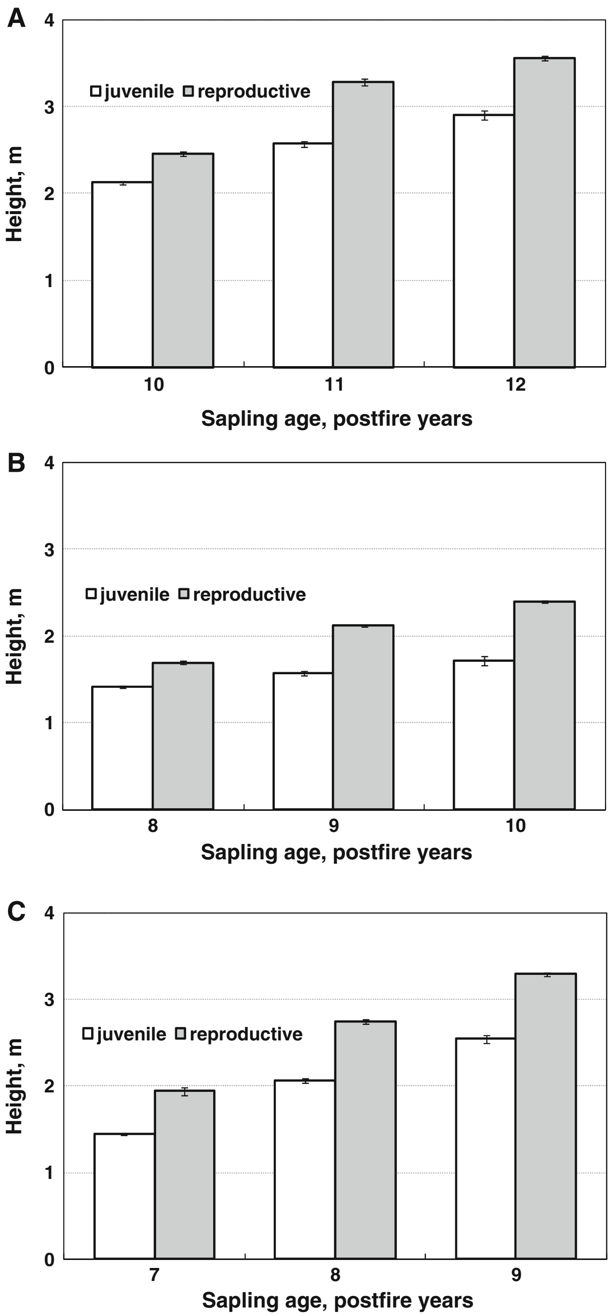
Results

The mean sapling height was found to be 3.34 ± 0.02, 2.23 ± 0.01 and 3.04 ± 0.02 m (n = 100, in each postfire population: Gouves, Rovies and Pili, at the end of the twelfth, tenth and ninth postfire year, respectively) while the mean annual growth increment for the particular growth seasons was 0.38 ± 0.01, 0.31 ± 0.01 and 0.61 ± 0.01 m. Height increased over time ($P < 0.001$) in all three postfire populations and was different between the populations, i.e. saplings were highest in Gouves and lowest in Rovies ($P < 0.001$). Furthermore, the reproductive saplings (Fig. 2) were significantly taller than the vegetative ones in all three populations (*t* test, $P < 0.005$). This result was confirmed by the repeated measures analysis and post hoc tests ($P < 0.001$). The reproductive saplings were also the most vigorously growing ones in the larger sample of 500 pine saplings in each postfire population (data not presented).

A considerable fraction (44 %) of pine population had already produced cones, as early as 10 years after fire (Fig. 3a); a dramatic increase was recorded in Gouves (59–66 % at sapling age of 11–12 years), closely corresponding to both population age and average height. Similarly to this, reproductive pines reached up to 45–75 % of the tagged saplings just 8–10 years after fire (in Rovies, Fig. 3b), while even earlier, the corresponding percentages for Pili (7–9 years old, Fig. 3c) were 20–67 %.

Cone and seed biometrical characteristics (Table 2) indicated that cones from three postfire populations became larger in size, i.e. in length and width, and mass during the three successive maturation years ($P < 0.05$). Mean seed mass varied from 12.57 ± 0.13 to 22.06 ± 0.96 mg in the three postfire populations and the mean number of seeds per cone ranged from 42.67 ± 1.22 to 72.88 ± 0.42. Furthermore, the collected cone samples have been found to bear viable and germinable seeds in all cases (Fig. 4) with mean values ranging from 34.1 ± 3.9 to 61.2 ± 0.5 germinable seeds per cone, 9–12 years after fire. Consequently, seed germination was adequately high, from 70 to 90 % in all three sapling populations, while by excluding empty and dead seeds, the final percentages were maximal, i.e. up to 99 %, on seedlots from young, postfire, Aleppo pine sapling populations 7–12 years old, tending to increase with time (data not presented).

Fig. 2 Sapling height of even-aged Aleppo pine individuals (**a**–**c** Gouves, Rovies and Pili, respectively, n = 100). The saplings were tagged and monitored for 3 consecutive years. *Vertical lines* represent ± SE



To estimate the postfire regeneration potential (Table 4) in the case of a second, recurrent fire event in all three Aleppo pine populations, the following parameters have been taken into consideration: mean sapling density per m^2, number of cones produced per sapling, number of sound seeds extracted per cone and seed germinability, all these

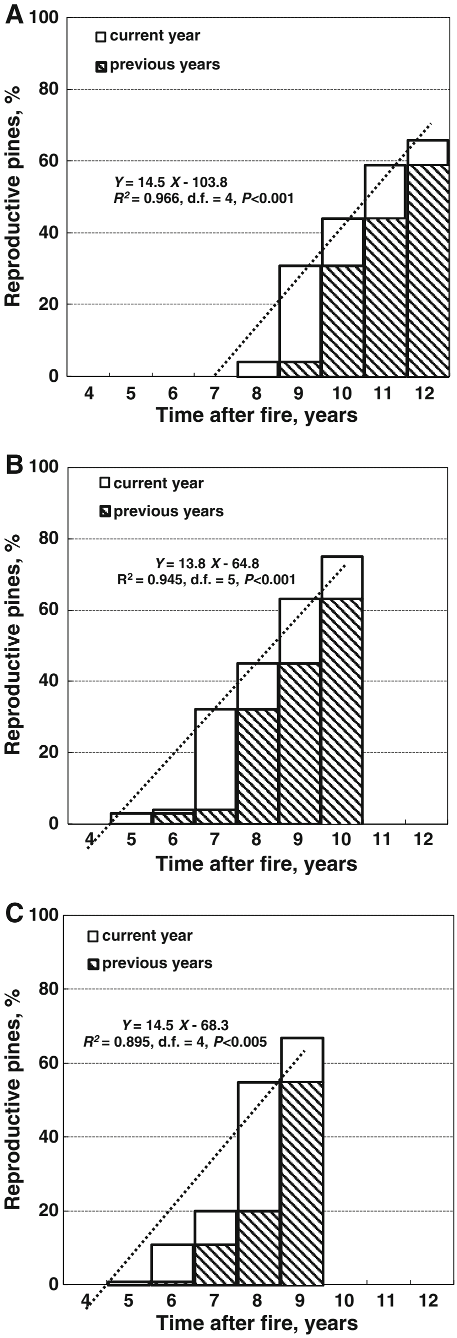


Fig. 3 Dynamics of the transition from the juvenile to the reproductive phase, for the same saplings of Fig. 2 (**a–c** Gouves, Rovies and Pili, respectively). *White* and *striped columns* represent the current year's 'first-time reproducers' and the accumulated value of the previous years, respectively

variables shown in bold in Table 3. The product of these actually measured parameters, namely the regeneration potential (RP), can be calculated, for any postfire year, by the formula:

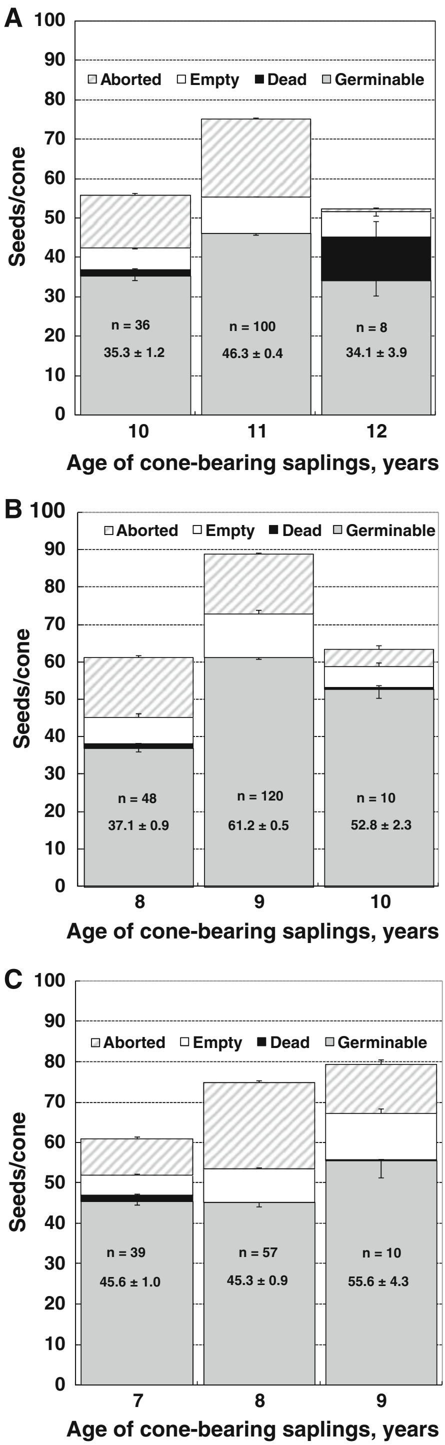


Fig. 4 Seeds per cone extracted from collections of freshly matured cones during three consecutive postfire years (**a–c** Gouves, Rovies and Pili, respectively); the postfire age is shown at the *bottom* of the bars. *Vertical lines* represent ±SE

Table 4 The regeneration potential (RP, germinable seeds m^{-2} stored in the canopy seed bank) in the three postfire regenerating forests, calculated for a 5-year-long period (Eq. 1)

Forest	Postfire year	Density (saplings m^{-2})	Cones/sapling (mean ± SE)	Seeds/cone (mean ± SE)	Germinable seeds/cone (% ± SE)	Postfire regeneration potential (seeds m^{-2})	Predicted postfire density (trees ha^{-1})
Gouves	10	1.03 ± 0.01 (n = 200, 0–6)	0.04 ± 0.004 (n = 100, 0–1)	42.67 ± 1.22 (n = 36, 1–84)	77.79 ± 2.91	1.4	4.8–133.0
	11		0.58 ± 0.02 (n = 100, 0–6)	55.48 ± 0.44 (n = 100, 7–110)	76.74 ± 0.36	25.4	88.7–2,474.3
	12		1.02 ± 0.03 (n = 100, 0–10)	51.75 ± 5.42 (n = 8, 17–82)	71.88 ± 9.27	39.1	136.3–3,801.7
	13		2.42 ± 0.07 (n = 100, 0–21)	53.62	74.74	99.9	348.4–9,716.6
	14		4.23 ± 0.12 (n = 100, 0–39)			174.6	609.0–16,984.0
Rovies	8	1.58 ± 0.02 (n = 200, 0–10)	0.04 ± 0.004 (n = 100, 0–1)	44.10 ± 0.95 (n = 48, 8–109)	56.82 ± 3.78	1.6	5.5–154.1
	9		0.76 ± 0.004 (n = 100, 0–18)	72.88 ± 0.42 (n = 104, 33–141)	73.08 ± 0.45	64.0	223.1–6,221.6
	10		1.19 ± 0.05 (n = 100, 0–20)	58.90 ± 2.52 (n = 10, 36–80)	94.01 ± 2.01	104.1	363.2–10,127.8
	11		2.46 ± 0.07 (n = 100, 0–20)	65.89	79.38	203.3	709.2–19,776.8
	12		6.82 ± 0.18 (n = 100, 0–42)			563.6	1,966.1–54,828.5

Table 4 continued

Forest	Postfire year	Density (saplings m^{-2})	Cones/sapling (mean ± SE)	Seeds/cone (mean ± SE)	Germinable seeds/cone (% ± SE)	Postfire regeneration potential (seeds m^{-2})	Predicted postfire density (trees ha^{-1})
Pili	7	0.85 ± 0.01 (n = 200, 0–5)	0.01 ± 0.002 (n = 100, 0–1)	50.54 ± 0.98 (n = 39, 10–83)	73.89 ± 3.23	0.3	1.1–30.9
	8		0.17 ± 0.01 (n = 100, 0–3)	57.11 ± 0.92 (n = 53, 15–109)	79.25 ± 0.60	6.5	22.8–636.2
	9		0.49 ± 0.02 (n = 100, 0–7)	67.30 ± 4.70 (n = 10, 34–110)	98.85 ± 1.03	27.7	96.7–2,695.4
	10		2.52 ± 0.08 (n = 100, 0–27)	62.21	92.70	123.5	430.9–12,015.8
	11		5.74 ± 0.15 (n = 100, 0–41)			281.3	981.4–27,369.4

Minimum and maximum values in parentheses (cones/sapling, seeds/cone) represent the observed range of each sample. Predicted densities after a recurrent fire are shown at marginal postfire conditions (highest and lowest values) on the basis of minimum and maximum values of RF (Table 3, Eq. 2)

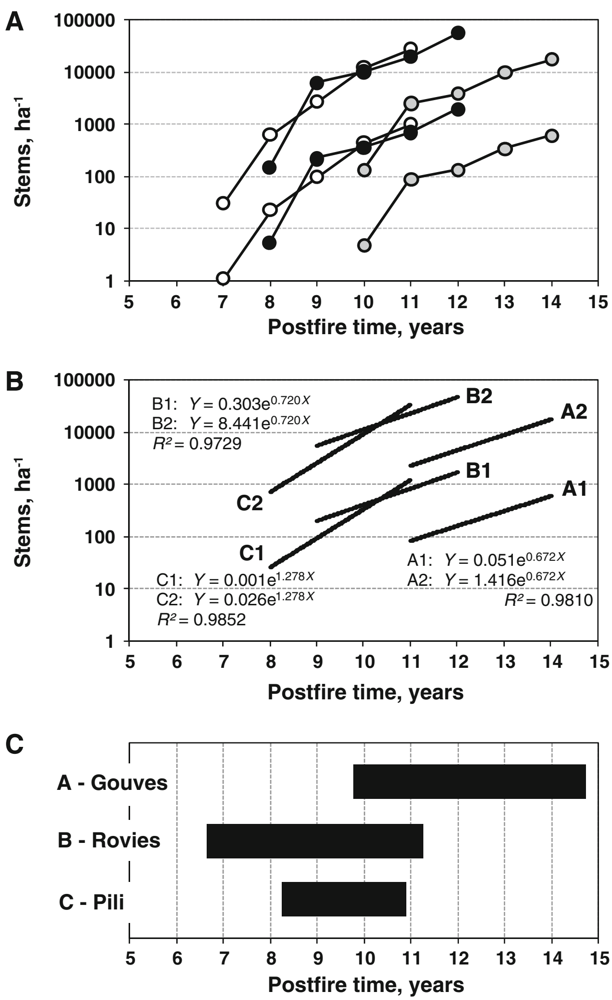


Fig. 5 Predicted density of a mature pine forest (PDRF) as a function of age at the hypothetical recurrent fire (Eq. 2). **a** Predicted highest and lowest values for Gouves (*grey*), Rovies (*black*) and Pili (*white*). **b** Linear regressions for predicted densities for the last 4 years of the period examined (*A1*, *A2* Gouves, *B1*, *B2* Rovies, *C1*, *C2* Pili). **c** *Horizontal bars* represent interfire time windows (based on regressions of Fig. 5b) allowing for full recovery (set at 1,000 mature stems established per hectare)

$$\mathrm{RP} = \sum (\mathrm{D} \times \mathrm{C_n} \times \mathrm{S_n} \times \mathrm{G_n}) \quad (1)$$

where: n refers to all yearly measurements prior to the age of the calculated RP. By applying Eq. (1), an increasing RP value (0.3–563.6 seeds m^{-2}) is obtained for all sites with postfire time. Eventually, the estimated RP value for 2008 amounts to 174.6, 281.3 and 563.6 seeds m^{-2}, for each of the three forests and at a postfire age of 14, 11 and 12 years, respectively.

The rest, relevant postfire estimators of Table 3 are combined into a product of either their min or max values (termed the RF) and, based on the assumptions made, the RF marginal values are 0.00033 and 0.00924. Therefore, the predicted density after a recurrent fire (PDRF) is given by the following formula:

$$\mathrm{PDRF} = \mathrm{RP} \times \mathrm{RF} \tag{2}$$

and actual estimations for the three forests studied are shown in the last column of Table 4 as well as in Fig. 5a, drawn semi-logarithmically versus age-at-a-second-wildfire. These estimations follow a statistically significant linear regression (Fig. 5b, for the last 4 years of the monitoring period) and it is postulated that these curves may be extrapolated in the future, for a few years at least. Assuming that full postfire recovery is attained with 1,000 established mature stems ha^{-1}, the time windows of the minimal intervening period for full recovery of each of the three forests examined is predicted, in Fig. 5c, to be as short as 10–15 years (Gouves), 8–11 years (Pili) and 7–11 years (Rovies) respectively, with marginal values corresponding to best and worst postfire scenarios, respectively.

Discussion

The Euboean provenance of Aleppo pine has been cited (Panetsos 1981) as a ‘superior’ one in growth and the best in straightness among numerous Mediterranean provenances tested in experimental, clonal seed orchards. This conclusion is supported by to the present study as sapling heights for the naturally, postfire growing pines in Euboea Island sites are dramatically higher than those recorded for similarly aged populations in several, burnt forests in southern Greece (Thanos et al. 1998). In addition, the annual growth increments observed, ca 0.30–0.60 m $year^{-1}$, are considerably larger than those reported in other studies (e.g. Eugenio et al. 2006).

A good relationship between sapling height, which constitutes a reliable proxy for plant biomass, and the onset of the reproductive stage was observed for the Euboean populations investigated. In agreement to previous reports (Thanos and Daskalakou 2000; Ne’eman et al. 2004), most of the vigorously growing saplings were found to be reproductive.

Aleppo pine, a well-studied Mediterranean pine, is characterised by a remarkably short juvenile phase. Early cone and seed production is a trait of high adaptive value with respect to fire recurrence, as well as to other disturbances related to climate change (e.g. severe drought episodes negatively affect the size of the canopy cone bank and thus the quality of included seeds; Espelta et al. 2011); furthermore, young reproductive saplings function initially as females (Ne’eman et al. 2004; Climent et al. 2008). In addition to observations from garden experiments (e.g. Climent et al. 2008), Aleppo pine field studies have also revealed an early reproductive transition, even at 3–4 years of age (Thanos and Daskalakou 2000). Postfire population dynamics in northern Euboea Island showed that most pine saplings have already turned reproductive at 9–12 years after fire, with particularly low values of J_{50}, a parameter denoting the age when half of the population individuals enter the reproductive stage (Thanos and Daskalakou 2000): i.e. 10.6, 8.3 and 8.2 years for Gouves, Rovies and Pili, respectively, in agreement with similar values, 10–11 years, reported for the Iberian Peninsula (Moya et al. 2008).

On the basis of previously published work, it has been suggested that cones formed at an early sapling age are relatively smaller than those produced by mature plants in the same location. Smaller cones contain fewer and smaller seeds but, nevertheless, almost equally germinable to those produced by mature trees (Thanos 2000). This suggestion is strongly supported by the findings of the present study: cone size, seeds per cone and seed mass all tend to increase with age, while a large fraction of seeds per cone are germinable and germination is nearly maximal. Furthermore, the importance of the cones as a reproductive structure that safeguards the enclosed seeds, and hence the species survival and proliferation, is particularly accentuated in bradychorous pines; in the case of Aleppo pine, seed mass as a fraction of cone mass is impressively small, as previously reported elsewhere (Thanos 2000).

Recurrent wildfires are well known to constrain the long-term regeneration ability of *P. halepensis* (e.g. Espelta et al. 2008), where twice-burnt areas show lower pine density, growth and reproductive ability, as well. An accumulated canopy seed bank, consisting of mature, serotinous cones, with 12.5–92.5 seeds m^{-2} is empirically considered sufficiently large to ensure forest regeneration after a recurrent fire (Moya et al. 2007). It is interesting to note that the values obtained with the proposed RF (10.8–301.8 seeds m^{-2}) are very close to this postulation. The estimation of the regeneration potential in all studied sites of the 10–13 years old, Aleppo pine postfire populations reached considerably high values (99.9–203.3 seeds m^{-2}), higher by far than the values previously reported (Moya et al. 2007). The proposed regenerator predictor (Table 3) aims at assessing the time window for full recovery of a pine population (1,000 stems ha^{-1}) in the case of a recurrent fire in the future, on the basis of the actually measured or bibliographically estimated following parameters: tree or sapling density, cones per tree, non-aborted conelets, sound seeds per cone, non-opened cones (e.g. the measured opened cones in this study account for 5 % of the total cone production, thus the essential parameter of the produced cones per sapling, remaining closed in the canopy seed bank and 'waiting' for the next fire event, will be corrected by a factor 0.95), seed viability within cones, seeds surviving fire, seed surviving post-dispersal, germinable seeds per cone, successful germination in the field, seedling survival to sapling stage and development of saplings to mature trees. In conclusion, for even-aged, postfire Aleppo pine populations the interfire period required for full recovery can be predicted as the product of the accumulated canopy seed bank (regeneration potential) and a number of estimators (RF, with min–max values).

The application of this RP tool is suggested to require data that span over at least two years (consecutive or a few years apart) and include annual measurements both in the field (sapling density, vegetative to reproductive shift dynamics, cones/sapling) and in the laboratory (sound and germinable seeds/cone) at a suggested time period 7–12 years after the first fire, when seed bank data is available and the minimal interfire period for full recovery may be approaching, if not already reached. Overall, the regeneration potential, RP, expressed as seeds ha^{-1} and projected for a particular year, when multiplied by the regeneration factor, RF, marginal values (0.00033 or 0.00924, corresponding to the worst and best postfire scenarios, respectively) results in a mature pine population density (1,000 stems ha^{-1}), after a hypothetical recurrent fire, at surprisingly short inter-fire time windows for the three, robustly growing forests studied. The required postfire RP value, ca 10–300 seeds m^{-2}, stored in the canopy seed bank, is considered to be the threshold for 'full recovery' in case of a recurrent fire event. This threshold is reached at a dramatically short time window (7–12 years after the first fire) for northern Euboea populations. On the other hand, fire intervals lower than either 10–15 years (Rodrigo et al. 2004), 20 years (Eugenio et al. 2006) or 12–23 years (Thanos and Daskalakou unpublished data) have been reported to result in a decline of recruitment and eventual recovery of *P. halepensis* populations, a fact that can be attributed to specific, adverse site conditions. The validation of the RP tool is obviously necessary (together with a more solid documentation of the RF) and a preliminary assessment can be made in wildfire cases where an adjoining significant part of the forest is not affected by fire.

Acknowledgments We acknowledge financial support of the "Strategic management plan of *P. halepensis* forests", a task implemented within the framework of TWIG (Transnational Woodland Industries Group) project under RECITE II Programme, European Commission, DG XVI. We are grateful to our colleagues: George Vassilopoulos, Katerina Koutsovoulou, Marios Andreou, Argyro Zerva and Athanasia Pikradi for their contribution to field data collection and laboratory experiments. We also thank Ioannis Tsaprounis, Forest Department of Limni, Euboea Island, for his assistance and Dr Pinelopi Delipetrou for her valuable help in statistical analysis. We finally acknowledge the helpful comments and suggestions of two anonymous reviewers.

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