

## Similar Gender Dimorphism in the Costs of Reproduction across the Geographic Range of *Fraxinus ornus*

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• **Background and Aims** The reproductive costs for individuals with the female function have been hypothesized to be greater than for those with the male function because the allocation unit per female flower is very high due to the necessity to nurture the embryos until seed dispersal occurs, while the male reproductive allocation per flower is lower because it finishes once pollen is shed. Consequently, males may invest more resources in growth than females. This prediction was tested across a wide geographical range in a tree with a dimorphic breeding system (*Fraxinus ornus*) consisting of males and hermaphrodites functioning as females. The contrasting ecological conditions found across the geographical range allowed the evaluation of the hypothesis that the reproductive costs of sexual dimorphism varies with environmental stressors.

• **Methods** By using random-effects meta-analysis, the differences in the reproductive and vegetative investment of male and hermaphrodite trees of *F. ornus* were analysed in 10 populations from the northern (Slovakia), south-eastern (Greece) and south-western (Spain) limits of its European distribution. The variation in gender-dimorphism with environmental stress was analysed by running a meta-regression between these effect sizes and the two environmental stress indicators: one related to temperature (the frost-free period) and another related to water availability (moisture deficit).

• **Key Results** Most of the effect sizes showed that males produced more flowers and grew more quickly than hermaphrodites. Gender differences in reproduction and growth were not minimized or maximized under adverse climatic conditions such as short frost-free periods or severe aridity.

• **Conclusions** The lower costs of reproduction for *F. ornus* males allow them to grow more quickly than hermaphrodites, although such differences in sex-specific reproductive costs are not magnified under stressful conditions.

**Key words:** Costs of reproduction, *Fraxinus ornus*, meta-analysis, sexual dimorphism.

### INTRODUCTION

Many different breeding systems have evolved in plants, including sexually monomorphic (hermaphroditism, monoecy, andromonoecy, gynomonoecy) and polymorphic (androdioecy, gynodioecy, dioecy, polygamodioecy) systems (Webb, 1999; Barrett, 2002). The evolution from monomorphic to polymorphic breeding systems has probably been driven by selective forces avoiding inbreeding and favouring sexual specialization (Bawa, 1980; Freeman *et al.*, 1997; Gleiser and Verdú, 2005; Pannell and Verdú, 2006; Verdú and Gleiser, 2006).

The separation of the sexes following the evolution from monomorphic to polymorphic breeding systems has traditionally been thought to lead to differences in the costs of reproduction among individuals of the same species. This hypothesis states that the costs for those individuals assuming the female function are greater than those assuming the male function (Lloyd and Webb, 1977; Delph, 1999). The underlying reasoning is that females would invest a lot of resources into reproduction because the allocation unit per flower (which is a large component of the overall reproductive investment) is very high due to the necessity to nurture the embryos until seed dispersal

occurs. In contrast, the male's reproductive allocation per flower is lower because it finishes once pollen is shed. This would allow the males to invest the saved resources in more vegetative growth, as occurs in many dioecious species [for an experimental demonstration that controls for genotype, age, habitat and reproductive history, see Wheelwright and Logan (2004), and also see reviews in Delph (1999) and Obeso (2002)]. This is not necessarily true if male plants are undergoing sexual selection on floral display for increased mating success (Bond and Maze, 1999; Delph *et al.*, 2005). Under this scenario of sexual selection, male reproductive costs may be greater than those of females.

The study of gender-related differences in reproductive allocation between individuals allocating more to reproduction versus individuals allocating less constitutes a non-manipulative experiment to study the costs of reproduction (Obeso, 2002). *Fraxinus ornus* (Oleaceae) is a sexually dimorphic species in which males coexist with hermaphrodites and therefore differences in reproductive costs between genders may be expected, because males only invest in one (the cheapest) sexual function whereas hermaphrodites invest in both functions. Verdú (2004) has recently shown that *F. ornus* males from Spanish populations produce more flowers but grow similarly to

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hermaphrodites. Nothing is known about the geographical variation of these reproductive costs associated with gender. The range of distribution of *F. ornus*, extending across south and central Europe and western Asia, provides a good research system for looking at the geographical variation of the gender-associated costs of reproduction in a species with a strongly asymmetric breeding system.

Intraspecific variability in the costs of reproduction associated with geographical and ecological conditions has been found for several species (see Obeso, 2002, and references therein). The main hypothesis regarding the geographical variability of gender-associated differences is that: costs will be more apparent under harsh conditions, and that females are more affected by them if they maintain greater reproductive investment than males under those conditions (Cox, 1981; Reznick, 1985; Bierzychudek and Eckhart, 1988). The costs of reproduction may be not revealed because they can be compensated for by phenological or physiological mechanisms (for a discussion of compensating mechanisms, see Obeso, 2002).

The present study specifically tested: (a) whether *F. ornus* hermaphrodites have higher costs of reproduction than males and (b) whether increased climatic stress across much of the geographic range of the species magnifies the differences in sex-specific reproductive costs, as has been predicted. These issues were addressed by summarizing the gender-related differences of reproductive and vegetative characters in ten populations from three countries located at the northern (Slovakia), south-eastern (Greece) and south-western (Spain) limits of the *F. ornus* European distribution. A random-effects meta-analysis approach was used to calculate the direction and magnitude of the gender-related differences while accounting for both the

sampling error and the variability among populations (Rosenberg *et al.*, 2000).

## MATERIAL AND METHODS

### *Study species and sites*

*Fraxinus ornus* L. (Oleaceae) is a deciduous, small, wind-dispersed tree pollinated by both insects and wind, inhabiting mixed woods, thickets and rocky places from southern and central Europe and western Turkey (Fig. 1) (for a description of the natural history of the species, see Verdú, 2004). The species is morphologically androdioecious (i.e. males coexist with hermaphrodites) but functionally dioecious because the pollen from hermaphrodites, although viable, has a low siring success in the population (Verdú *et al.*, 2004; Spanos and Gaitanis, 2005; Verdú *et al.*, 2006). The clear signature of the functional dioecy in this species is the 1 : 1 sex ratio consistently found in all the populations studied (Verdú *et al.*, 2006). Fluctuation in the numbers of inflorescences between years follows a biannual cycle typical of masting species (see fig. 4 in Verdú, 2004). Flowers of both sexes are similarly sized except for the gynoecium, which is rudimentary in males (Domme *et al.*, 1999; Wallander, 2001). The sex of the trees does not change between years (Verdú, 2004). No spatial segregation of the sexes occurs.

Data on reproductive and vegetative traits of ten *F. ornus* populations were collected from three different countries located at the south-western (Spain), northern (Slovakia) and south-eastern (Greece) limits of its distribution range in Europe (Fig. 1). These populations had contrasting climatic and ecological characteristics

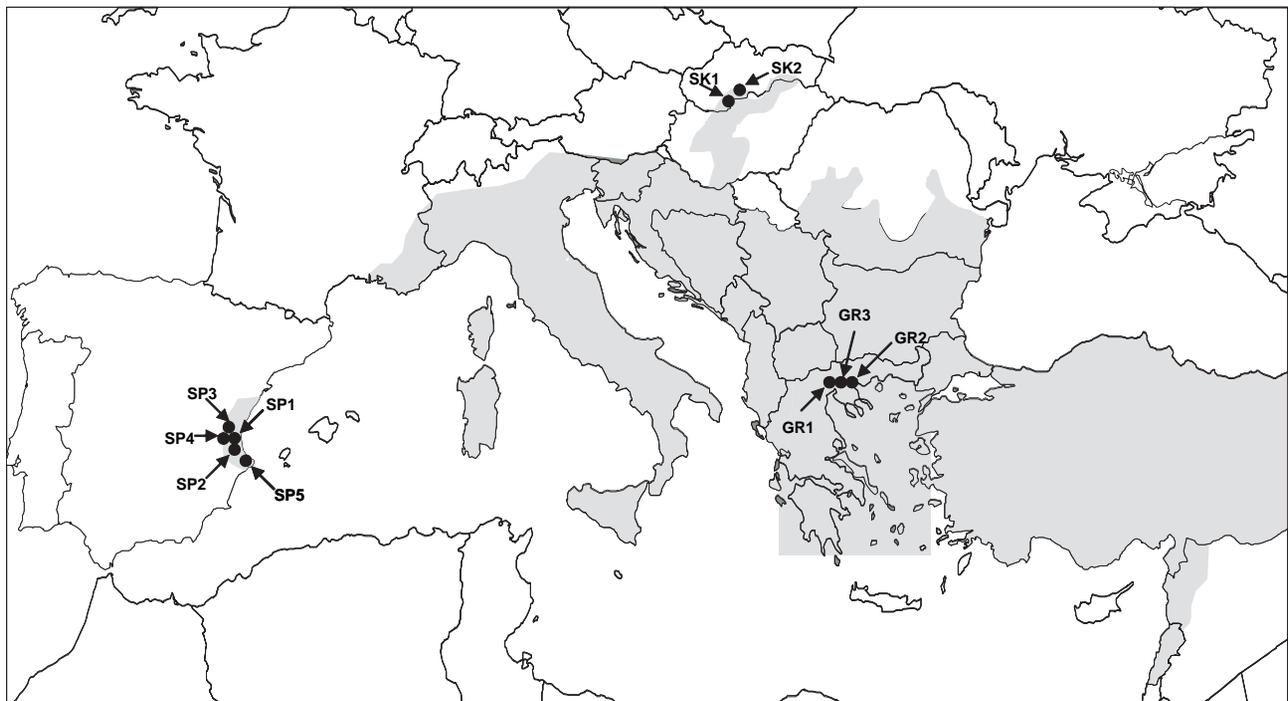


FIG. 1. Distribution map of *Fraxinus ornus* showing the study populations: SP1–5 (Spain); SK1 and 2 (Slovakia); GR1–3 (Greece).

(Table 1). Data were mainly collected between 2002 and 2004, with older data coming from Verdú (2004) having also been included.

#### Reproductive characters

The first 60 trees found along a linear transect were tagged and the number of flowers per inflorescence counted in populations from Spain (Bunyol, Font Roja and Sella), Greece (Chortiatis) and Slovakia (Kováčov and Príbelce) over several years. In each population, the numbers of flowers were counted in five to ten inflorescences uniformly spaced around the canopy for ten males (range 6–14) and ten hermaphrodites (range 6–13).

The number of inflorescences per tree was directly counted in Spanish populations or estimated by category from 0 to 4 (0 = no inflorescences at all; 1 = <10 % of the branches had inflorescences; 2 = 10–50 %; 3 = 50–90 %; 4 = >90 %) in the rest of populations. On average, 18 males (range 11–32) and 22 hermaphrodites (range 18–32) per population were sampled. Due to the lack of flowering of the trees from the two Slovakian populations in 2004 and in most of the Spanish populations in 2000 these sites/years were not included from the analysis.

The number of pollen grains per flower was assessed in one to four flowers of 27 trees (14 males and 13 hermaphrodites) randomly selected in the Font Roja population with the help of a haemocytometer of 0.0025, mm  $2 \times 0.1$  mm depth (Neubauer Improved, Marienfeld, Germany; see Verdú, 2004).

#### Vegetative characters

Primary growth, measured as the mean length of ten current year shoots uniformly spaced around the canopy of each tree, was estimated in one Spanish (Font Roja) and two Slovakian (Kováčov and Príbelce) populations after the end of the growing season. On average, 27 males (range 10–34) and 25 hermaphrodites (9–31) were randomly sampled in each population.

Secondary growth was measured in two different forms: DBH increment and annual ring growth of the last 5 years. DBH increment was measured as the difference in the trunk diameter between 2003 and 2004 in the two Slovakian populations (34 males and 28 hermaphrodites in Kováčov and 29 males and 31 hermaphrodites in Príbelce). The width of the last five annual rings of ten one-stemmed trees of each gender was measured in a Greek population (Petrokerasa). Woody stem sections were taken at about 1 m height from the stem base and the total growth of the last five rings was measured at 0.1 mm precision, as well as the age of each tree. There were no significant differences in the age of males ( $27.4 \pm 5.9$  years) and hermaphrodites ( $29.8 \pm 9.8$  years) ( $F_{1,18} = 0.43$ ;  $P = 0.51$ ).

#### Compensatory mechanisms (length of photosynthetic period)

It was hypothesized that hermaphrodites may compensate for their higher reproductive investment by producing

their leaves earlier in the spring or retaining them later in the autumn when compared with males. The length of the photosynthetic period was recorded as the time elapsed between the start and the end of the leafing period in two Spanish (Alzira and Font Roja), two Greek (Doubia and Petrokerasa) and two Slovakian (Kováčov and Príbelce) populations. The length of the photosynthetic period was recorded in 29 males (range 23–33) and 28 hermaphrodites (range 17–35) per population. The trees were the same individuals as the ones in which reproductive characters were monitored. Each population was visited every week.

#### Climatic predictors

To study the variation in the gender-associated costs with stressful conditions, two indices of stress were used: one related to temperature (the frost-free period) and another related to water availability (moisture deficit). The frost-free period was calculated as the number of days between the last freezing temperature (0 °C) of the spring and the first frost in the autumn. The moisture deficit was calculated as the difference between the potential and the real evapotranspiration calculated following the Thornthwaite method (Thornthwaite, 1948). Data correspond to an historical series obtained from the nearest climatic stations (Table 1).

#### Statistical methods

Due to the great heterogeneity in the type of measurement, sites, years and data gatherers, it was decided to use meta-analytical tools for the statistical analyses (Verdú and Traveset, 2005). The purpose of a meta-analysis is to examine the magnitude of an effect and its consistency among studies when there is a body of experimental data that measures the same effect in different ways (Rosenberg *et al.*, 2000). Random-effects models, which conceptualize the study sites as a random sample of all existing sites, were applied, increasing the generalizability of the results to the rest of the sites not included in the present study (Kalaian, 2003).

The effect size selected for summarizing the gender-related differences across studies was Hedges'  $d$ , which estimates the standardized mean difference between males and hermaphrodites ( $X^H - X^M$ ) and is not biased by small sample sizes (Hedges and Olkin, 1985). Hedges'  $d$  was calculated by means of the following equation:

$$d = \frac{(\bar{X}^H - \bar{X}^M)}{S} J$$

where  $S$  is the pooled standard deviation and  $J$  is the correction factor accounting for the small samples sizes (see Rosenberg *et al.*, 2000). Negative effect sizes indicate that males have larger trait means (e.g. longer shoots or more flowers) than hermaphrodites. All the individual effect sizes were summarized by calculating a cumulative effect size, which is a simple weighted mean. The weight is a

TABLE 1. *Ecological and climatic characteristics of the study populations of F. ornus*

Country	Population	Code	Co-ordinates	Altitude (m a.s.l.)	$T$ (°C)	Prec. (mm)	$T_c$ (°C)	$T_h$ (°C)	FFP (days)	MD (mm)	Other dominant species
Spain	Alzira	SP1	39°09'N 0°26'W	300	15.5	802	8.7	23.6	291	340	<i>Pinus halepensis</i> , <i>Quercus coccifera</i>
Spain	Font Roja	SP2	38°42'N 0°28'W	1350	11.6	825	7.5	23.6	278	304	<i>Quercus ilex</i> , <i>Acer opalus</i>
Spain	Bunyol	SP3	39°25'N 0°57'W	800	13.9	505	6	22.6	235	245	<i>Quercus faginea</i> , <i>Q. ilex</i>
Spain	Bicorp	SP4	39°09'N 0°48'W	600	17	630	10	25.6	289	254	<i>P. halepensis</i> , <i>Q. ilex</i>
Spain	Sella	SP5	38°38'N 0°18'W	450	17.5	388	10.7	25.9	356	324	<i>P. halepensis</i> , <i>Pistacia lentiscus</i>
Slovakia	Kováčov	SK1	47°50'N 18° 49'E	180	10.2	551	-1.4	20.4	183	200	<i>Quercus pubescens</i> , <i>Quercus cerris</i>
Slovakia	Príbelce	SK2	48°12'N 19°15'E	420	9.4	631	-2.4	19.7	162	200	<i>Quercus petraea</i> , <i>Q. cerris</i>
Greece	Chortiatis	GR1	40°38'N 23°08'E	350–400	14.6	496	0.4	30.2	355	500	<i>Q. coccifera</i> , <i>Q. Pubescens</i> , <i>Carpinus orientalis</i> , <i>Quercus conferta</i>
Greece	Doubia	GR2	40°30'N 23°17'E	300–350	15.3	455	0.6	31.2	361	500	<i>Q. coccifera</i> , <i>Q. pubescens</i> , <i>C. orientalis</i>
Greece	Petrokerasa	GR3	40°31'N 23°16'E	420–472	14.8	484	0.5	30.5	357	500	<i>Q. pubescens</i> , <i>Q. Coccifera</i> , <i>C. orientalis</i> , <i>Q. conferta</i>

Data correspond to historical series obtained from the nearest climatic stations.

$T$ , Mean annual temperature; Prec, mean annual precipitation;  $T_c$ , mean temperature of the coldest month;  $T_h$ , mean temperature of the hottest month; FFP, frost-free period (the number of days between the last freezing temperature (0 °C) of the spring and the first frost in the fall); MD, moisture deficit (ETP – ETR).

function of the individual variances plus a random component (for mathematical details, see Rosenberg *et al.*, 2000). To test for the cumulative effect size differing from zero, bootstrap 95 % confidence intervals (999 iterations) were calculated to estimate if zero was contained in such intervals.

To test if the effect sizes were homogeneous across the studies, the total heterogeneity ( $Q_T$ ) of the sample, which is tested against a  $\chi^2_{n-1}$  distribution under the null hypothesis of no heterogeneity among studies, was calculated.

The traits indicating costs of reproduction were grouped into two categories: vegetative and reproductive. The trait indicating a possible compensation mechanism (length of photosynthetic period) was analysed separately.

To study the variation of the gender-associated costs with stressful conditions, a random-effects meta-regression was performed between the effect sizes and both the frost-free period and the moisture deficit. The meta-regression, similar to the standard ANOVA, makes a partition of the total heterogeneity ( $Q_T$ ) into the heterogeneity due to the model ( $Q_M$ ) and due to the residual error ( $Q_E$ ). The significance level of  $Q_M$  is tested against a  $\chi^2$  distribution. This procedure takes into account the hierarchical structure of the meta-analytic data by adding a 'between-sites' model which specifies the distribution of the site-effect sizes as a function of the site characteristics and random errors (Raudenbush and Bryk, 2002). All these analyses were run with the help of the MetaWin 2.0 statistical program (Rosenberg *et al.*, 2000).

As the dataset included multiple data points from the same population, either from different years or different measures, the lack of statistical independence may bias the statistical tests. To control for this effect, we reran all the analyses by means of a meta-analytical general linear model in which population and year were considered as blocks. The population was dummy coded before entering into the mixed meta-regression, which was fitted with the help of the MetaReg macro for SPSS available at the D. B. Wilson's homepage (<http://mason.gmu.edu/~dwilsonb/ma.html>).

## RESULTS

The mean number of reproductive structures as well as the flowering intensity varied largely between populations and years, as expected in a masting species like *F. ornus* (Table 2). For example, Greek populations flowered with low intensity (1.78–2.31 in the scale 0–4) and few flowers per inflorescence (825) whereas the Slovakian population flowered more intensively (3.26–3.24) and with more flowers per inflorescence (1000–1500). The number of inflorescences per tree in Spanish populations varied among years and populations, ranging from 5 to 84. Despite all this variability among years and populations, males produced significantly more reproductive structures than hermaphrodites (Table 2). On average, males produced 41 % more flowers per inflorescence, 60 % more inflorescences per tree and 12 % more pollen grains per flower than hermaphrodites. The flowering intensity scale

also showed that males flowered 2 % more intensively than hermaphrodites. The meta-analysis of all these data (Fig. 2) revealed a significant gender effect size on the reproductive output [Hedges'  $d = -0.31$ ; 95 % bootstrap CI (-0.46, -0.19)], indicating that males have more reproductive structures than hermaphrodites. This pattern was consistent across years and populations as indicated by the non-significant total heterogeneity ( $Q_T = 22.15$ ; d.f. = 23;  $P = 0.45$ ). When the general linear model including year and population as statistical blocks was run to account for the effect of possible non-independence of the data points, the estimation of the magnitude of the sexual dimorphism on the reproductive output was very similar to that obtained in the simpler model (Hedges'  $d = -0.32$ ).

Temporal and spatial variability among populations in the mean shoot growth rates occurred, ranging from 2.2 cm in one Slovakian population (Kovakov) to 3.2 cm in the Spanish (Font Roja) and the other Slovakian population (Pribeľce) (Table 2). The primary and the secondary growth were significantly greater for males [Hedges'  $d = -0.45$ ; 95 % CI (-0.83, -0.07)]. On average, male tree ring growth for the last 5 years was 76 % greater than that of hermaphrodites. Similarly, annual shoot growth was 22 % greater in males. DBH increments were larger for males in one population while the reverse was true in the other study population. Despite the geographical and temporal variability depicted (Fig. 3), the set of effect sizes across populations were homogeneous, as the non-significant total heterogeneity reveals ( $Q_T = 8.93$ ; d.f. = 7;  $P = 0.25$ ). The estimation of the magnitude of the sexual dimorphism on the vegetative output remained very similar after blocking by population and year (Hedges'  $d = -0.46$ ).

The length of the photosynthetic period ranged from 188 d in a Slovakian population (Pribeľce) to 252 d in a Spanish population (Alzira) with a negligible difference between sexes (0.47 %). Therefore, the costs of reproduction were not compensated for by longer photosynthetic periods of hermaphrodites relative to males, as shown by the non-significant gender effect [Hedges'  $d = 0.04$ ; 95 % bootstrap CI (-0.17, 0.31)], which was consistent across populations and years ( $Q_T = 9.36$ ; d.f. = 9;  $P = 0.40$ ). Blocking by population and year did not result in a substantial change of our estimate of the gender effect on the length photosynthetic period (Hedges'  $d = 0.05$ ).

The frost-free period ranged from a very short growing season in the northern populations (162 d) to long seasons in the south-eastern populations (361 d) (Table 1). The gender-associated costs on reproductive characters did not decrease under restrictive climatic conditions imposed by shorter growing seasons, as the non-significant meta-regression between the gender effect size on reproduction and the frost-free period indicated ( $y = -0.68 + 0.001x$ ;  $Q_M = 1.47$ ;  $P = 0.22$ ). Similarly, the stress imposed by aridity, which ranged from 200 to 500 mm (Table 1), did not explain the differences in the effect that gender has on the reproductive costs because the gender effect size was not correlated with the moisture deficit ( $y = -0.64 + 0.001x$ ;  $Q_M = 2.41$ ;  $P = 0.12$ ). The

TABLE 2. Raw data of the study variables across sites and years

Population	Year	Country	Category	Trait	$X_{\text{male}}$	s.d. <sub>male</sub>	$n_{\text{male}}$	$X_{\text{herm}}$	s.d. <sub>herm</sub>	$n_{\text{herm}}$	$P$
Chortiatis	2004	GR	Reproductive	Flowers/inflorescence	925	484	11	726	306	10	0.27
Kováčov	2003	SK	Reproductive	Flowers/inflorescence	1959	955	10	1117	292	10	0.01
Príbelce	2003	SK	Reproductive	Flowers/inflorescence	1208	391	10	812	195	10	0.01
FontRoja	2002	SP	Reproductive	Flowers/inflorescence	894	577	14	859	598	13	0.87
Sella	1999	SP	Reproductive	Flowers/inflorescence	1559	647	6	908	541	6	0.08
Bunyol	1999	SP	Reproductive	Flowers/inflorescence	1511	880	10	1277	531	10	0.48
FontRoja	2002	SP	Reproductive	Pollen grains/flower	65296	16176	14	58133	19965	13	0.31
Kováčov	2003	SK	Reproductive	Flowering intensity (0–4)	3.35	0.73	34	3.17	0.90	28	0.38
Príbelce	2003	SK	Reproductive	Flowering intensity (0–4)	3.27	0.88	29	3.29	0.74	31	0.92
Doubia	2003	GR	Reproductive	Flowering intensity (0–4)	2.37	0.97	32	2.25	0.75	28	0.59
Petrokerasa	2003	GR	Reproductive	Flowering intensity (0–4)	1.75	0.64	28	1.81	0.69	32	0.72
FontRoja	1999	SP	Reproductive	Inflorescences/tree	27.11	53.84	18	9.22	19.84	18	0.19
FontRoja	2001	SP	Reproductive	Inflorescences/tree	14.33	32.17	18	3.22	6.76	18	0.16
FontRoja	2002	SP	Reproductive	Inflorescences/tree	68.44	77.3	18	56.38	66.33	18	0.61
Alzira	1999	SP	Reproductive	Inflorescences/tree	31.87	30.14	16	27.23	42.96	21	0.71
Alzira	2001	SP	Reproductive	Inflorescences/tree	97.93	98.08	16	71.19	79.63	21	0.36
Alzira	2002	SP	Reproductive	Inflorescences/tree	31.93	44.27	16	26.42	43.74	21	0.70
Bicorp	1999	SP	Reproductive	Inflorescences/tree	28.90	58.99	11	5.22	8.47	22	0.07
Bicorp	2001	SP	Reproductive	Inflorescences/tree	26.90	36.79	11	25.72	25.59	22	0.91
Bicorp	2002	SP	Reproductive	Inflorescences/tree	11	20.99	11	11.5	25.93	22	0.25
Bunyol	1999	SP	Reproductive	Inflorescences/tree	10.38	18.18	13	5.94	10.29	19	0.38
Bunyol	2000	SP	Reproductive	Inflorescences/tree	18.84	40.8	13	8.15	22.96	19	0.35
Bunyol	2001	SP	Reproductive	Inflorescences/tree	24.07	28.83	13	0.78	3.44	19	<0.01
Bunyol	2002	SP	Reproductive	Inflorescences/tree	11.15	21.43	13	0.47	1.83	19	0.03
FontRoja	2002	SP	Vegetative	Annual shoot growth (cm)	2.94	1.06	10	3.45	3.77	9	0.68
Kováčov	2003	SK	Vegetative	Annual shoot growth (cm)	2.46	1.17	34	2.01	0.97	28	0.10
Kováčov	2004	SK	Vegetative	Annual shoot growth (cm)	3.04	0.92	34	2.15	1.03	28	<0.01
Príbelce	2003	SK	Vegetative	Annual shoot growth (cm)	3.10	1.38	29	2.66	1.62	31	0.26
Príbelce	2004	SK	Vegetative	Annual shoot growth (cm)	4.01	1.96	29	2.48	1.38	31	<0.01
Kováčov	2004	SK	Vegetative	DBH increment	0.91	1.04	34	1.161	0.97	28	0.33
Príbelce	2004	SK	Vegetative	DBH increment	1.71	1.27	29	1.05	1.01	31	0.02
Petrokerasa	2004	GR	Vegetative	5-year annual ring growth (mm)	7.46	1.19	5	4.24	1.37	5	<0.01
Kováčov	2003	SK	Photosynthetic period	Photosynthetic period (days)	221	13	33	226	11	27	0.11
Kováčov	2004	SK	Photosynthetic period	Photosynthetic period (days)	195	5	33	196	5	27	0.44
Príbelce	2003	SK	Photosynthetic period	Photosynthetic period (days)	205	12	29	204	12	28	0.75
Príbelce	2004	SK	Photosynthetic period	Photosynthetic period (days)	188	6	29	188	8	31	1.00
Doubia	2003	GR	Photosynthetic period	Photosynthetic period (days)	214	2	32	216	2	28	<0.01
Petrokerasa	2003	GR	Photosynthetic period	Photosynthetic period (days)	246	5	28	245	6	32	0.48
FontRoja	2002	SP	Photosynthetic period	Photosynthetic period (days)	192	8	29	191	8	35	0.62
FontRoja	2003	SP	Photosynthetic period	Photosynthetic period (days)	208	8	29	209	9	30	0.65
Alzira	2002	SP	Photosynthetic period	Photosynthetic period (days)	252	20	23	243	22	17	0.18
Alzira	2003	SP	Photosynthetic period	Photosynthetic period (days)	229	13	28	222	12	26	0.04

Mean ( $\bar{X}$ ), standard deviation (s.d.) and sample size ( $n$ ) are shown for males and hermaphrodites.

Country: SP, Spain; SK, Slovakia; GR, Greece.

$P$  refers to the one-way ANOVA traditional tests for the differences between males and hermaphrodites.

slopes of the meta-regressions remained non-significant after blocking by year and population ( $-0.003 \pm 0.004$ ;  $P = 0.38$  for the frost-free period and  $-0.005 \pm 0.006$ ;  $P = 0.38$  for the moisture deficit).

Sexual dimorphism on vegetative traits did not change with the frost-free period ( $y = 0.23 - 0.004$ ;  $Q_M = 0.75$ ;  $P = 0.38$ ) nor with the moisture deficit ( $y = 0.45 - 0.004$ ;  $Q_M = 1.93$ ;  $P = 0.16$ ). Blocking by year and population did not result in significant slopes of such meta-regressions ( $-0.009 \pm 0.005$ ;  $P = 0.10$  for the frost-free period and  $-0.006 \pm 0.003$ ;  $P = 0.10$  for the moisture deficit).

## DISCUSSION

A lot of variability in the reproductive and vegetative output across populations and years can be envisioned from this study. This is not surprising, especially in a

masting species like *F. ornus* in which low-producing years alternate with mast years. Despite this temporal and spatial variability, most of the estimates of sexual dimorphism point in the direction of males growing more than hermaphrodites, as expected under the hypothesis of lower cost of male reproduction. This fact suggests that gender-associated costs of reproduction in *F. ornus* are present in good and bad years and populations. This finding is consistent with many studies from dioecious species, although some others have failed to find such differences (Delph, 1999; Obeso, 2002; Delph *et al.*, 2005).

Interspecific differences in the gender-associated costs of reproduction may come from different selective pressures in each species. For example, males from some species may be strongly selected for massive pollen production. Zahoueh *et al.* (1991) showed that males of



males consistently grow more quickly than hermaphrodites across years and at the extremes of the species range.

In some cases, the failure to detect gender-associated costs of reproduction may come from a lack of statistical power rather than a reduced effect of gender on reproductive and vegetative traits (see the *P*-values of the ANOVA traditional tests in Table 2). This situation is particularly evident when the distribution of effect sizes that are non-significant under traditional statistical tests is not centred around zero (Osenberg *et al.*, 1999). In the absence of gender effects, the expected distribution of data would be 50 % negative and 50 % positive values. A single small positive mean may fail to reject the null hypothesis because of low statistical power. However, the meta-analysis may accumulate the evidence pointing towards the same direction by averaging many small positive means and then reject the null hypothesis. For example, Verdú (2004) failed to detect significant differences in vegetative growth between both genders of *F. ornus* in spite of the trend of males growing more than hermaphrodites. Now, meta-analytical tools have allowed us not only to reject the null hypothesis (i.e. males and hermaphrodites do not differ in vegetative and reproductive parameters) but also to quantify how large the difference between genders is.

In the context of behavioral sciences, Cohen (1988) defined three cut points that allow the separation of small ( $d = 0.2-0.5$ ), medium ( $d = 0.5-0.8$ ) and large ( $d > 0.8$ ) effect sizes. These are standardized mean difference effect sizes that can be converted to correlation coefficients (Verdú and Traveset, 2004) corresponding to percentages of the explained variance of 1–6.24 %, 6.25–16 % and >16 %, respectively. The usual values of explained variance in ecological and evolutionary meta-analyses only range from 2.5 to 5.4 % (Møller and Jennions, 2002). The effect sizes shown here for reproductive and vegetative characters are  $d = -0.31$  and  $d = -0.45$  respectively, which accounts for 2.3 % and 4.8 % of the variance respectively. These magnitudes are small in the traditional Cohen's scale, but in an ecological context the effects of gender should be considered as relatively small for reproductive traits but medium to high for vegetative characters.

Contrasting ecological conditions may produce intraspecific variation in the gender-associated costs of reproduction. Some authors have stated that harsh conditions may promote gender differences because the gender with greater reproductive costs is more affected by such conditions (Dawson and Bliss, 1989; Dawson and Ehleringer, 1993; Dawson and Geber, 1999; Delph, 1999; Obeso, 2002). No evidence has been found in *F. ornus* for such a prediction because the gender-associated differences observed in vegetative and reproductive characters were independent of the stress conditions like short frost-free periods or high moisture deficits. Other factors like herbivory, soil characteristics, competition, etc. could also be acting as stressors; it would be interesting for future studies to relate these factors with sexual dimorphism in reproduction and growth.

In summary, the lower costs of reproduction for males allows them to grow more quickly than hermaphrodites, although such differences in sex-specific reproductive costs are not magnified under stressful conditions.

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