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**Relictual distribution reaches the top: elevation constrains fertility  
and leaf longevity in *Juniperus thurifera*.**

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ABSTRACT: *Juniperus thurifera* populations are scattered throughout the western Mediterranean basin and are relictual from its Tertiary distribution due to progressive climatic warming since the last glacial period. To disentangle the factors responsible for its extremely low fertility we combined a microscale experimental design with a macroscale study. At the microscale we experimentally alleviated environmental stress by watering and fertilizing during two years a set of trees in one population. At macroscale we selected 11 populations across a geographical range and sampled them for three years.

1           Macroscale patterns evidenced that both plant fertility and leaf  
2 longevity diminished with increasing elevation. Both microscale and  
3 macroscale illustrated the importance of water and nutrient availability on leaf  
4 growth and plant fertility: On the microscale experiments, regular supply of  
5 water and nutrients increased fruit set by 300%. Macroscale showed that  
6 increases in resource availability (precipitation) resulted in reductions of seed  
7 abortion, although paralleled by increases in seed predation.

8           Altogether, our results indicate that fertility is constrained both by  
9 elevation and by resource limitation. Therefore any potential lift in the  
10 elevational distribution limits will result in synergistic fertility reductions due to  
11 harder physical conditions and lower water and nutrient availability. Both will  
12 compromise future regeneration of this relictual species, although population  
13 decline might be buffered temporary thanks to longevity of adult trees.

14

15   Keywords: altitude; parthenocarpy, treeline, leaf longevity, leaf growth, seed  
16 predation, migration.

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## **Introduction**

19

20           Elevational migration of high mountain flora is a common response to  
21 environmental warming (Grabherr *et al.*, 1994; Klanderud & Birks, 2003;  
22 Walther, 2003). Warming of the environmental conditions increases the  
23 elevation of both lower and upper plants distribution limits. Increase of lower  
24 distribution limits of a species is not normally due to heat stress but rather to

1 an increase of the upper elevational limit of competitor species with faster  
2 growth rates (Loehle, 1998; Walther, 2003; Alward *et al.*, 2006). On the other  
3 hand, to increase the elevation of their upper distribution limits plants have to  
4 face a set of increasingly harsh environmental factors characteristic of higher  
5 elevations, like lower CO<sub>2</sub> and O<sub>2</sub> partial pressure, higher UV, IR and visible  
6 radiation, and sometimes shorter growth seasons, stronger winds and more  
7 frequent drought events (Barceló *et al.*, 1992; Körner, 2003; De Lillis *et al.*,  
8 2004; Körner, 2007).

9         Ultraviolet radiation from the sun is considered to be particularly  
10 intense at high elevations, increasing by 25% from 200m to 1500m  
11 (Caldwell, 1968). In addition, reduction of stratospheric ozone due to human  
12 release of chlorofluorocarbons to the atmosphere has increased UV radiation  
13 by 6-14% (UNEP, 2002). Although some plant species have the ability to  
14 adapt to high UV levels (Teramura & Sullivan, 1991), UV radiation can be a  
15 significant stress factor for leaves (Caldwell, 1968; Robberecht & Caldwell,  
16 1980; Teramura & Sullivan, 1991) resulting in reduced leaf lifespan and leaf  
17 growth (Ortiz *et al.*, 2002) and reducing flowering frequency and whole plant  
18 fertility (Caldwell, 1968; Koti *et al.*, 2005).

19         Altogether high mountain conditions can inhibit photosynthetic activity  
20 (Kofidis *et al.*, 2003) and reduce net primary productivity (Luo *et al.*, 2004).  
21 Under such unfavorable circumstances reproductive allocation tends to  
22 decrease with increasing elevation (Ortiz *et al.*, 2002; Obeso, 2002; Sakai *et*  
23 *al.*, 2006) and sometimes plants mitigate their reproductive effort by  
24 producing low quality seeds (Houle & Barbeux, 1994). Seed predator species

1 can also migrate to higher elevations due to temperature increases, and  
2 elevate their elevational distribution faster than plants do, increasing  
3 predation rates of previously unaffected populations and species (Hódar &  
4 Zamora, 2004).

5 *Juniperus thurifera* (Cupressaceae) is a dioecious tree inhabiting  
6 semiarid cold environments of the Holartic region and originated during the  
7 Tertiary (Suárez Cardona *et al.*, 1991). It attained its maximum distribution  
8 during the cold periods of the Pleistocene, since then, progressive warming  
9 has reduced its distribution to scattered populations restricted to the high  
10 mountains of the western Mediterranean Basin (Terrab *et al.*, 2008).  
11 Therefore its present day habitats represent a compromise between  
12 environmental harshness and low presence of competitor species (Gómez-  
13 Manzaneque, 1997). Livestock has controlled competition traditionally, but  
14 land abandonment has reduced grazing in recent times, leading to increased  
15 interspecific competition (DeSoto *et al.*, 2009). Like many junipers, *J. thurifera*  
16 presents low seed viability rates (e.g. Roques *et al.*, 1984; García, 1998). A  
17 positive relationship between *J. thurifera* vegetative growth and current year  
18 precipitation was already known (Montesinos *et al.*, 2006). However,  
19 geographical and environmental factors responsible for junipers' low fertility  
20 are unclear (García *et al.*, 2000). Juniper seed viability can be limited by  
21 environmental harshness (García *et al.*, 2000; Ortiz *et al.*, 2002; Wesche *et*  
22 *al.*, 2005), nutrient and water availability (Stephenson, 1981; García *et al.*,  
23 1999; Drenovsky & Richards, 2005) and pollination failure (Ortiz *et al.*, 2002),  
24 although experimental manual pollinations indicate that pollen is not limiting

1 *J. thurifera* fertility (Montesinos unpublished data). Junipers typically present  
2 a very high proportion of parthenocarpic seeds (Fuentes, 2000) and moderate  
3 to high rates of abortion and predispersal seed predation (Rappaport *et al.*,  
4 1993; García, 1998; El Alaoui El Fels *et al.*, 1999). Explanations for  
5 parthenocarpy include frost damage to the ovule, nutrient limitation and  
6 defense against seed predators (Traveset, 1993; Verdú & García-Fayos, 1998  
7 and references therein).

8 In this work we try to elucidate factors responsible for *J. thurifera's*  
9 present day low fertility and to infer the reproductive consequences of an  
10 upward migration as a response to a hypothetical rise in temperature. We  
11 studied variation in seed fate (viability, abortion, predation and  
12 parthenocarpy), leaf longevity and leaf growth at two different scales of  
13 environmental variation: at macroscale, by sampling 11 populations along a  
14 latitudinal range across the Iberian Peninsula; and at microscale, by  
15 experimentally modifying water and nutrient availability on a set of individuals  
16 in one population.

17

## 18 **Material and Methods**

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### 20 *Study species*

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22 *Juniperus thurifera* lives in the calcareous high-mountains of the  
23 western Mediterranean Basin. It is found in the Alps (France and Italy), across  
24 the mountains of the Iberian Peninsula (Spain and French Pyrenees), in the

1 Atlas Mountains (Morocco) and in two small populations in Corsica and Algeria  
2 (Gauquelin *et al.*, 1999). Together with two closely related species with  
3 similar biology (*J. excelsa* and *J. procera*) they are scattered all along the  
4 Mediterranean basin, western Asia and eastern Africa. It forms low-density  
5 pure stands or mixed open forests with *Quercus ilex*, *Q. faginea*, *Pinus nigra*,  
6 *P. sylvestris* and *P. pinaster*. It is often found as a treeline edge species. Trees  
7 are 5-10m high (exceptionally 20m) and often live for centuries (Bertaudière  
8 *et al.*, 1999). Cones take 22 months to develop and ripen and they contain on  
9 average 3.5 (1-7) seeds (Montesinos pers. obs. and Adams *et al.*, 2003).  
10 Viability and germination of *J. thurifera* seeds is extremely low due to high  
11 rates of parthenocarpy, abortion and predation (Ceballos & Ruiz de la Torre,  
12 1979; Melero & García-Fayos, 2001) and seedling recruitment is severely  
13 limited by drought and nutrient availability, which can be partially alleviated  
14 by sex-biased self-facilitation (Montesinos *et al.*, 2007).

15 Fleshy cones are attacked by a variety of pests, but main seed  
16 predators are the chalcid *Megastigmus bipunctatus* (hereafter *Megastigmus*)  
17 and the mite *Trisetacus quadrisetus* (hereafter *Trisetacus*). *Megastigmus*  
18 oviposites on unripe seeds the first summer after pollination and larvae  
19 develop and grow for one more year before they emerge from the seed  
20 leaving a characteristic exit hole (Roques *et al.*, 1984). *Trisetacus* oviposition  
21 occurs much earlier, often before pollination occurs. Mites live in colonies and  
22 use seeds as growth chambers often leading to the destruction of the totality  
23 of the seeds in a cone. Seeds affected by *Trisetacus* colonies present a  
24 characteristic brown "fibrous" morphology (Roques *et al.*, 1984).

1

## 2 *Study sites*

3

4 From French Pyrenees to southern Spain eleven populations (see Fig.  
5 1) were sampled for seeds during three years (2002-2004) and for leaf  
6 growth and longevity in 2004. Sampled populations cover a wide range of  
7 environmental characteristics (Table 1). In each population, we estimated  
8 tree density by counting every individual taller than 2 m in 10 randomly  
9 distributed transects each of 100 m long and 10 m wide.

10 Simultaneously, we randomly selected and permanently marked 20  
11 female trees at population three (Puebla de S. Miguel, Valencia) for the  
12 microscale experiment of water and nutrient addition. This population  
13 corresponds to a *J. thurifera* forest with intermediate precipitation,  
14 temperatures and density in a typical calcareous soil (Table 1). From April  
15 2003 to March 2005, half of the trees were watered and fertilized monthly,  
16 except in June and July, the driest months, when they were watered and  
17 fertilized fortnightly. This method alleviates resource limitation in the broad  
18 sense but does not allow for discrimination of the effect of a particular  
19 resource (i.e. the effect of water alone, or N or P alone). On each date every  
20 tree was supplied with 100 L of 200 ppm balanced fertilization solution  
21 (Universol Blue 18N:11P:18K plus oligoelements, Scotts, USA) according to  
22 manufacturer recommended concentrations. Water was distributed on 20m<sup>2</sup>  
23 around trunks resulting in an approximate increase in precipitation of 50 L ·

1  $\text{m}^{-2} \cdot \text{year}^{-1}$ . This resulted in a net yearly dose of 1000 L of water and 2 Kg of  
2 fertilizer per tree.

3

#### 4 *Seed fate*

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6 We collected 10 ripe cones from each of 20 female trees randomly  
7 chosen each year across every population. Cones were collected from all  
8 around the tree to avoid orientation effects on seed viability and seed set.  
9 Ripe cones were collected in October 2002, 2003 and 2004. Seeds were cut  
10 to expose the embryo and visually assigned to one of five categories: viable  
11 seeds, aborted, parthenocarpic, preyed upon by *Megastigmus* and preyed  
12 upon by *Trisetacus*. Previous tests with 300 seeds showed that estimations of  
13 seed viability by visual identification and with tetrazolium tests did not differ  
14 (t-test comparing 3+3 sets of 50 seeds each;  $t=0.339$   $df=4$ ,  $p<0.751$ ).

15 At the experimentally watered set of trees, three individual branches  
16 were marked in each marked tree and the total number of flowers was  
17 counted in January 2002, before experimental addition of water with fertilizer  
18 started. At the end of the experiment, in October 2004, fruit-set was  
19 estimated following the same procedure, and seeds collected to study  
20 viability.

21

#### 22 *Branch growth and leaf longevity*

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1            *J. thurifera* presents a year-long continuous branch growth occasionally  
2 limited by high temperatures in summer and low temperatures in winter (D.  
3 Montesinos pers. obs.). Natural defoliation due to age and shading from  
4 foliage (Montès *et al.*, 2000) results in feather-duster like branches. In  
5 October 2004, we collected one branch from each of ten male and ten female  
6 trees from each of the 11 populations, and also from the experimental trees  
7 at population 3, by cutting them up to the defoliation point. Stems and leaves  
8 from the last year (bright green leaves on non lignified stems) were manually  
9 separated from older stems and leaves (dark green leaves on dark lignified  
10 stems), dried at 60°C for 48 h and weighed to the nearest 0.0001 g. Yearly  
11 branch growth was compared between populations comparing dry weight of  
12 last year growths. Leaf lifespan estimation method was inspired by the  
13 principles proposed by Mediavilla and Escudero (2003). The ratio between the  
14 dry weight of last year growth and the dry weight of growth from previous  
15 years is a convenient approximation to leaf longevity in scale-like leaved  
16 plants under the assumption that leaf growth is similar among years. This  
17 might be a difficult assumption in Mediterranean environments; however, it  
18 can be a useful approximation when used to compare qualitatively between  
19 watered and not watered plants.

20

21 *Statistical analyses*

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1           Several types of analyses were used to suit different types of data at  
2 macro, and microscale and depending on the number of years available for  
3 each variable.

4           Linear Mixed Models (LMM) permit the study of time-series accounting  
5 for temporal autocorrelations among years; therefore they were used when  
6 data from more than one year were available. LMM with an autoregressive  
7 covariance structure of order one and year as repeated measure were fitted  
8 to the data to analyze the effect of populations' environmental characteristics  
9 (elevation, latitude, mean temperature and precipitation, previous year  
10 precipitation and tree density) on each year's seed fate.

11           Linear Regressions were used to study the effect of different  
12 environmental factors (elevation, latitude, precipitation, etc.) on leaf longevity  
13 and leaf growth, from which data were obtained only once, at the end of the  
14 longevity study. Linear Regressions were also used to study the  
15 autocorrelation between the environmental factors.

16           Finally, for the microscale data, General Linear Models with Gaussian  
17 distribution of errors were fitted to the data to determine if seed viability,  
18 abortion, parthenocarpy, predation or fruit-set were affected by regular  
19 watering with fertilizer.

20           Statistical values throughout the text show the mean $\pm$ SD. Statistical  
21 analyses were performed with SPSS 15.0.

22

23

## Results

24

1 *Seed fate*

2

3 Seed viability averaged  $9.5 \pm 8.8$  % (Mean  $\pm$  SD) among populations and  
4 presented a negative relationship with elevation (Table 2). There were no  
5 other significant relationships between seed viability and any other  
6 environmental or geographical variable (Table 2).

7 Seed abortion averaged  $19 \pm 11$  % among populations and correlated  
8 negatively with previous year precipitation (Table 2 and Fig. 2). Seed  
9 predation averaged  $13.6 \pm 8.7$  % among populations. Two seed predators  
10 were identified: *Trisetacus* ( $6.3 \pm 10$  %) and *Megastigmus* ( $7.3 \pm 4.6$  %). The  
11 first did not show any relationship with climate while the second correlated  
12 positively with previous year precipitation (Table 2 and Fig. 2). The rate of  
13 parthenocarpy averaged  $58.7 \pm 11.9$  % and did not correlate with any other  
14 variable. There were no significant relationships between mean number of  
15 seeds per cone, proportion of filled seeds or seed fate with any other  
16 environmental or geographical variable (data not shown).

17 Regarding the microscale watering and fertilizing experiment at  
18 population 3, seed fate rates were unaffected by watering and fertilization  
19 (Table 3) although watered and fertilized trees produced three fold more ripe  
20 cones per flower ( $0.28 \pm 0.19$  cones/flower) than controls ( $0.09 \pm 0.05$   
21 cones/flower;  $F=6.3$ ;  $df=1$ ;  $p=0.028$ ). It is remarkable that the proportion of  
22 viable seeds was similar on both groups.

23

24 *Branch growth and leaf longevity*

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2           Across the geographical range there were no significant differences  
3 between sexes on branch growth ( $F=0.228$ ;  $df=1$ ;  $p=0.639$ ) or leaf longevity  
4 ( $F=0.755$ ;  $df=1$ ;  $p=0.396$ ) (Table 1). Since our study was focused on seed  
5 production, subsequent analyses on branch growth and leaf longevity  
6 considered only females' leaves. Branch growth did not present any  
7 correlation with any environmental or geographical factor; however leaf  
8 longevity was negatively correlated to elevation (Table 4).

9           Microscale experiments of watering and fertilization significantly  
10 increased branch growth from  $2.8\pm 2.6$  g to  $4.7\pm 3.9$  g ( $F_1=6.15$ ;  $p=0.015$ )  
11 although mean leaf longevity ( $2\pm 0.3$  years) was not affected ( $F_1=0.33$ ;  
12  $p=0.57$ ).

13

#### 14 *Independence of factors*

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16           Regarding the independence of the environmental and geographical  
17 factors, elevation was not correlated with any other variable. However  
18 precipitation and temperature were significantly correlated with latitude, with  
19 higher precipitations and lower mean temperatures at northern latitudes  
20 (none of them affected seed viability). Mean annual precipitation and mean  
21 annual temperature were negatively correlated. Finally, tree density was  
22 independent of any other factor studied (Table 5).

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## **Discussion**

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Elevation significantly reduced both seed viability and leaf longevity of *J. thurifera* trees, as expected for increasingly harsh environments (Caldwell & Robberecht, 1980; Teramura & Sullivan, 1991; Hemborg & Karlsson, 1998; Kofidis *et al.*, 2003; Körner, 2003; Sakai *et al.*, 2006) including light levels which may induce photoinhibition (Close *et al.*, 2003) and low primary productivity (Luo *et al.*, 2004). Similarly, the congeneric *J. communis* also experienced reductions in fertility and branch growth across a single-population elevational transect (Ortiz *et al.*, 2002).

On the microscale, branch growth was increased by water and nutrient supply while leaf longevity was not, in concurrence with other studies (e.g. Jonasson *et al.*, 1997) but see Aerts (1995). Combined, the data suggest that *J. thurifera* branch growth might be more affected by nutrient limitation than by water scarcity, while resource availability is not limiting leaf longevity. Differences in chemical composition in leaves and reproductive cones were likely to alleviate reproductive vs. growth trade-offs as previously suggested by Montès *et al.* (2002), facilitating increases in both branch growth and fruit set when watered and fertilized.

It is remarkable that in our study, both at the microscale experiment and along the macroscale geographical range, parthenocarpy rate was high and regular ( $58.7 \pm 11.9$  %) and was not correlated with any geographical or environmental variable. Trees experimentally supplied with extra water and nutrients maintained both high seed parthenocarpy and low seed viability rates, even though they increased fruit-set more than three fold. Across the

1 macroscale geographical range, precipitation in a given year significantly  
2 reduced *J. thurifera* seed abortion of the following seed crop, indicating that  
3 water stress can be an important limitation for seed viability. However, this  
4 reduction in seed abortion did not result in an increase in seed viability  
5 because it was paralleled by a similar increase in seed predation by *M.*  
6 *bipunctatus*. This agrees with evolutionary explanations of parthenocarpy:  
7 Seed predators have a long evolutionary history in common with junipers  
8 (Roques, 1983; Turgeon *et al.*, 1994; Roux & Roques, 1996) and  
9 parthenocarpy might be a by product of seed predation, reducing both pre  
10 and postdispersal seed predation because predators spend time and eggs in  
11 unviable seeds, thus increasing survival probability of viable seeds (Traveset,  
12 1993; Verdú & Garcia-Fayos, 2000).

13         Increases in water availability both across the macroscale and  
14 experimentally at the microscale did not affect seed viability rates, however at  
15 microscale they dramatically increased fruit-set. We therefore can infer that  
16 resource availability affects fertility through variation in crop size rather than  
17 seed viability. This could be the result of selection for high seed  
18 parthenocarpy (Traveset, 1993; Verdú & García-Fayos, 1998), since there  
19 seems to be a threshold above which additional viable seeds have low  
20 probability of escaping from seed predators.

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## Conclusions

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1 High elevation *J. thurifera*'s populations present significant reductions  
2 in fertility and leaf longevity compared to that of populations from the lower  
3 part of the elevational range. Parthenocarpy seems to be pretty stable among  
4 populations and environments and experimental data indicate that variation in  
5 fertility comes from variation in fruit set size as response to variation in  
6 available resources.

7 Plants are expected to perform better when centered on their original  
8 elevational range (Yakir *et al.*, 1986; Körner & Diemer, 1987; Angert, 2006;  
9 Körner, 2007). Our results permit to hypothesize that *J. thurifera*'s original  
10 distribution range could be centered at lower elevations. Phenotypic plasticity  
11 might partially buffer the consequences of living in a suboptimal environment,  
12 giving room to natural selection to act and favor individuals with  
13 characteristics more suitable for harsher habitats. However, rate of adaptation  
14 can be extremely slow in long-lived conifers, too long for some species to  
15 adapt (Davis *et al.*, 2005 and references therein).

16 On the other hand, some recent studies indicate that faster growing  
17 species like *Quercus ilex* and *Pinus sylvestris* are extending their distribution  
18 limits and transforming nearly monospecific *J. thurifera* forests into mixed  
19 stands with high interspecific competition (Olano *et al.*, 2008; DeSoto *et al.*,  
20 2009).

21 Any additional increase in temperature (e.g. due to global warming)  
22 will fasten *J. thurifera* populations into an "environmental clamp": on one side  
23 faster-growing species are likely to push upwards by competition (Loehle,  
24 1998; Walther, 2003; Alward *et al.*, 2006); on the other side a series of

1 environmental factors associated with high elevations (UV irradiance, lower  
2 resource availability, etc.) are likely to constrain colonization of higher  
3 populations by reproductive downsizing. Besides, previous studies show that  
4 seedling recruitment is severely affected by drought and nutrient limitation  
5 (Montesinos *et al.*, 2007).

6 Altogether, this will compromise the species future, although some  
7 authors point to persistence through longevity as a survival strategy during  
8 interglacial periods (Bennet *et al.*, 1991) and the immediate effect will be  
9 attenuated by the long lifespan (>200 years) of junipers (Garcia & Zamora,  
10 2003).

11

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Population	Latitude (nearest °)	Elevation (m a.s.l.)	Mean annual temperature (° C)	Mean annual precipitation (mm)	Tree density (trees/ha)	Branch growth (g) (2004) (Mean±SD)	Leaf longevity (years) (2004) (Mean±SD)
1.- Nerpio	38°N	1285	14.6	466	690	4.7±2.29	2.26±0.42
2.- Ossa de Montiel	39°N	1000	12.8	448	905	5.01±1.60	2.17±0.42
3.- Puebla de S. Miguel	40°N	1500	12.6	535	423	4.62±1.70	2.03±0.47
4.- Saldón	40°N	1420	10.8	470	596	5.2±2.63	2.71±0.23
5.- Portell de Morella	41°N	1120	11.2	665	178	2.21±1.05	2.41±0.36
6.- Hornuez	42°N	1130	11.4	510	350	5.96±2.39	2.51±0.50
7.- Purburrell	42°N	350	15.2	360	104	6.1±2.30	3.23±1.62
8.- Calatañazor	42°N	1100	9.8	700	429	3.69±1.03	2.44±0.44
9.- Barrios de Luna	43°N	1200	9.4	848	267	6.29±2.01	2.46±0.39
10.- Crémenes	43°N	1150	8.8	1274	327	8.42±3.75	2.38±0.48
11.- Mt. de Rie	43°N	850	11.0	1050	925	-	-

**Table 1:** Sampled populations and their environmental characteristics ordered by latitude (Mean±SD values).

**Table 2:** Macroscale evaluation of seed fate determinants. F values for the Linear Mixed Models (df=1,20). \*p<0.05; \*\*p<0.01; \*\*\*p<0.001

	<b>Viability</b>	<b>Abortion</b>	<b>Parthenocarpy</b>	<b>Predation by <i>Trisetacus</i></b>	<b>Predation by <i>Megastigmus</i></b>
<b>Elevation</b>	<b>9.00**</b>	0.03	0.03	1.97	2.82
<b>Latitude</b>	1.46	2.65	0.09	0.09	0.07
<b>Mean precipitation</b>	1.47	2.23	0.02	0.06	1.48
<b>Pp. prev year</b>	0.27	<b>4.16*</b>	1.75	0.15	<b>8.4*</b>
<b>Mean temperature</b>	0.38	1.40	0.22	0.39	1.11
<b>Density</b>	0.42	0.93	0.60	0.30	3.44
<b>Sex ratio</b>	0.06	0.73	1.92	1.08	0.27

**Table 3:** Microscale watering and fertilization experiments. F values for the Linear Mixed Model 2003-2005 (df=1,13). \*p<0.05; \*\*p<0.01; \*\*\*p<0.001

	<b>Watering with fertilization</b>
<b>Viability</b>	0.23
<b>Abortion</b>	0.92
<b>Parthenocarpy</b>	0.46
<b>Predation <i>Trisetacus</i></b>	0.75
<b>Predation <i>Megastigmus</i></b>	0.04

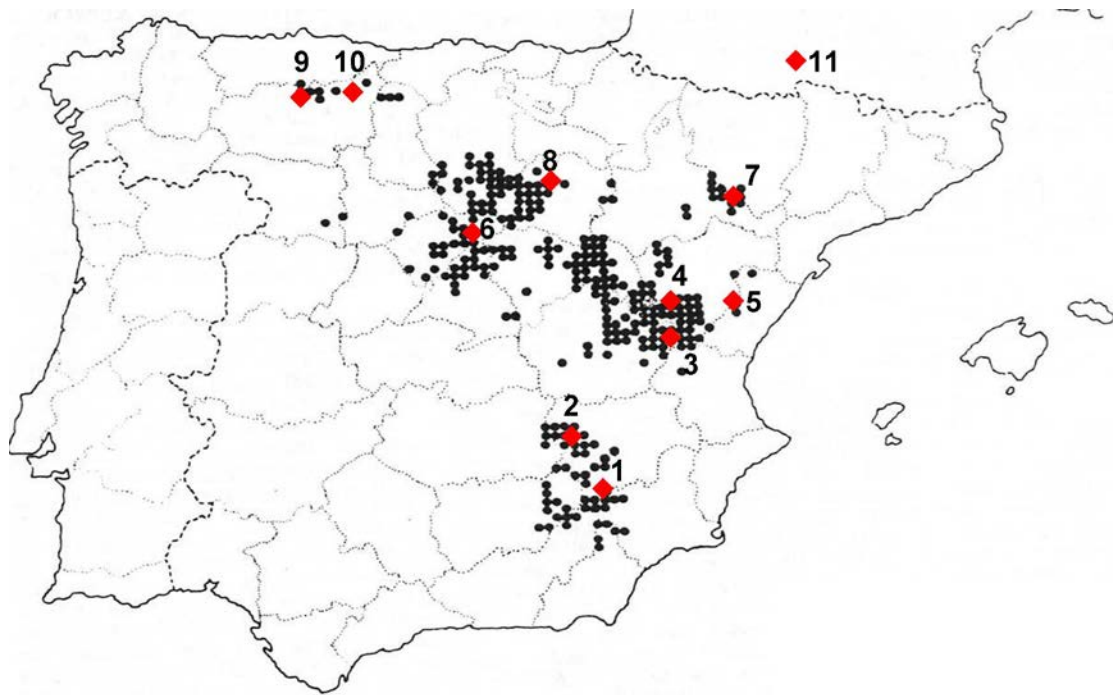
**Table 4:** Macroscale F values for Linear regressions (df=9, notice the absence of samples from population 11). \*p<0.05; \*\*p<0.01; \*\*\*p<0.001

	<b>Branch growth</b>	<b>Leaf longevity</b>
<b>Elevation</b>	0.21	<b>9.47** (R<sup>2</sup>=0.54; B=-0.74)</b>
<b>Latitude</b>	2.55	1.19
<b>Mean precipitation</b>	2.43	0.44
<b>Pp. prev. year</b>	0.41	1.19
<b>Temperature</b>	0.37	0.45

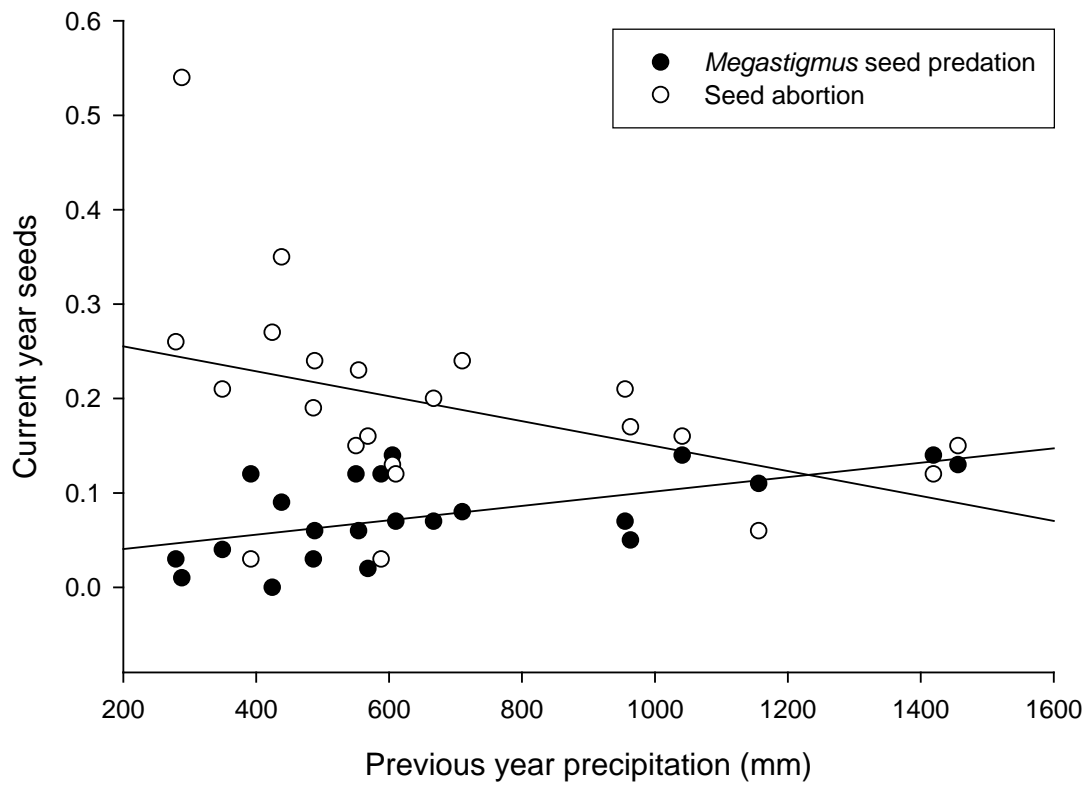
**Table 5:** F values for Linear regressions testing for independence of macroscale factors (df=10). \*p<0.05; \*\*p<0.01; \*\*\*p<0.001

	<b>Latitude</b>	<b>Mean precipitation</b>	<b>Mean temperature</b>	<b>Tree density</b>
<b>Elevation</b>	1.03	0.03	1.47	0.26
<b>Latitude</b>	-	<b>9.39*</b> (B=0.72; R <sup>2</sup> =0.51)	<b>6.35*</b> (B=-0.64; R <sup>2</sup> =0.41)	1.10
<b>Mean precipitation</b>	-	-	<b>10.92**</b> (B=-0.74; R <sup>2</sup> =0.55)	0.01
<b>Mean temperature</b>	-	-	-	0.07





**Fig. 1:** *J. thurifera* Iberian distribution (dots, based on Gómez Manzanque *et al.*, 1993) and studied sites (diamonds): 1-Nerpio; 2-Ossa de Montiel; 3-Puebla S. Miguel; 4-Saldón; 5-Portell de Morella; 6-Hornuez; 7-Purburrell; 8-Calatañazor; 9-Barrios de Luna; 10-Crémènes ; 11-Mt. de Rie.



**Fig. 2:** Precipitation in a given year correlates negatively with following year seed abortion ( $p < 0.05$ ; estimate =  $-1.3 \cdot 10^{-4} \pm 6.5 \cdot 10^{-5}$ ) and positively with seed predation ( $p < 0.05$ ; estimate =  $7.7 \cdot 10^{-5} \pm 2.6 \cdot 10^{-5}$ ) (LMM statistical values shown on table 2). Open dots represent seed abortion rates (0-1), filled dots represent seed predation by *Megastigmus*.