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**Positive coupling between growth and reproduction in young post-fire
Aleppo pines depends on climate and site conditions**

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26 **Abstract**

27 In fire- and drought-prone Mediterranean forests tree growth and regeneration depend on
28 the moisture regime between fires. Therefore, post-fire tree regeneration will depend on
29 moisture conditions and how they are altered by fire recurrence and climate warming.
30 Aleppo pine forests are the most abundant Circum-Mediterranean ecosystems subjected to
31 frequent wildfires and summer droughts. Since both stressors constrain their reproduction
32 and growth patterns across diverse ecological conditions, these forests represent a suitable
33 system to test how moisture availability drives post-fire regeneration. Aleppo pine is an
34 obligate seeder species that reproduces at an early age after fire. Such precocious behaviour
35 poses the question as to whether post-fire regeneration depends on moisture conditions and
36 the coupling between female cone production and growth. Here, we evaluate if female cone
37 production and radial growth are linked at the tree level in post-fire Aleppo pines by
38 comparing a dry vs. a very dry site and considering stands with three different tree densities
39 in SE Spain. We found that trees with higher basal areas produced more female cones and
40 this positive association intensified as the water balance improved. Aleppo pines from the
41 very dry site were more precocious in reproductive terms than pines of the same age from
42 the dry site, but long-term cone production was lower at the very dry site. Lower tree
43 density enhances the resilience of xeric post-fire Aleppo pine forests, in growth and
44 reproduction terms, but this effect can be reversed by droughts. Overall, a more positive
45 water balance improves post-fire regeneration by enhancing growth and cone production.
46 Thus, silvicultural treatments as thinning should be applied by taking into account the post-
47 fire water balance to maximise growth and cone production in Aleppo pine stands. Our
48 findings illustrate how climate warming could hamper post-fire tree regeneration by
49 aggravating drought stress.

50 **Keywords:** post-fire reproduction; *Pinus halepensis*; drought; radial growth; serotiny.

51

52 **Introduction**

53 If climate warming leads to increased aridification this could modify how post-fire climatic
54 conditions determine tree regeneration in drought-prone areas such as Mediterranean pine
55 forests (Pausas 2004). Since these forests are characterised by frequent wildfires and
56 recurrent summer droughts (Naveh 1974; Trabaud 1987) warmer and drier conditions could
57 hamper post-fire reproduction and growth thus constraining tree regeneration at stand and
58 tree levels. Warming-induced aridification increases the fire hazard in the Mediterranean
59 Basin (Piñol *et al.* 1998; Pausas 2004), but extreme climatic events such as severe droughts
60 are also expected to increase their frequency in this area throughout this century (Meehl and
61 Tebaldi 2004). However, we still lack datasets to evaluate how those adverse climatic
62 conditions affect post-fire regeneration. Such evaluation should be performed at the stand
63 and tree levels considering how post-fire growth and reproductive performance are related.
64 First, if rising temperatures magnify drought severity and increase fire frequency, this
65 would constrain tree growth or reduce the reproductive potential of stands, particularly in
66 the case of non-sprouting tree species (Corona *et al.* 1998; Thanos and Daskalakou 2000).
67 But how growth and reproduction are modified by post-fire moisture availability could also
68 depend on regional climatic conditions or be modulated by stand features such as density
69 which modifies the actual availability of water to trees (Linares *et al.* 2010). Second,
70 secondary growth and reproduction have a similar and low priority for allocating available
71 carbohydrates so varying drought stress could alter their phenology or modify the preferred
72 allocation sink and determine the associations between the two processes at the tree level
73 (Klein *et al.* 2014). For instance, if moist conditions enhance growth but not reproduction
74 (or vice-versa) this could produce a negative correlation that may be spuriously interpreted
75 as a trade-off (Knops *et al.* 2007). Alternatively, if a more positive water balance enhances

both growth and reproduction this pattern could obscure actual trade-offs (Thomas 2011). To test these ideas it is therefore important to have annually and seasonally resolved variables of reproduction and growth such as cone production and earlywood and latewood production.

To address these questions, we selected Aleppo pine (*Pinus halepensis* Mill.), which is the most widely distributed pine species throughout the Mediterranean Basin and one of the best-adapted tree species to fire and drought (Pausas 2004). Aleppo pine is a pioneer (shade-intolerant), obligate seeder, short-lived conifer species that shows high post-fire seeding capacity and precocious reproduction (Richardson 2000). Small trees tend to produce only female cones, and this female-first strategy enhances population spread (Ne'eman *et al.* 2011). In *P. halepensis*, pollination occurs in spring, fertilisation follows 1 year later and seed dispersal takes place 3 years after pollination (Panetsos 1981). Serotiny (long-term retention of seeds in the canopy) is also frequent in Aleppo pine (Daskalakou and Thanos 1996, Tapias *et al.* 2001), and serotiny levels increase as fire recurrence does (Ne'eman *et al.* 2004; Hernández-Serrano *et al.* 2013). However, dry and hot climatic conditions also induce seed release (xeriscense *sensu* Nathan *et al.*, 1999; see also Espelta *et al.* 2011). Aleppo pine tolerates marked water deficit during several seasons (Borghetti *et al.* 1998), and the main peaks of radial growth occur in spring and autumn with a reduced growth rate during dry summers (de Luis *et al.* 2007; Camarero *et al.* 2010). Furthermore, longitudinal or radial growth and cone production are reduced by drought (Girard *et al.* 2012; Pasho *et al.* 2012).

Since post-fire young Aleppo pines show very high growth rates and start reproducing very early, this poses the question as to whether growth and reproduction are positively or negatively associated. Furthermore, the high density of post-fire Aleppo pine

stands can intensify conspecific competition among neighbouring trees, leading to a reduction in growth and reproduction levels in very dense stands. Both tree size and interactions with neighbours must be taken into account in order to understand how reproduction varies among individuals within the same population (Haymes and Fox 2012). Aleppo pine is a suitable tree species to study these issues given its ability to fruit at early ontogenetic stages and because crop amount can be enhanced either through thinning (González-Ochoa *et al.* 2004; De las Heras *et al.* 2004, 2007; Moya *et al.* 2008; Ruano *et al.* 2013) or fertilization (Ortiz *et al.* 2011). In addition, there is evidence for wide geographical variability of Aleppo pine reproductive traits (Climent *et al.* 2008) and growth-related wood-anatomical features (Esteban *et al.* 2010). Such variability suggests that this species presents adaptive responses in growth and reproductive terms in response to different stressful climatic conditions. Consequently, growth-reproduction associations must be assessed in stands with different densities and subjected to contrasting water balances.

Our aim was to evaluate how climate conditions control post-fire tree regeneration by quantifying radial growth and female-cone production in young Aleppo pines recruited after fires in south-eastern Spain. We evaluated how growth and reproduction respond to climate and conspecific competition by comparing two climatically contrasting sites (dry vs. very dry site) and by considering stands with three different tree densities.

Material and methods

Study sites and experimental design

Twenty-one rectangular plots (10 m × 15 m) per site were set up in 1999 in two post-fire naturally-regenerating Aleppo pine stands in south-eastern Spain, close to the villages of

Yeste and Calasparra. Both locations were burned in summer 1994. Fire severity was heterogeneous in the burned area (Ruiz-Gallardo et al. 2004), but only high severity areas without surviving trees were selected for this study. Before the wildfires the study areas were covered by mature stands of *P. halepensis* mixed with *Pinus pinaster* Ait. and *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. (the latter species was only found at Yeste).

The average annual rainfall and temperature are 595 mm and 340 mm, and 13.6°C and 16.5°C, respectively, in Yeste and Calasparra (Supporting Information, Fig. S1). Following Rivas-Martinez et al. (1999), the ombrothermic indices pointed to an upper dry type at Yeste and a lower semiarid type at Calasparra (hereafter referred to as the dry site and the semiarid (or very dry site), respectively).

Study plots presented high initial sapling densities and were subjected to thinning treatments in 1999 and 2004 to reach two final densities: (i) nine high-density plots per site with density ranges of 1,600-2,400 trees ha⁻¹ and 1,600-9,500 trees ha⁻¹ at the dry and the very dry site, respectively; (ii) nine moderate-density plots per site with density values of 800 trees ha⁻¹. At both sites, three plots remained unthinned (termed control plots) which resembled the very high initial densities found (7,000 and 130,000 trees ha⁻¹ at the dry and the very dry site, respectively).

Dendrochronological analysis

We used dendrochronology to quantify the temporal patterns of radial growth expressed as earlywood and latewood production (hereafter abbreviated as EW and LW, respectively). We randomly selected 90 trees per site (30 trees per each tree density group), although for the moderate- and high-density groups we selected trees only from plots treated in 2004. The selected trees were cored near the tree base (height ca. 0.3 m) using a Pressler

increment borer. Two perpendicular cores per tree were sampled with at least one of them reaching the pith. When trees were too small to be cored (diameter < 5 cm), a wood disk was obtained by sawing them. Cores and disks were air-dried and sanded until the EW and LW boundaries became clearly visible under a stereomicroscope. All the samples were visually cross-dated, i.e. they were synchronized to assign the year of formation to each tree ring by comparing characteristic narrow rings present in all trees. The EW and LW widths series were then measured to the nearest 0.001 mm with a LINTAB measuring device (Rinntech, Heidelberg, Germany). We visually distinguished EW and LW based on the cross-sectional area of tracheid lumens and the thickness of their cell walls (de Luis *et al.* 2007; Camarero *et al.* 2010). Despite the assumption that the likelihood of cross-dating errors is low in short tree-ring width series of *P. halepensis* (Eugenio *et al.* 2006), we further checked cross-dating quality using the COFECHA software (Holmes 1983). The trend due to the geometrical constraint of adding a volume of wood to a stem of increasing size was corrected by converting the EW and LW widths into area increments.

Structure variables and cone production

Plots were sampled in the years 1999, 2000, 2001, 2005, 2007, 2009 and 2011, which correspond to pine ages of 5 (1999) to 17 (2011) years. A representative number of trees per plot was tagged and monitored during the study period (n=24 for the very high and high-density plots, and n=12 for the moderate-density plots), accounting for a total number of ca. 1,000 trees monitored per year. The structural variables measured in those trees were: stem diameter at 0.3 m above ground (*d*), total height (*h*), dominant height (*H_d*, defined as the total height of the tallest tree located in each plot) and the number of cones visible in the

crown. We calculated a distance-independent competition index k for each plot and study year as follows:

$$k = (d/dg) - 1 \quad (1)$$

where dg is the mean square diameter of the trees located in each plot.

Trees were considered reproductive when they bore at least one conelet. In the samplings performed in 2005, 2007, 2009 and 2011, cones were also classified according to their age and were differentiated by size and colour as: red conelets or female strobili (cone age < 1 year), green or immature cones (cone age < 2 years), brown or mature (cone age = 2-3 years), grey or serotinous and open cones (cone age > 3 years). In 2013, we also counted and classified the cones present in the crowns of the 90 trees selected for the dendrochronological analyses. The serotiny level for each tree was estimated from 2005 onwards as the number of serotinous cones related to the total number of cones (open plus serotinous cones) observed in each tree (Tapias *et al.* 2001).

To determine the relationships between the onset of reproduction and tree height, we defined the following ratios obtained at the plot level:

$$H_{R-NR} = 100 \times (H_{Ri} - H_{NRi}) / H_{Ri} \quad (2)$$

$$H_{R-d} = 100 \times (H_{Ri} / H_d) \quad (3)$$

where H_{Ri} and H_{NRi} are the average tree heights measured in the sampling year i (1999, 2000, 2001, 2005, 2009, 2011) for reproductive and non-reproductive trees, respectively, and H_d is the dominant height measured for each plot in the last inventory carried out in 2011. The ratio H_{R-NR} focuses on the differences in height between reproductive and non-reproductive trees, whereas the H_{R-d} function centres on the relative height of reproductive trees. Note that these metrics are widely used in forest inventories and they are linked to the minimum size at reproductive onset (Wright *et al.* 2005).

195

196 *Climatic effects on growth and reproduction*

197 We obtained monthly climatic variables (mean temperature and total precipitation) for the
198 study period (1994-2012) from nearby meteorological stations (data provided by the
199 Spanish National Meteorological Agency). We used water balance instead of precipitation
200 because the former represents more accurately the available water for growth and
201 reproduction in accordance with rainfall and thermal conditions than the latter. The water
202 balance (P-PET) was calculated as the difference between monthly precipitation (P) and
203 potential evapotranspiration (PET), where the last variable was estimated using the method
204 proposed by Hargreaves and Samani (1985).

205 To quantify how these climatic variables affect radial growth (EW and LW area
206 increments) or cone production, we calculated Pearson and Spearman correlation
207 coefficients between climate and the corresponding variable, respectively. Since growth
208 and reproduction show lagged responses to climate, we calculated those correlations up to 1
209 (from the previous September to the current October) or 2 years (from the previous January
210 to the current August) prior to the formation of tree ring or green cones, respectively. For
211 the climate-cone associations we excluded non-reproductive trees from the analyses, thus
212 maintaining 262 and 233 trees at the dry and the very dry site, respectively. To obtain
213 consecutive series of green cone production, we assumed that the green cones of year t
214 corresponded to the brown cones of year $t+1$ in those years when green cones had not been
215 directly counted.

216

217 *Statistical analyses*

Significance levels for the Pearson and Spearman correlation coefficients were set at $P < 0.05$ and corrected for the presence of temporal autocorrelation following Mudelsee (2003). ANOVAs and *post hoc* comparisons (Tukey-Kramer HSD test) were used to evaluate if there were differences between sites in terms of several variables (H_{R-d} , number of cones; $P < 0.05$). Generalized linear mixed models (GLMMs) were calculated to model (i) the presence or absence of cones and (ii) the total production of cones or green cones. The GLMMs were fitted according to: tree age, tree height, basal area, plot tree density, competition intensity and presence of mature or serotinous cones (only for green cone production). Factors plot and tree were introduced as random effects to account for the spatial and temporal autocorrelation in cone production. The probability of presence versus absence was modelled using a binomial error distribution (logit link). The tree size at which the probability to have reached sexual maturity was 50% (hereafter abbreviated as J_{50}) was also obtained from the binomial GLMMs. To model the production of either all or green cones, a negative binomial error distribution (log link) was used to account for overdispersion in the count data. GLMMs were fitted by using maximum likelihood methods. The best fitted models were considered those showing the lowest Akaike Information Criterion (AIC) (Burnham and Anderson 2002). Since the difference between the best model and the alternative ones was > 2 AIC units, we report only the best-fitted models. GLMMs were fitted using the *lme4* package (Bates *et al.* 2013) in the R package, version 3.1 (R Core Development Team 2014).

Results

Radial growth, thinning and climate

During the study period, the EW and LW area increments were higher at the dry than at the very dry site (Fig. 1). For instance, EW (LW) reached median values of up to 3.5 (0.3) and 1.2 (0.1) cm² yr⁻¹ at the dry and the very dry site, respectively. Those maximum growth values were observed in the moderate-density plots at both sites after the 2004 thinning. The minimum growth rates were observed in the highest-density control plots at the very dry site. The EW response to thinning peaked in the moderate-density plots, but such a response was modulated by climate. For instance, the EW area increment was low in 2005, particularly at the dry site, but was high in 2007-2008; these two periods were characterised by dry and wet conditions, respectively (Supporting Information, Fig. S1). However at the very dry site, thinning enhanced EW growth and the drought-induced growth decline in 2005 was delayed, as observed mainly in 2006.

Climate-growth-cone relationships

Wet and cool conditions in the previous autumn (September, November) and the current spring (March) were associated with improved EW growth (Fig. 2). These climatic effects were more evident at the very dry site plots.

Green cone production was related mainly to the wet and cool conditions in the spring and summer of the year $t-2$ and to September temperatures of year $t-1$ at the dry site (Fig. 3). The wet conditions in September of year $t-2$, but the negative responses to the dry May conditions of year $t-1$, were related to higher cone production at the very dry site.

Reproductive patterns

Five years after post-fire natural regeneration, the percentage of reproductive trees was higher at the very dry site than at the dry site (15% vs. 7%, respectively) (Fig. 4a).

However, this pattern reversed later, i.e., from 7 to 17 years after a fire, when the percentage of reproductive trees at the dry site exceeded that at the very dry site. In particular, at 17 years post-fire, 83% and 60% of all the trees were reproductive at the dry and the very dry site, respectively.

In general, contrasting frequencies in the production of different cone types were observed at the two study sites with time. For instance, the highest percentages of conelets production were observed in 2005 and 2009, two particularly dry years, at the dry and the very dry sites, respectively (Table 1). Furthermore, a higher percentage of brown (mature) cones was recorded in the thinned plots, i.e., with moderate or high tree densities, than in the control plots. These differences were significant ($P<0.005$) at the dry site in 2005 and at the very dry site in 2007 and 2011. We also detected significantly ($P<0.05$) higher serotinous cone crops for the years 2007, 2009 and 2011 in the control plots than in the other thinned plots at the very dry site. Serotiny was very high (70-100%) for each year and study site, excepting for the dry year 2005 at the very dry site. Save this year, serotiny remained very high at the very dry site ($>96\%$), but slightly decreased over at the dry site (from 88% to 80%).

Effects of tree size, plot density and competition intensity on cone production

The H_{R-NR} ratio continuously increased with time, but more at the dry site than at the very dry site (Fig. 4b). For instance, at the age of 5, the mean ($\pm$ SE) heights of the reproductive trees from both the dry and very dry sites were 147 ± 4 and 90 ± 2 cm, respectively. Consequently, the height at which the probability to have reached sexual maturity was 50% (J_{50}) differed between sites when pines were young, but later converged at older ages (Fig 4c). Thus from post-fire years 5 to 7, J_{50} was higher at the dry site than at the very dry site,

while this trend reversed later. When considering the relative height of reproductive trees (H_{R-d}), we found no significant differences between sites (Fig. 4d). Therefore, the height of the reproductive trees seems to be proportional to the dominant height of the plot, suggesting that microsite effects mainly drive the height at which reproduction starts.

GLMMs confirmed tree height as the main factor to positively drive the presence of cones, while tree height, tree density and competition were driving cone production (Table 2). Taller trees were more likely to be reproductive than smaller trees. Conversely, cone abundance was negatively related to plot tree density. The positive coefficients of the years in the models of presence or cone production indicated an ontogenetic effect in the reproductive trends of trees from the dry site. Conversely at the very dry site, the models revealed a progressive reduction in the number of new reproductive trees since 2001. Finally, the best explanatory variables of green cone production were similar, as in the case of all the cones, but also including the presence of other cone types.

Associations between radial growth and cone production

We found positive and significant ($P < 0.05$) relationships between green cone production and EW area increments at the dry site (Spearman $r_s = 0.75$, $n=10$, period 2003-2013), and also between green cone production and LW area increments at the very dry site ($r_s = 0.85$). Regarding lagged growth-cone production associations, green cone production was significantly and positively related to the EW and LW area increment of the year $t-1$ in 12% of trees from the dry site and was positively related to LW in 11% of trees from the very dry site. Green cone production was significant and correlated positively with EW formation growth in the year $t-2$ in 11% of trees from the very dry site.

As Aleppo trees aged and their stems thickened, they produced more cones. However, wide variation was noted in this basal area-cone numbers association between sites, density levels, and even among the trees growing at the same site and plot with similar basal areas (Fig. 5). We observed the lowest cone production at the very dry site, irrespectively of tree basal area. Furthermore, stand attributes modulated this association since the highest cone production was observed in the thinned plots with moderate to high tree densities.

Discussion

We found positive associations between reproduction and growth at the tree level in young Aleppo pines. This corresponds with observations at the branch level when comparing reproductive (either male or female) vs. non-reproductive branches (Ne'eman *et al.* 2011). Those years characterized by large area increments corresponded to years of abundant cone formation and wet conditions immediately before or during the early growing season. Consequently, we can state that the larger the basal area, the higher the cone production, but that there was considerable among-tree variability within stands.

The response of cone production to climatic variability was greater at the dry site than at the very dry site. The year-to-year variability of cone production in Aleppo pine has been related to climate, specifically water availability, and tree vigour or size (Girard *et al.* 2012). Cone development depends mainly on resource availability during the 2 years after pollination when the largest carbon investment during cone ripening occurs (Ne'eman *et al.* 2011). Accordingly, cone production responds to lagged climatic effects related to the phenological stages of the fruiting processes in *P. halepensis*, such as conelet induction (spring to early autumn in year $t-2$) and conelet formation (winter in year $t-1$). Climatic

control on fruit production has been identified mainly in less productive areas (Calama *et al.* 2011), yet we found responses of cone production to water availability at both the dry and very dry sites, suggesting that additional environmental factors, that were not accounted for (light, air or soil temperature, etc.), also determined reproductive success.

In Mediterranean Aleppo pine forests, winter-spring water availability is a main driver of radial growth and EW formation (Pasho *et al.* 2012). Accordingly, radial growth was lower at the very dry site than at the dry one (see also Moya *et al.* 2008b). The negative impact of drought on EW growth was also detected during the dry year 2005 in the unthinned plots. However, a lagged growth response to drought was also observed in the thinned plots, where warmer summer conditions enhanced LW formation. This suggests that improved radial growth due to thinning can enhance the sensitivity of young Aleppo pines to climate (Olivar *et al.* 2012).

The pines from the very dry site showed a shorter non-reproductive juvenile period than pines from the dry site, which was also reported by González-Ochoa *et al.* (2004). Stressful environments may elicit phenotypic reproductive responses in Aleppo pine for instance by inducing earlier reproduction or by responding to frequent fire (Climent *et al.* 2008; Moya *et al.* 2008). Accordingly, the height threshold for reproduction (J_{50}) was higher at the dry site than at the very dry site. At the site level, stressful water-deficit conditions induced earlier reproduction, which does not agree with the tree level observations showing that the most vigorous trees begin reproduction earlier in even-aged populations (Thanos and Daskalakou 2000; Ne'eman *et al.* 2004).

Despite the mentioned precocity in the very dry site, long-term cone production was higher at the dry site in both tree and basal-area bases than at the very dry site. Lastly, thinning improved radial growth and the amount of cones produced per tree (see also

Verkaik and Espelta 2006). This effect was noticeable at the dry site because, at the very dry site, the advantages of thinning for growth and reproduction were probably obscured by stressful site conditions (Misson *et al.* 2003).

Therefore, reproductive precocity and investment, which are sometimes tightly linked (Santos-del-Blanco *et al.* 2013), are highly dependent on climate and site conditions other than fire recurrence (Keely and Zedler 1998; Espelta *et al.* 2008). Climatic conditions, coupled with site conditions (e.g., poor water-holding capacity), can together induce earlier onset of reproduction or reduce long-term cone production. Presence and abundance of cones were dependent mainly on tree height, as previously reported in other tree species (Thornley and Johnson 1990). Furthermore, trees bearing mature, serotinous or open cones in the crown were more likely to bear new cones. Consequently, once the tree had left the juvenile phase, it was more likely that abundant annual crops were yielded as trees enlarged. However, cone abundance was also largely influenced by tree-to-tree competition, which confirms that thinning does not only improve growth, but also cone production (Calama *et al.* 2011).

In Aleppo pine, raised population levels of serotiny are associated with high fire recurrence (Keeley and Zedler 1998; Ne'eman *et al.* 2004; Hernández-Serrano *et al.* 2013). The negative correlation of serotiny with tree height observed at the very dry site agrees with smaller pines' tendency to generally produce more serotinous cones, especially in post-fire stands (Goubitz *et al.* 2004). This further supports specific serotiny selection by fire rather than by other disturbances (Ne'eman *et al.* 2004). Climatic harshness in water availability terms played a minor role as a driver of serotiny because we found very high serotiny levels at both study sites. However, we detected that tree density had a significant effect on the serotiny levels at the dry site.

Forest managers can improve the resilience of Aleppo pine stands in a warming and drying climate by reducing tree density through thinning and taking into account the post-fire climatic conditions, specifically the water balance. Thinning is useful to improve growth and to promote a large canopy seed bank in young post-fire stands (Verkaik and Espelta 2006; Moya *et al.* 2008, 2008b). Our results indicate that applying similar forest treatments after years of favorable climate conditions, i.e. wet years, would allow maximizing the positive effects on growth and cone production. Conversely, post-fire thinning treatments should be avoided after dry years since these conditions constrain conelets formation.

Finally, extreme climate events, such as severe droughts, alter the reproductive patterns of young Aleppo pine stands. For example, the xeriscense phenomenon (*sensu* Nathan *et al.* 1999) detected in 2005 at the very dry site was due to hot, dry conditions, which promoted the seed release of all the serotinous cones and reduced the potential for post-fire regeneration in that site (Ne'eman *et al.* 2004). In particular, this massive seed release did not result in new cohort recruitment due to the unfavourable climatic conditions for tree recruitment (Alfaro-Sánchez *pers. observ.*). Successful post-fire regeneration in similar xeric areas not only depends on water availability and soil conditions (ash, litter cover, etc.), but it is also conditioned by seed dispersal and viability (Nathan *et al.* 2000). For example, the latter was moderate at the very dry site (64%, cf. Moya *et al.* 2008)

Conclusions

In post-fire young Aleppo pine stands growth and cone production were positively linked and enhanced by wet conditions and lower tree density. Trees with larger basal areas produced more female cones and this positive association intensified as the water balance

improved. Young Aleppo pines produced cones earlier in the very dry site than in the dry site. However, long-term cone production was higher at the dry site than at the very dry site. Lower tree density in post-fire young Aleppo pine stands also enhances growth and cone production thus improving the resilience of these forests facing recurrent fires and droughts. Post-fire thinning should be applied after years of positive water balance in order to maximize the growth and reproductive potentials of Aleppo pine stands.

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575 **Tables**

576 **Table 1.** Percentage of different cone types produced per tree and serotiny (standard errors
577 are provided in parentheses) for different tree densities in study years 2005, 2007, 2009 and
578 2011. Lowercase letters show significant ($P<0.05$) differences for each site and date
579 between density levels.

580

Yeste (dry site)							
Year	Density	Conelets	Green cones	Brown cones	Serotinous cones	Open cones	Serotiny
2005	Moderate	74 (3) ^a	5.0 (1.0)	7.5 (1.1) ^b	12.6 (1.9) ^{ab}	1.4 (0.4)	88 (3)
	High	80.8 (1.5) ^b	3.2 (0.6)	5.9 (0.8) ^b	8.8 (1.0) ^a	1.3 (0.5)	88 (3)
	Control	80 (5) ^{ab}	2.0 (1.0)	1.0 (0.8) ^a	17 (5) ^b	1.0 (0.2)	91 (7)
2007	Moderate	23 (3) ^a	4.3 (0.7) ^b	47 (3)	22.5 (2.3) ^b	2.8 (0.7)	90.4 (2.3)
	High	31.8 (2.1) ^b	2.8 (0.5) ^{ab}	47.5 (2.0)	15.7 (1.3) ^a	2.1 (0.5)	87.3 (2.3)
	Control	23 (6) ^{ab}	0.4 (0.3) ^a	57 (6)	18 (4) ^{ab}	1.9 (1.1)	93 (4)
2009	Moderate	7.3 (1.3) ^{ab}	25.5 (1.9) ^b	9.7 (1.2)	47 (3)	11.0 (1.9) ^b	82 (3)
	High	5.3 (0.7) ^a	29.5 (1.5) ^b	12.9 (1.2)	45.8 (1.8)	6.5 (0.9) ^a	87.8 (1.5)
	Control	12 (4) ^b	15 (3) ^a	10 (3)	54 (6)	9 (3) ^{ab}	81 (5)
2011	Moderate	25 (3)	12.5 (1.5) ^a	17.9 (1.5)	32.0 (2.4)	12.7 (1.4) ^b	71 (3) ^a
	High	23.5 (1.6)	14.4 (1.0) ^{ab}	16.5 (1.0)	37.5 (1.7)	8.1 (0.9) ^a	82.7 (1.7) ^b
	Control	21 (5)	21(4) ^b	13 (4)	38 (6)	7 (3) ^{ab}	84 (7) ^{ab}

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Calasparra (very dry site)							
Year	Density	Conelets	Green cones	Brown cones	Serotinous cones	Open cones	Serotiny
2005	Moderate	5.6 (2.0)	5.8 (1.6)	11 (3) ^{ab}	0 (0)	78 (3) ^b	0 (0)
	High	4.5 (1.0)	5.0 (1.0)	9.0 (1.4) ^a	0.3 (0.2)	81.3 (1.7) ^b	0.4 (0.2)
	Control	8.0 (4)	8 (3)	21 (5) ^b	0 (0)	63 (4) ^a	0 (0)
2007	Moderate	27.0 (3) ^{ab}	12 (5)	22 (3) ^b	39 (6) ^a	0.4 (0.4)	99.2 (0.8)
	High	27.8 (2.0) ^b	7.8 (2.2)	22.4 (2.2) ^b	42 (4) ^a	0.3 (0.3)	98.5 (1.5)
	Control	15 (5) ^a	1.7 (1.7)	3.3 (2.3) ^a	80 (7) ^b	0 (0)	100 (0)
2009	Moderate	60 (5)	2.5 (0.7)	9 (3)	28 (5) ^{ab}	0.08 (0.08)	98.9 (1.1)
	High	67 (3)	3.7 (0.9)	4.7 (1.1)	24.8 (2.4) ^a	0.3 (0.3)	99.5 (0.5)
	Control	49 (8)	1.9 (1.1)	2.5 (1.5)	47 (9) ^b	0 (0)	100 (0)
2011	Moderate	32 (5)	9.4 (1.9) ^a	33 (4) ^b	25 (4) ^a	0.12 (0.12)	97 (3)
	High	25.8 (2.3)	15.7 (1.5) ^b	35 (3) ^b	23.0 (2.3) ^a	0.23 (0.14)	99.1 (0.6)
	Control	25 (13)	0 (0) ^a	7 (5) ^a	68 (4) ^b	0 (0)	100 (0)

Table 2. Coefficients obtained for the best-fitted generalized linear mixed models for the presence or production of cones (a) or for the production of green cones (b) by young Aleppo pines at the two study sites (Yeste, dry site; Calasparra, very dry site) according to fixed (age, tree height, tree density, competition intensity and presence of brown, serotinous or open cones (only for the green cone production)) and random (σ^2_{plot} , σ^2_{tree}) effects.

(a)	Presence of cones		Cone production	
	Yeste (dry site)	Calasparra (very dry site)	Yeste (dry site)	Calasparra (very dry site)
Fixed effects	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)
Intercept	-15.21 (0.01)	-5.3 (0.9)	-1.12 (0.18)	0.01 (0.17)
2000*	8.79 (0.01)	1.2 (0.5)	1.51 (0.16)	0.25 (0.14)
2001	10.89 (0.01)	0.8 (0.5)	1.84 (0.16)	0.21 (0.14)
2005	11.81 (0.01)	-8.1 (1.3)	2.70 (0.18)	-0.76 (0.18)
2007	19.26 (0.02)	-6.0 (1.2)	2.77 (0.18)	0.10 (0.18)
2009	20.62 (0.02)	-7.9 (1.3)	2.88 (0.18)	0.93 (0.18)
2011	18.63 (0.01)	-8.2 (1.5)	2.89 (0.19)	0.83 (0.21)
Tree height	11.80 (0.01)	9.7 (0.9)	0.38 (0.03)	0.28 (0.05)
Tree density	n.s.	n.s.	-0.15 (0.05)	-0.18 (0.08)
Competition intensity	n.s.	n.s.	0.25 (0.03)	0.32 (0.04)
Random effects				
σ^2_{plot}	2	0.4	0.09	0.09
σ^2_{tree}	214	185	0.5	0.4

* 1999 was considered the reference level; n.s. stands for non-significant

(b)	Green cone production	
	Yeste (dry site)	Calasparra (very dry site)
Fixed effects	Estimate (SE)	Estimate (SE)
Intercept	-2.07 (0.01)	-2.9 (0.3)
2007 [†]	-0.20 (0.01)	-0.35 (0.23)
2009	1.74 (0.01)	-0.11 (0.23)
2011	1.02 (0.01)	0.80 (0.30)
Tree height	0.48 (0.01)	0.33 (0.11)
Tree density	-0.23 (0.01)	-0.28 (0.13)
Competition intensity	0.23 (0.01)	0.35 (0.08)
Presence of brown, serotinous or open cones	1.19 (0.01)	1.49 (0.21)
Random effects		
σ^2_{plot}	0.07	0.15
σ^2_{tree}	0.22	0.30

[†]2005 was considered the reference level.

Figures

Figure 1. Trends in area increment of earlywood (EW) and latewood (LW) in both study sites after considering the three density classes. Box plots show: the median (horizontal line within the box), the 25th and 75th percentiles (lower and upper box boundaries), the 10th and 90th percentiles (error bars), and the 5th and 95th percentiles (outliers). The vertical dashed line indicates the thinning treatment carried out in 2004. Note the different scales in the EW area increment of the two study sites.

Figure 2. Relationships (Pearson correlation coefficients) observed between the earlywood –EW, white bars– or latewood –LW, striped bars– area increments and the monthly climatic variables data (T, mean temperature; P-PET, water balance) at both study sites after considering the three density classes (control or very high tree density, high and moderate tree densities). Growth is related with the climatic data from previous (months abbreviated by lowercase letters) and current (months abbreviated by uppercase letters) years, where the current year is the year of tree-ring formation. The bars surpassing dashed lines indicate significance at $P < 0.05$. Values area means $\pm$ SE.

Figure 3. Percentage of trees showing significant ($P < 0.05$) Spearman correlation coefficients between the number of produced green cones and the monthly climatic data (precipitation and water balance). Correlations were calculated for the years of cone formation (t), and also for 1 ($t-1$) and 2 years before ($t-2$). Black and grey bars indicate the positive and negative correlations, respectively.

Figure 4. Relative frequency of reproductive trees according to tree age (a), relative differences in height between the reproductive and non-reproductive trees (H_{R-NR} , see Equation 2) (b), mean tree height at which the probability to have reached sexual maturity was 50% (J_{50}) for each age (different line colours and types) and site (c) and mean ratios ($\pm$ 95% confidence intervals) of relative height of reproductive trees (H_{R-d} , see Equation 3) (d). Quadratic functions are plotted in Figure 4a for illustrating the differences between the two study sites.

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632

633 **Figure 5.** Female cones produced by each tree according to its basal area. The results are
634 presented for the two study sites and the three density levels (control or very high tree
635 density, high and moderate tree densities).

Supporting Information

Figure S1. (a) Annual and seasonal precipitation and mean temperatures measured during the study period at the Yeste (dry site) and Calasparra (very dry site) locations. (b) Climatic diagrams of both study sites show pronounced dry summer periods.