



## Original article

# 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.

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

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

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## 1. Introduction

Elevational migration of high mountain flora is a common response to environmental warming (Grabherr et al., 1994; Klannerud and Birks, 2003; Walther, 2003). Warming of the environmental conditions increases the elevation of both lower and upper plants distribution limits. Increase of lower distribution limits of a species is not normally due to heat stress but rather to an increase of the upper elevational limit of competitor species with faster growth rates (Loehle, 1998; Walther, 2003; Alward et al., 2006). On the other hand, to increase the elevation of their upper distribution limits plants have to face a set of increasingly harsh environmental factors characteristic of higher elevations, like lower CO<sub>2</sub> and O<sub>2</sub> partial pressure, higher UV, IR and visible radiation, and sometimes shorter growth seasons, stronger winds and more frequent drought events (Barceló et al., 1992; Körner, 2003, 2007; De Lillis et al., 2004).

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

Altogether high mountain conditions can inhibit photosynthetic activity (Kofidis et al., 2003) and reduce net primary productivity (Luo et al., 2004). Under such unfavorable circumstances reproductive allocation tends to decrease with increasing elevation (Ortiz et al., 2002; Obeso, 2002; Sakai et al., 2006) and sometimes plants mitigate their reproductive effort by producing low quality seeds (Houle and Barbeux, 1994). Seed predator species can also migrate to higher elevations due to temperature increases, and elevate their elevational distribution faster than plants do, increasing predation rates of previously unaffected populations and species (Hódar and Zamora, 2004).

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*Juniperus thurifera* (Cupressaceae) is a dioecious tree inhabiting semiarid cold environments of the Holarctic region and originated during the Tertiary (Suárez Cardona et al., 1991). It attained its maximum distribution during the cold periods of the Pleistocene, since then, progressive warming has reduced its distribution to scattered populations restricted to the high-mountains of the western Mediterranean Basin (Terrab et al., 2008). Therefore its present day habitats represent a compromise between environmental harshness and low presence of competitor species (Gómez-Manzaneque, 1997). Livestock has controlled competition traditionally, but land abandonment has reduced grazing in recent times, leading to increased interspecific competition (DeSoto et al., 2009). Like many junipers, *J. thurifera* presents low seed viability rates (e.g. Roques et al., 1984; García, 1998). A positive relationship between *J. thurifera* vegetative growth and current year precipitation was already known (Montesinos et al., 2006). However, geographical and environmental factors responsible for junipers' low fertility are unclear (García et al., 2000). Juniper seed viability can be limited by environmental harshness (García et al., 2000; Ortiz et al., 2002; Wesche et al., 2005), nutrient and water availability (Stephenson, 1981; García et al., 1999; Drenovsky and Richards, 2005) and pollination failure (Ortiz et al., 2002), although experimental manual pollinations indicate that pollen is not limiting *J. thurifera* fertility (Montesinos unpublished data). Junipers typically present a very high proportion of parthenocarpic seeds (Fuentes, 2000) and moderate to high rates of abortion and predispersal seed predation (Rappaport et al., 1993; García, 1998; El Alaoui El Fels et al., 1999). Explanations for parthenocarpy include frost damage to the ovule, nutrient limitation and defense against seed predators (Traveset, 1993; Verdú and García-Fayos, 1998 and references therein).

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

## 2. Material and methods

### 2.1. Study species

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

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

### 2.2. Study sites

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

Simultaneously, we randomly selected and permanently marked 20 female trees at population three (Puebla de S. Miguel, Valencia) for the microscale experiment of water and nutrient addition. This population corresponds to a *J. thurifera* forest with intermediate precipitation, temperatures and density in a typical calcareous soil (Table 1). From April 2003 to March 2005, half of the trees were watered and fertilized monthly, except in June and July, the driest months, when they were watered and fertilized fortnightly. This method alleviates resource limitation in the broad sense but does not allow for discrimination of the effect of a particular resource (i.e. the effect of water alone, or N or P alone). On each date every tree was supplied with 100 L of 200 ppm balanced fertilization solution (Universol Blue 18N:11P:18K plus oligoelements, Scotts, USA) according to manufacturer recommended concentrations. Water was distributed on 20 m<sup>2</sup> around trunks resulting in an approximate increase in precipitation of 50 L m<sup>-2</sup> year<sup>-1</sup>. This resulted in a net yearly dose of 1000 L of water and 2 kg of fertilizer per tree.

### 2.3. Seed fate

We collected 10 ripe cones from each of 20 female trees randomly chosen each year across every population. Cones were

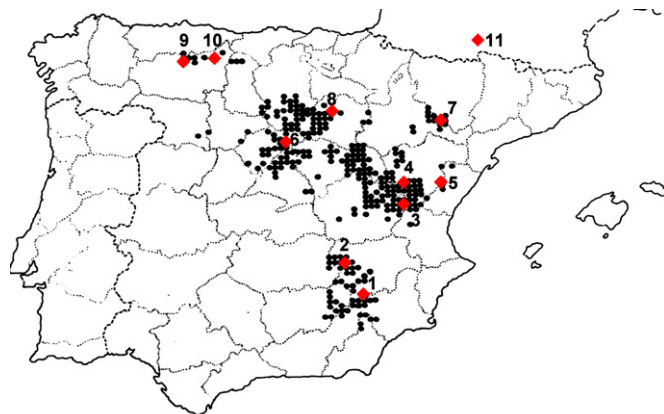


Fig. 1. *J. thurifera* Iberian distribution (dots, based on Gómez Manzaneque et al., 1993) and studied sites (diamonds): 1 – Nerpio; 2 – Ossa de Montiel; 3 – Puebla S. Miguel; 4 – Saldón; 5 – Portell de Morella; 6 – Hornuez; 7 – Purburrell; 8 – Calatañazor; 9 – Barrios de Luna; 10 – Crémenes; 11 – Mt.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

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