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The greater growth rate of male over female of the dioecious tree *Juniperus thurifera* only in worse habitat conditions

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Abstract: Dioecy is a mating system in which a greater reproductive effort has been observed in one sex than the other. This is expressed in differences between the sexes in growth rate and spatial segregation. The spatial structure of *Juniperus thurifera* subsp. *thurifera* and *Juniperus communis* subsp. *communis* and growth rate of tree-ring width of *J. thurifera* were tested in different habitat conditions in Santo Domingo de Silos in northern Spain. We analyzed junipers growing on the eastern slope, with better habitat conditions, and the western, with poorer habitat conditions. The studies found that males of *J. communis* were taller when compared to the females, both on the eastern and the western slope. *J. thurifera* females were taller on the eastern slope (the better habitat), but shorter on the western slope as compared to males. *J. thurifera* males and females on the eastern slope had the greater tree-ring width in comparison with those on the western slope. The annual tree–ring width of males dominated over females on both slopes at first, probably from the time of sexual maturation. However, these differences persisted to the end of the analyzed period only on the poorer western slope. The growth rate of females and males after several years was equal on the eastern slope. Spatial segregation has not been shown, probably due to the homogeneity of the habitat on both slopes. Studies have shown that the decrease of growth rate in *J. thurifera* females can occur only in the poorer habitat conditions.

Additional key words: reproductive effort; sex segregation; tree-ring width; *Juniperus communis* subsp. *communis*

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Introduction

Dioecy ensures cross-pollination of plants. However, only 6% of the world flora has this mating system (Givnish 1980). In addition, plants with a dioecious mating system are considered more vulnerable to extinction as compared with other mating systems (Heilbuth 2000, Vamosi and Vamosi 2005). Besides reduced mate assurance and the seed-shadow handicap (Pannell and Barrett 1998, Heilbuth et al.

2001), the probability of extinction can be increased by differences between male and female individuals (Iszkuło et al. 2009). These differences result from a greater reproductive effort incurred mostly by females, with few exceptions in which a greater reproductive effort was recorded for males (Obeso 2002, Leigh et al. 2006, Massei et al. 2006, Ortiz-Pulido and Pavón 2010).

The spatial segregation of the sexes is a quite frequently observed phenomenon in dioecious species (Bierzychudek and Eckhart 1988, Freeman et al. 1997, Queenborough et al. 2007, Schmidt 2008). Spatial segregation may result from several factors and can be associated with the division of ecological niches between individuals of different sexes.

The differences in mortality between male and female, competition between sexes, the heterogeneity of the environment and possibility of sex change in some species can be factors influencing the spatial "mutual repulsion" of sexes (Bierzychudek and Eckhart 1988, Freeman et al. 1997, Hughes et al. 2010).

The occurrence of gender segregation may reflect physiological, phenological and ecological divergences between individuals of different sexes (Freeman et al. 1997). The literature frequently highlights that the females often occupy places with better conditions for growth and development, while males are more common in areas with less favorable conditions (Freeman et al. 1993, Freeman et al. 1997, Faliński 1998, Queenborough et al. 2007, Ueno et al. 2007, Hughes et al. 2010). Costs associated with the reproduction and mortality rate among them may be higher in females than in males. Gender segregation relieves reproductive costs of female individuals, reducing competition between individuals of different sexes (Bierzychudek and Eckhart 1988, Schmidt 2008).

Slope aspect has a very important influence on habitat conditions (e.g. Desta et al. 2004, Chmura 2008). Particularly contrasting climatic differences were found between the northern and southern slopes. This trend is caused by the greater solar radiation received by south-facing compared to north-facing slopes, resulting in a relatively warmer and drier south-facing slope microclimate (e.g. Desta et al. 2004, Warren 2008). However, the water deficit in the Mediterranean area often makes too big a difference on the north and south slopes for growth of the same species (Peñuelas et al. 1999, Cantón et al. 2004). Nevertheless, the eastern aspect has a much better habitat condition in comparison with the western (Bochet et al. 2009). Soil and plants are frequently moist in the morning. On east slopes the sun's energy has to evaporate this water before the slope can heat appreciably. When the sun reaches the west facing slope, the moisture has already evaporated, so the sun's energy more effectively heats the slope (Price 1981).

To answer the question as to how males and females respond to the different habitat conditions, the following hypotheses were tested: 1) due to improved habitat conditions the eastern slope is better for the colonization of the female specimens, 2) the growth rate of males compared to females is greater on the western slope, and smaller on the eastern, and 3) male and female specimens of *J. thurifera* and *J. communis* exhibit spatial segregation of sexes.

Material and methods

Studied species

Juniperus thurifera L. subsp. *thurifera* is a medium-size, 8–15(20) m tall, dioecious tree (Farjon 2005, Adams 2008). Its range covers the whole Western Mediterranean region, from the western Alps and Corsica in the east, to the Pyrenees, the Cantabrian range, central Iberian ranges and the Andalusian mountains in the west. The centre of the species' presence covers the western part of the Mediterranean, mostly the Iberian Peninsula (Quézel and Médail 2003, Farjon 2005, Adams 2008), and the African *J. thurifera* is recognized as a different taxon (Romo and Boratyński 2007).

Juniperus communis L. subsp. *communis* is a dioecious shrub to 1–3 m tall. It is widely distributed in the Eurosiberian region from Siberia in the Far East, across Central and Western Asia to W Europe (Farjon 2005). In the Mediterranean region it seeks refuge in mountain areas of Anatolia, the Balkans, the Italian Peninsula, Sicily, Corsica, Sardinia and the Iberian Peninsula (Quézel and Médail, 2003, Farjon 2005, Adams 2008); in Morocco and Algeria it is known only from a few localities (Charco 2001, Quézel and Médail 2003).

Since *J. thurifera* and *J. communis* have not been planted very extensively, their seeds have not been transported for long distances (Santos et al. 1999), and the pattern of geographic differentiation of the species has not been disturbed, as has been the case with more important forest trees. For this reason, they provided a good object for investigation of the pattern of growth rate variation in the Mediterranean region.

Study site

J. thurifera and *J. communis* (under the name *J. hemisphaerica*) are dominant in the more continental areas of the Sistema Ibérico range (Rivas Martínez 1987) in northern Spain. They occur in wide areas of the Duriense ecoregion (Alonso Ponce et al. 2010).

The lower mountains towards the south of the northern Sistema Ibérico range mark the Duero Basin margins, and they are oriented from NW to SE, an orientation that appears to be controlled by old tectonic structures (Cortés et al. 2003). These marginal southern Sierras (or lower mountains) are submitted to very dry and continental climatic conditions, and the foehn effect (Romo 1989; 2000). They are protected by the highest cordillera, situated further north, and formed by the Sierras of Demanda and Urbión.

The juniper woodlands dominated by *J. thurifera* subsp. *thurifera* and *J. communis* are found in the more marginal southern mountains of the northern Sistema Ibérico range and the selected station is a good representative of these mountains in contact with the Duero Basin. For this reason, the study plot was established in Santo Domingo de Silos (N 41°58', E 3°25') in northern Spain, at an altitude of about 1190 meters above sea level.

The bedrock of the study site is formed of limestone-marl from the Palaeocene, which in turn are in contact with upper Cretaceous limestone (Quintero et al. 1972), and the soils formed over this subtract are leptic calcisols (FAO 2006).

The average annual temperature in 1950-2006 (results obtained from the data provided by the "Centro Meteorológico de Castilla y León") was 10.8°C with an average rainfall of 681 mm (Fig. 1). The period of probable below-zero temperatures extends from October to May, and the time of sure freeze spans from the beginning of December to the end of February.

The rainy season is autumn, followed by spring and winter; the driest season is summer. The period of summer drought (Walter and Lieth 1960) is estimated at two months. The climatic condition of this station is Mediterranean with a strong continental influence.

The transect was 30 m wide across a small valley, so that its length was equal (50 m) on both the eastern and western slopes. The east slope inclination was 17° and west 15°. Trees were composed of *J. communis* and *J. thurifera* and one individual of *J. oxycedrus*.

In all individuals of *J. communis* and *J. thurifera*, the height and crown width were measured, and for *J. thurifera*, the trunk diameter at 1.3 m high was measured. The presence of male and female cones was used to determine the sex of every individual sampled for this study.

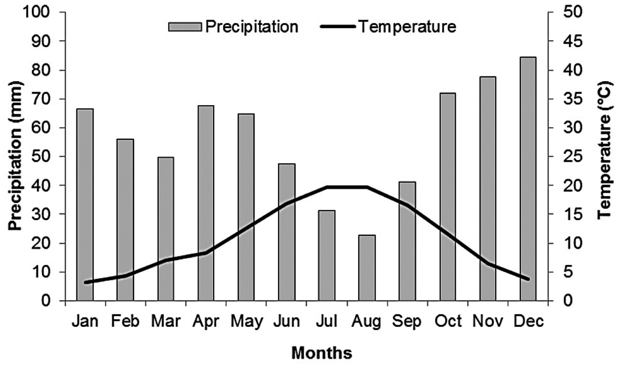

Fig. 1. Average temperature and average total precipitation between 1950 and 2006 at Santo Domingo de Silos meteorological station

In the case of *J. thurifera* on each slope 7 dominant males and 7 females (28 total) were selected. Samples were collected using the Pressler borer. Trees were selected according to the dendrochronological methodology (Schweingruber 1988): dominant trees growing next to each other to avoid differences in environmental conditions.

Tree-ring width and growth rate were analyzed using WinDendro software (Regent Inc.) The samples were scanned at 1200 dpi and a ring-width analysis was conducted on the samples using a WinDendro™ Image analyzing system. Signal homogeneity was subsequently verified using the COFECHA software (Holmes 1994).

Spatial structure

The type of spatial distribution of trees on the plots was analyzed using Ripley's K(d) function. This method is based on the counting of individuals within the circle of radius "d", centred on each individual. The K(d) function analyzes the distances between all trees in the population, which allows us to define the spatial pattern of individuals at different spatial scales. The estimator of Ripley's function has the form: $K(d) = \frac{R}{N^2}\sum_i\sum_j I_d(d_{ij})$ where: R – plot area, N – number of trees, $I_d(d_{ij}) = 1$ if $d_{ij}<0$, $I_d(d_{ij}) = 0$ otherwise, d_{ij} – distance between "*i*" and "*j*" trees.

To stabilize the variance of the function and to make the interpretation easier, the square root transformation of K(d) was applied: $L(d) = \sqrt{\frac{K(d)}{\pi}} - d$.

First, the initial null hypothesis is usually the hypothesis of assumed random spatial distribution of trees (CSR hypothesis), described by the Poisson model. Significance of the departures from the null model can be tested by Monte Carlo simulations. If individuals are randomly distributed in space then $K(d)=\pi d^2$ and $L(d)=0$. If the number of trees within the radius "d" is higher than the expected value for null model, then $L(d)>0$ and it indicates the clumping of trees. If $L(d)<0$, this indicates that trees are evenly spaced within the population (Szwagrzyk and Ptak 1991, Haase 1995, Goreaud and Pélissier 1999, Youngblood et al. 2004, Szmyt and Korzeniewicz 2007, Illian et al. 2008, Dounavi et al. 2010).

To analyze the spatial relationships between trees belonging to two different populations (e.g. two different species, size classes etc.) one can apply the Ripley's K_{12}(d) function for bivariate analysis, this being the modification of the function for univariate analysis (Szwagrzyk 1992, Szwagrzyk and Czerwczak 1993, Haase 1995, Goreaud and Pélissier 2003, Wiegand 2004, Wiegand and Moloney 2004, Fortin and Dale 2005, Perry et al. 2006, Dounavi et al. 2010, López et al. 2010). Function $K_{12}(d)$ can be defined as the expected number of trees of 2nd type within the radius "d" of the circle centred on a tree of 1st type divided by the intensity (e.g. number of trees on the plot area). Similarly to the univariate analysis, $K_{12}(d)$ is then transformed to the form of $L_{12}(d)$ (Wiegand and Moloney 2004, Rozas et al. 2009):

$$L_{12}(d) = \sqrt{\frac{K_{12}(d)}{\pi}} - d$$

In the case of bivariate analysis there is the possibility of applying two different null hypotheses (null models) according to the ecological questions answered (Goreaud and Pélissier 2003, Wiegand and Moloney 2004, Perry et al. 2006, Schmidt 2008, Rozas et al. 2009). Selection between two null models is not an easy task. Misunderstanding in that selection can lead to a wrong interpretation of the obtained results. More detailed information on the appropriate selection of null models can be found in Goreaud and Pélissier (2003).

The hypothesis of spatial independence between individuals belonging to two different populations (independence hypothesis) assumes that both investigated populations result from two different stochastic processes, independently from each other. This theoretical model postulates the lack of spatial relationships between trees from two populations corresponding to their spatial independence in their distribution. If so, the value of $K_{12}(d)=\pi d^2$ and $L_{12}(d)=0$. If $K_{12}(d)>\pi d^2$ and $L_{12}(d)>0$ this suggests that individuals of different populations tend to form intertype aggregations, and if $K_{12}(d)=\pi d^2$ and $L_{12}(d)<0$ it suggests intertype spatial segregation (Baddeley and Turner 2005).

The second null model – random labelling hypothesis – assumes random distribution of labels of individuals of two different populations. The distribution of individuals belonging to two different categories results from the same stochastic process, but their labels (e.g. sex) attributed to each tree are randomly dispersed in the whole population. If $K_{12}(d)=K(d)$ and $L_{12}(d)=L(d)$ then it suggests independence in spatial distribution of labels and the hypothesis of random labelling cannot be rejected. If $L_{12}(d)>L(d)$ we can state that there is a positive spatial correlation between individuals of both types. Negative spatial correlation is stated when $L_{12}(d)<L(d)$ (Goreaud and Pélissier 2003). The significance of departures from null models can be evaluated using Monte Carlo simulations (Szwagrzyk and Ptak 1991, Haase 1995, Goreaud and Pélissier 2003, Wiegand and Moloney 2004, Baddeley and Turner 2008).

To conduct the spatial analysis, SpPack ver. 1.39 software was used (Perry 2004).

Results

Species influenced significantly on the height and breadth of the crown (Table 1), and sex influenced only on the height of trees. However, a significant interaction between sex and species and sex and slope indicates a different response of sexes, in both species and both slopes. *J. communis* males are taller on the eastern and western slope (Table 2). *J. thurifera* females are taller only on the eastern slope. Conversely, on the western slope, females are lower in comparison with males (Table 2).

On the eastern slope were more *J. thurifera* females (46) than males (32). On the western slope the number of individuals is similar in both sexes. *J. communis* females prevailed on both slopes (Table 2).

There were no statistically significant differences in tree-ring width and age between the sexes in *J. thurifera*. Only tree-ring width was significantly wider on the eastern as compared with the western slope in males and females (Table 3). Greater growth rate on the eastern slope confirmed cumulative figure (Fig. 2). However, at the age of about five on the eastern slope and about eleven on the western slope, the differentiation of tree-ring width between males and females was observed. Females experienced lower growth rates than males. However, the growth rate of females and males was equal on the eastern slope at the age of about 25 years. The differences between males and females on the western slope persisted until the end of the analyzed period (Fig. 2).

Spatial pattern

Separate analysis for sexes L(d) function showed that male and female individuals of *J. thurifera* were randomly distributed (Figs. 3A, B). Random type of spatial organization was also confirmed by analysis with respect to the slope exposition (graphs are not presented here).

Analysis of the spatial distribution of *J. communis* sexes indicated that both females and males were distributed in clumps (Figs. 3C, D). However, there were differences between sexes in the spatial scales at

Table 1. Significance of effects of species, sex and slope on height and breadth of crown (ANOVA). Indeterminate individuals were excluded from analysis

		Height		Breadth	
	DF	F	P	F	P
Species	1	3.878	**0.050**	9.747	**0.002**
Sex	1	4.358	**0.038**	0.035	0.852
Species × sex	1	4.946	**0.027**	0.733	0.393
Slope	1	0.239	0.626	0.285	0.594
Species × slope	1	0.044	0.833	4.714	**0.031**
Sex × slope	1	3.472	**0.044**	1.108	0.294
Species × sex × slope	1	2.159	0.143	1.359	0.245

Table 2. Average height and breadth of crown for *J. thurifera* and *J. communis* and trunk diameter at 1.3 m (DBH) and standard error (SE) for females, males and indeterminate individuals in western and eastern slopes

Species	Trait	Slope	Females (SE)		Males (SE)		Indeterminate (SE)	
Juniperus thurifera	N	E	46		32		100	
		W	31		30		143	
	Height (m)	E	4.18	(0.25)	3.36	(0.25)	1.90	(0.12)
		W	3.33	(0.20)	4.09	(0.24)	1.51	(0.08)
	DBH (cm)	E	9.15	(0.78)	7.12	(0.88)	3.87	(0.39)
		W	8.02	(0.72)	8.38	(0.63)	3.32	(0.31)
	Crown width (m)	E	2.69	(0.11)	2.25	(0.15)	1.40	(0.07)
		W	2.55	(0.18)	2.73	(0.16)	1.24	(0.05)
Juniperus communis	N	E	35		18		24	
		W	20		6		24	
	Height (m)	E	0.64	(0.05)	0.81	(0.08)	0.35	(0.03)
		W	0.59	(0.06)	0.80	(0.10)	0.33	(0.03)
	Crown width (m)	E	1.25	(0.13)	1.38	(0.18)	0.45	(0.05)
		W	0.96	(0.13)	1.07	(0.23)	0.40	(0.03)

Table 3. Average (and standard error – SE) tree-ring width and age of analyzed 28 *Juniperus thurifera* trees. Different letters mean significant differences between females and males and west and east slopes (P=0.05, Tukey-Kramer test)

Slope	East				West			
Sex	Female (SE)		Male (SE)		Female (SE)		Male (SE)	
N	7		7		7		7	
Tree-ring width (mm)	1.157a	(0.027)	1.127a	(0.028)	0.900b	(0.017)	0.967b	(0.034)
Age (years)	66.57a	(7.81)	62.83a	(6.27)	60.62a	(7.35)	73.83a	(6.10)

which clumps were observed. In the case of *J. communis* females, clumping could be seen in almost all of the spatial scales taken into consideration (Fig. 3C). On the contrary, males showed random distribution at the scales of 2–8 meters (Fig. 3D).

Spatial relationships between the location of both species females and males did not show any significant differences from the null model assuming the independent distribution of sexes. Thus, no spatial segregation of sexes was observed (Fig. 4).

Analyzing the spatial correlations of between females and males in the dependence on the slope exposition the obtained results did not prove the spatial segregation of sexes of *J. thurifera*. Both on the eastern slope and the western one, the function revealed lack of spatial correlations of sexes (Figs. 5A, B). There was probably no spatial correlation between sexes in the case of *J. communis* on western and eastern slopes. The fact of negative correlations found on the western slope should be attributed to the small number of males on the plot (Figs. 5C, D).

Fig. 2. Relationship between cumulative tree-ring width and tree age of males and females of *Juniperus thurifera* on east and west slope

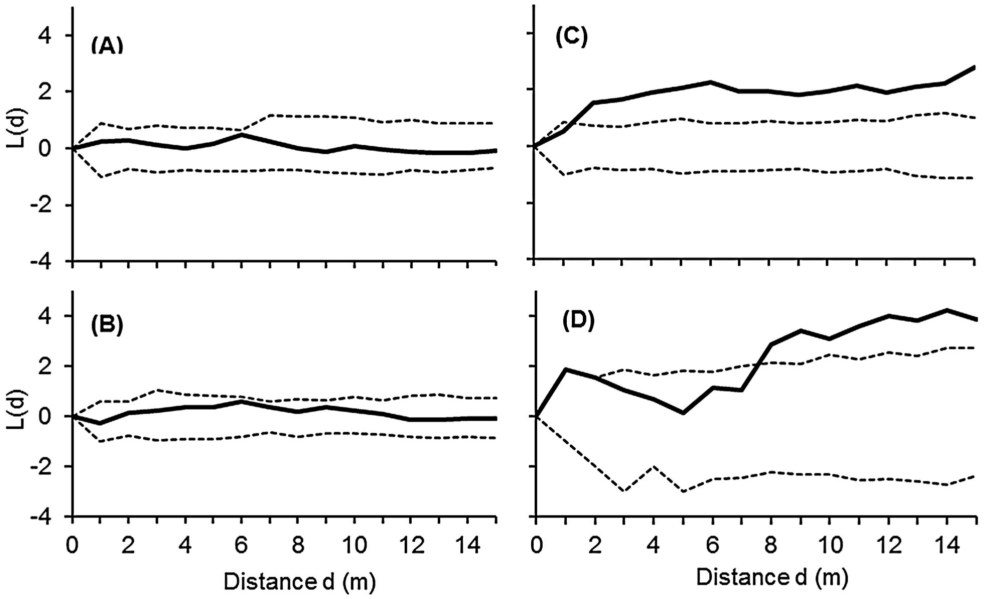

Fig. 3. Spatial pattern for *Juniperus thurifera* females (A) and males (B) and *Juniperus communis* females (C) and males (D) based on L(d) function. Bold solid line means the values for an empirical L(d). Dashed lines are 95% confidence envelopes for the spatial randomness hypothesis

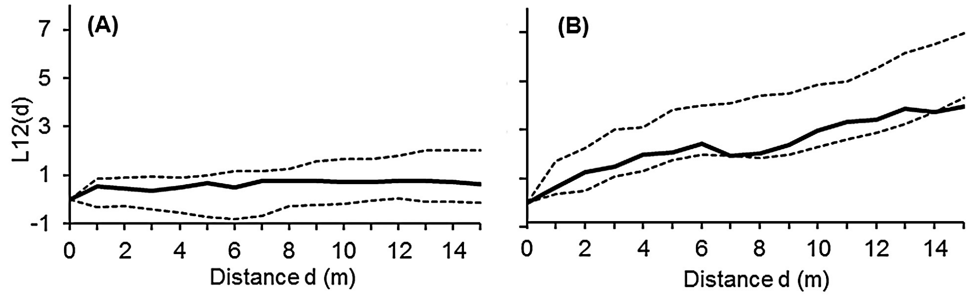

Fig. 4. Interaction between females and males of *J. thurifera* (A) and *J. communis* (B) independently of the slope exposition. Bold solid line is an empirical $L_{12}(d)$ values and dashed lines are 95% confidence envelopes for the random labelling null models

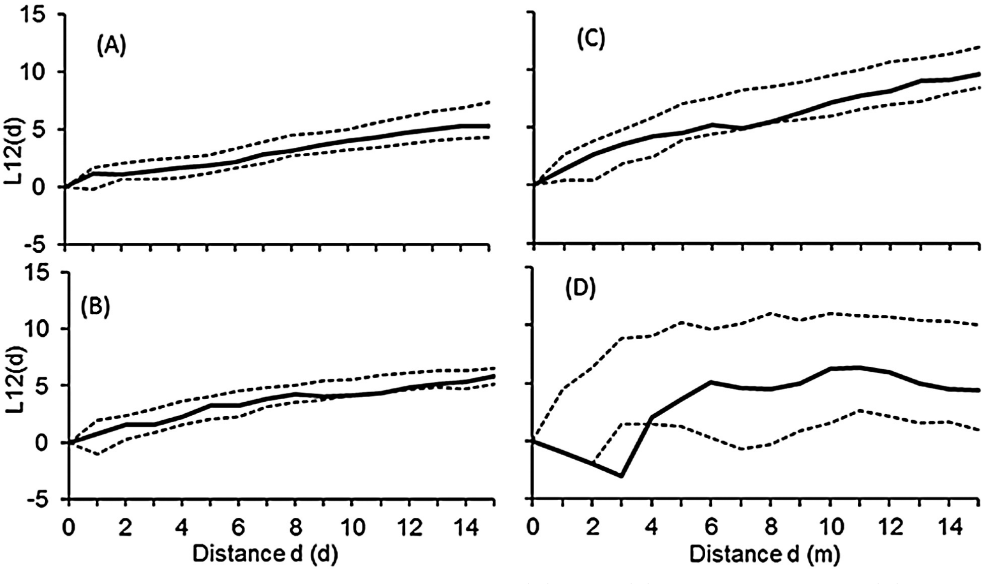

Fig. 5. Interaction between females and males of *J. thurifera* east (A), west (B) and *J. communis* east (C) and west (D) slope exposition. Bold solid line is an empirical $L_{12}(d)$ and dashed lines are 95% confidence envelopes for the random labelling null models

Discussion

The study showed how different ecological conditions affected in the different sex expression in two species of the genus *Juniperus*. *J. communis* reacted like a typical dioecious species. Males were larger as compared to females (Obeso 2002, Ortiz-Pulido and Pavón 2010). *J. thurifera* was very interesting in this context, because its males and females reacted differently on the western and eastern slope. Previous studies of *J. thurifera* showed female-biased sex ratio and females were taller but with a lower radial growth in comparison with males. The habitat conditions were not taken into consideration (Gauquelin et al. 2002).

The western slope, having poorer habitat conditions, was better for the colonization of males. And vice versa, the eastern slope, having better habitat conditions, was better for the colonization of females. This was evidenced by a larger number of females and higher trees of females on the eastern slope and larger number and higher trees of males on the western slope. This confirms earlier reports that females are more demanding in relation to habitat conditions (Freeman et al. 1976, Li et al. 2007).

The poorer habitat conditions on the western slope confirmed a slower growth rate for both males and females. On the eastern slope (better habitat), the age of sexual maturity was probably achieved earlier than on the western, which is probably the cause of the observed differentiation of the growth rate. However, only in a worse habitat, differences in growth rates persisted to the end of the analyzed period.

The greater growth in the females compared to males was found in *Taxus baccata* (Cedro and Iszkuło 2011, Iszkuło et al. 2011), *Rhamnus cathartica* (Bañuelos and Obeso 2004), *J. communis* subsp. *communis* (Iszkuło and Boratyński 2011) and *J. thurifera* (Montesinos et al. 2006). However, for the first time it was proven that differences in growth rate between males and females may persist only in the poorer habitat conditions. This phenomenon is probably connected with the period of sexual maturation (Montesinos et al. 2006) and abundant flower production (Iszkuło and Boratyński 2011). The reduction of growth rate of vegetative organs caused by the production of generative organs was demonstrated in several studies (Morris 1951, Powell 1977, Koenig and Knops 1998). Females make a greater reproductive effort, because they have to produce not only flowers but also seeds over a much longer period (Obeso 2002, Leigh et al. 2006). It was found that the sex ratio favoured males in the more stressful environment. It has been proven that unfavourable conditions had a negative effect chiefly on females in *Hippophaë rhamnoides* (Li et al. 2007) and *Populus cathayana* (Zhao et al. 2011, Zhang et al. 2011, Chen et al. 2011).

However, no sex segregation was found in either of the species. This is probably related to the habitat homogeneity on the east and west slope aspects. The phenomenon of gender segregation is often demonstrated in species with unstable sex, whereas in species with a genetic sex determination, spatial segregation is often not proven (Bierzychudek and Eckhart 1988, Freeman et al. 1997, Nicotra 1998). The spatial segregation of the sexes was often regarded as a phenomenon specific to the dioecious species (Nicotra 1998), but a lack of segregation was often observed and individuals of different sexes showed mutual spatial independence in occurrence or they attracted each other to form clumps consisted of both sexes in the case of *Ceratiola ericoides* (Schmidt 2008), and *Corema conradii* (Rocheleau and Houle 2001).

Ueno et al. (2007) did not find gender segregation in *Salix sachalinensis* in riparian habitats in Japan, characterized by the homogeneity of site conditions. In the case of a greater variety of these conditions, little spatial segregation was found (Ueno and Seiwa 2003). However, a clear segregation of male and female was found in *Salix arctica* (Dawson and Bliss 1989) and *Salix glauca* (Dudley 2006). Gender segregation resulted from the variable site conditions, particularly humidity. Females often occurred in the flooded areas while males mainly inhabited drier sites. Similar relationships were found for *Salix lapponum* and *S. myrsinifolia-phylicifolia*, although gender segregation was not so clear on all tested sites (Hughes et al. 2010). Queenborough et al. (2007) found no clear gender segregation in the species from the family of Myristicaceae in Amazonian forests.

The study showed, that males and females of *J. thurifera* reacted in a different way to habitat conditions. In the Mediterranean area the eastern slope has better habitat conditions and females grow better in comparison with males. On the western slope, in worse habitat conditions males grow better when compared with females. Spatial segregation has been shown in neither of the species, probably due to the homogeneity of the habitat on both slopes.

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