1 # A test of the size-constraint hypothesis for a limit to sexual

2 # dimorphism in plants

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7 Anne-Marie Labouche[1] and John R. Pannell

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10 Department of Ecology and Evolution

11 University of Lausanne

12 CH-1015 Lausanne

13 Switzerland

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16 [1] Author for correspondence: annemarie.labouche@gmail.com

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20 Running header: A size-constraint hypothesis for sexual dimorphism in plants

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22 Author contributions: AML and JRP conceived and designed the experiment; AML

23 performed the experiment and analyzed the data. AML and JRP wrote the manuscript

Abstract

In flowering plants, many dioecious species display a certain degree of sexual dimorphism in non-reproductive traits, but this dimorphism tends to be much less striking than that found in animals. Sexual size dimorphism in plants may be limited because competition for light in crowded environments so strongly penalises small plants. The idea that competition for light constrains the evolution of strong sexual size dimorphism in plants (the size-constraint hypothesis) implies a strong dependency of the expression of sexual size dimorphism on the neighbouring density as a result of the capacity of plants to adjust their reproductive effort and investment in growth in response to their local environment. Here, we tested this hypothesis by experimentally altering the context of competition for light among male-female pairs of the light-demanding dioecious annual plant *Mercurialis annua*. We found that males were smaller than females across all treatments, but sexual size dimorphism was diminished for pairs grown at higher densities. This result is consistent with the size-constraint hypothesis. We discuss our results in terms of the tension between selection on size acting in opposite directions on males and females, which have different optima under sexual selection, and stabilizing selection for similar sizes in males and females, which have similar optima under viability selection for plasticity in size expression under different density conditions.

43   In organisms with separate sexes, males and females often differ from one another in

44   morphological, life-history and physiological traits that are not directly related to primary sex

45   expression or gamete production (Darwin 1871). Such secondary sexual dimorphism is

46   common in animals, but is also known to occur in plants for a wide range of characters

47   (reviewed in Barrett and Hough 2013), including life-history (reviewed in Delph 1999, Obeso

48   2002), morphological (reviewed in Dawson and Geber 1999), physiological (reviewed in

49   Dawson and Geber 1999) and defence traits (reviewed in Ågren et al. 1999). For example,

50   males usually have larger flowers and/or floral displays than females (e.g. *Silene latifolia*,

51   Meagher 1992; Delph et al. 1996), the sexes may display different leaf shapes and sizes (e.g.

52   *Simmondsia chinensis*, Wallace and Rundel 1979), males may grow more quickly (e.g. *Acer*

53   *negundo*, Jing and Coley 1981; *Dacryodes excelsa*) or more slowly than females (e.g. *Silene*

54   *latifolia*, Gross and Soule 1981; *Mercurialis annua*, Hesse and Pannell 2011) and males tend

55   to be more susceptible to herbivores than females (e.g. *Fragaria virginiana*, Ashman et al.

56   2004; reviewed in Ågren et al. 1999; Obeso 2002). Although sexual secondary dimorphism is

57   often extreme in animals (Darwin 1871; Fairbairn 1997;Moore and Pannell 2011), it is rarely

58   so in plants, and it is seldom possible to tell males and females apart on the basis of vegetative

59   traits (Lloyd and Webb 1977; Delph et al. 1996; Moore and Pannell 2011; Barrett and Hough

60   2013). A striking exception is offered by the differences in leaf and branching traits between

61   the sexes in several species of the Cape fynbos genus *Leucadenron* (Bond and Midgely 1988;

62   Bond and Maze 1999; Harris and Pannell 2010).

63

64   The fact that differences between males and females of dioecious plants tend often to be more

65   subtle than those found in many animal species probably reflects, in part, reduced

66   opportunities for sexual selection in plants (Skogsmyr and Lankinen 2002; Moore and Pannell

67   2011; Forrest 2014). The arena for female choice in plants is obviously much narrower than it

68   is in animals, being limited to the occasional influence females might exercise in which pollen

69   grains are allowed to fertilize their ovules (e.g. Lankinen and Madjidian 2011) and perhaps

70   aspects of the phenology of flowering (e.g. Brunet and Charlesworth 1995; Gleiser et al.

71   2008). Female choice would in any case likely affect floral rather than vegetative traits. Male-

72   male competition is more likely to occur in plants, and many floral adaptations have probably

73   evolved in response to selection for increased siring success, both in hermaphrodites and

74   dioecious plants (reviewed in: Moore and Pannell 2011; Barrett and Hough 2013). Again,

75   selection for siring success will tend to shape floral and inflorescence traits, e.g., by

76   increasing the size or number of flowers or inflorescences or the amount of pollen produced

77   and dispersed, rather than vegetative traits directly. However, because competition for siring

78   success may bring about selection for increased absolute investment by individuals in

79   flowering (Bond and Maze 1999), specifically in their male function, we would expect

80   allocation trade-offs to have indirect effects on vegetative traits that might differ between

81   males and females (Delph et al. 1996; Bond and Maze 1999; Delph et al. 2004; Harris and

82   Pannell 2010; Moore and Pannell 2011; Barrett and Hough 2013).

83

84   Differences in trade-offs between investment in reproduction and growth and/or maintenance

85   between males and females are probably the main reason for many of the traits for which

86   dioecious species show secondary sexual dimorphism (Barrett and Hough 2013). Thus, for

87   example, the oft-observed increased susceptibility by males to herbivores or pathogens may

88   be the outcome of steeper trade-offs between reproduction and defence in males than females

89   (reviewed in Ågren 1999). Similarly, different life-history schedules between males and

90   females (Delph 1999), including patterns of phenology and mortality, probably explain the

91   strong differences in secondary sex ratios in many dioecious plant populations, where the sex

92   making the heavier investment in reproduction flowers later or dies earlier (Pannell and Ojeda

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93   2000; Field et al. 2013). This sex is often female (leading to male-biased sex ratios), but may

94   also be male (reviewed in Delph 1999; Field et al. 2013).

95

96   The idea of trade-offs between sexual selection (and investment to enhance mating success)

97   and ecological (e.g., viability) selection lies at the heart of models for the evolution of sexual

98   dimorphism: the phenotype selected should be that for which marginal gains in fitness via one

99   component (e.g., through increased siring success) equal the marginal losses in another (e.g.,

100   through increased mortality; Andersson 1994; Shuster and Wade 2003). In this sense, sexual

101   dimorphism in plants might thus be limited either by low benefits accruing to individuals with

102   phenotypes that diverge from an ecological optimum (because the scope for sexual selection

103   is limited) or by high costs of such divergence (because of elevated risks of mortality or

104   reproductive failure for other reasons), or by both factors together. In cases where these

105   benefits and costs vary with environmental conditions (Delph and Bell 2008), we would

106   expect the phenotypes expressed by males and females to vary as a result of phenotypic

107   plasticity, so that measures of sexual dimorphism might vary among environments, too. Here,

108   we test this idea with particular reference to sexual size dimorphism in a wind-pollinated

109   annual plant growing at different densities. We label our hypothesis the 'size-constraint

110   hypothesis'.

111

112   The size-constraint hypothesis posits that ecological selection among plants under

113   competition for light will modulate the extent to which males and females can deviate from

114   one another in terms of their size. It is well known that plants often face strong asymmetrical

115   competition with both intraspecific and heterospecific neighbours for light, with the tallest

116   individuals gathering a disproportionate share of the resource (Schwinning and Weiner 1998).

117   In dioecious populations, intraspecific competition will occur both between plants of the same

118   sex and plants of the opposite sex. Plants possess a range of adaptations that allow them to

119   adjust their growth in response to their competitive environment. Preeminent among these is

120   their ability to increase growth in height in response to a shifted Red:Far-Red (R:FR) light

121   ratio, which serves as a signal for the presence of green neighbours (Ballare et al. 1990;

122   Schmitt and Wulff 1993; Ballare 1999). Responses to the R:FR light ratio allow plants avoid

123   competitive suppression that occurs when taller plants overshadow shorter ones (shade

124   avoidance response, Ruberti et al. 2012). A well-known consequence of competition for light

125   is the tendency for plants to reduce their reproductive effort in the face of competition for

126   light (Harper 1977), probably in response to life-history trade-offs associated with a higher

127   investment in growth. This trade-off partially explains the decrease in the seed yield of crops

128   per area planted with increases in plant density (Harper 1977, see also Sangoi et al. 2002). If

129   sexual dimorphism reflects a deviation by males and/or females from a common phenotype

130   that is optimal for success in competing for light, then the size-constraint hypothesis predicts

131   that sexual size dimorphism will be smaller in light-demanding dioecious plants at high

132   density (or, in general, under conditions where success at gaining access to light depends on

133   size); by contrast, plants growing at low density will be freer to deviate from the common

134   phenotype, and sexual size dimorphism will be more pronounced.

135

136   We tested the size-constraint hypothesis by manipulating the perceived density of plants of

137   the wind-pollinated herb *Mercurialis annua*, a dioecious annual that shows substantial sexual

138   size dimorphism, with males typically smaller than females in terms of biomass and often also

139   height (Harris and Pannell 2008; Sanchez et al. 2011; Sanchez and Pannell 2011). Our

140   experiment involved comparing sexual size dimorphism among plants expressing their

141   phenotypes at different experimental densities, and in the middle versus at the edge of

142   experiment plots. Because we were interested specifically in the response of males and

143   females in competition with one another for light, we grew plants in male-female pairs in

144   individual pots and varied the spacing between pots. Thus, all plants in our experiment were

145   subjected to the same competition for underground resources, but varied among treatment

146   densities in terms of their access to light. Because our focus was on sexual dimorphism, i.e.,

147   the difference between male and female phenotypes, we used male-female pairs as the unit of

148   replication. We predicted that, in dense situations, males and females would be constrained to

149   grow to similar sizes, whereas, in sparse situations, they could afford to deviate from a size

150   optimal for competition for light and hence potentially express greater sexual size

151   dimorphism. Previous work (Harris and Pannell 2008) has shown that males tend to be

152   smaller than females of *M. annua*, partially because of their particularly heavy investment in

153   reproduction, presumably a behaviour that has evolved under intense scramble competition

154   for siring success. Sexual selection thus appears to favour males with high reproductive effort

155   and thus smaller sizes. However, small sizes are expected to be strongly penalised in dense

156   situations under asymmetrical competition for light.

157

158   **Materials and methods**

159   Study system

160   *Mercurialis annua* (Euphorbiaceae) is a wind-pollinated annual herb that occupies disturbed

161   habitats in central and Western Europe, as well as around the Mediterranean Basin (Durand

162   1963, Tutin et al. 1968). The species shows remarkable variation in its sexual systems,

163   including monoecious, dioecious and androdioecious populations (where males co-occur with

164   hermaphrodites) in different parts of its range (Pannell et al. 2004). Here, we focus on the

165   dioecious populations, which are diploid and occur throughout much of Europe. These

166   populations are sexually dimorphic, with male plants typically shorter and lighter than

167   females and possessing pedunculate inflorescences that are held erect above the plant whereas

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168 females display sessile flowers at each leaf axil (Eppley and Pannell 2007). Reproduction

169 begins several weeks following germination, with males often commencing inflorescence

170 production a few days earlier than females (Harris and Pannell 2008). Flowering in *M. annua*

171 is indeterminate, with plants dispersing their pollen and seeds as they grow, meaning that

172 there is no clearly distinct vegetative and reproductive phases (Hesse and Pannell 2011). The

173 plants used in the study originated from seeds bulked from 25 naturally occurring diploid

174 dioecious populations, sampled across its native European range.

175

176 Experimental design and measurements

177 We tested the size constraint hypothesis by experimentally altering the context of light

178 competition for pairs of male and female plants. We established 18 plots, each comprising 25

179 male-female pairs in single pots (i.e., each pot comprised a male and a female together);

180 henceforth, 'pot' refers to male-female pairs. Seeds randomly picked from the bulk pool were

181 individually sown in peat pellets (Jiffy Products International), and 900 young plants (450 of

182 each sex) were transplanted in male-female pairs into 15 cm diameter pots at the onset of

183 flowering, three weeks after germination. To reduce asymmetries in competition caused by

184 slight differences in the timing of germination, we matched males and females of

185 approximately similar height for each pair. Plants were then moved out-of-doors in a

186 ploughed field on the campus of the University of Lausanne (Switzerland). Individuals were

187 supported with wooden stakes in their pots to prevent toppling in the wind.

188

189 Within each plot, the randomly assigned 25 pots were arranged in a square lattice (5 x 5) with

190 an inter-pot distance of 0 cm (pots touching), 5 cm, 15 cm, 25 cm, 35 cm, or 85 cm. These six

191 density levels represent our competition treatment. Each density level was replicated three

192 times. The lattice arrangement meant that there were nine internal pots and 16 edge pots in

193   each plot, and that competition for light experienced by the pots in the dense plots was

194   diminished for the pots placed at the edge. The experiment ran out-of-doors for eight weeks,

195   and plants were harvested when growth in size appeared to be levelling off and signs of

196   nitrogen limitation were being shown (a slight yellowing of the leaves). At harvest, we found

197   that pots were completely full of roots, pointing to the likelihood of strong belowground

198   competition. During growth, plants were watered daily, as necessary. There was very little

199   mortality during this period, with only two males and one female dying in plots of

200   intermediate density. At the end of week eight, all plants were measured for height, and

201   aboveground parts were then collected, bagged, dried and weighed.

202

203   <u>Statistical analysis</u>

204   To test for the effect of interplant competition on sexual dimorphism in plant height and mass,

205   we ran two separate linear mixed-models (LMM), with sex, distance and position (edge

206   versus central placement) and their interactions as fixed variables and replicate pots nested

207   within plot replicate as random effects. As we found a significant effect on plant mass of the

208   three-way interaction sex × distance × position ($\chi^2_5 > 15.6$; $p = 0.008$), we ran two separate

209   LMMs on plants reared in pots in the centre and at the edge of the plot, respectively. To test

210   whether male and female mass were differently affected by their position in the plot, we also

211   ran two separate LMMs on males and females, respectively.

212

213   To quantify more precisely the extent to which males and females differed within each pot,

214   we calculated a sexual dimorphism index (SDI; Lovich and Gibbons 1992) per pot by

215   subtracting the male trait value from the female trait value and dividing by the male trait

216   value, excluding the three pots in which one of the plants had died. We used separate

217   Wilcoxon tests for each density level to test whether mass SDI differed significantly from 0

218   (i.e., whether male and female masses were significantly different). We ran these tests

219   specifically on central pots where the effect of density was strongest. To compare SDI among

220   the different density levels, we used either a non-parametric Kruskal-Wallis test or a one-way

221   Welch's ANOVA, depending on the homogeneity of variances of SDI in the group of interest

222   (i.e. mass SDI or height SDI in the center or at the edge of the plot). Homogeneity of the

223   variances was tested with the non-parametric Flinger-Killeen test for homogeneity of

224   variance.

225

226   We used backward elimination (successively removing factors with $P > 0.10$) until we

227   obtained a minimal adequate model, comparing models with log-likelihood ratio tests

228   (LLRT). When necessary, we normalised the response variable using the Boxcox

229   transformation. Data are given as mean ± SE, unless specified. All analysis was conducted on

230   R 3.0.2 (R Core Team 2013), with LLMs implemented using the package lme4.

231

232   **Results**

233   <u>Effects of density on male and female plant mass and height</u>

234   Male and female plants were lighter when they experienced more competition for light (Fig.

235   1a) and female plants experienced a steeper decrease in mass with increased plant density

236   than males (Fig 1a). Distance between the pots and position of the pot within the plot both

237   affected plant mass differently in male and female plants, as revealed by a significant three-

238   way interactions (LLRT sex × position × distance: $\chi^2_5 > 15.6$; p = 0.008): while both male and

239   female plant mass decreased with increased competition for light, females placed in the center

240   of the plot were significantly lighter than the females placed at the edge when density

241   increased (Fig 1b; distance × position interaction: p < 0.001; Table 1). In contrast, this effect

242   of the position of the plant within the plot was only marginally significant for males (Fig. 1b;

243      $p = 0.07$; Table 1).

244

245   Males and females were taller when they experienced more competition for light (Fig. 2a).

246   The position of the plant in the plot (edge vs. center) did not significantly affect the pattern of

247   height variation in female plants (Fig. 2b, Table 2), but it did affect males. At higher densities,

248   males from the centre of plots were significantly taller than the males at their edge (Fig. 2b;

249   Table 2).

250

251   <u>Effects of density on sexual dimorphism within pots</u>

252   On average, mass SDI was positive, i.e., females were larger than males (Table 3). This

253   applied to total biomass, but also to vegetative parts after flowers and fruits had been

254   removed from females (seed and fruit mass accounted for about 10% of the female mass

255   in all densities, except for distance class 0 in which it accounted for 7.7% of the female

256   mass). However, because males were weighed with with their inflorescences, we

257   present mass SDI on the basis of a comparison between the sexes reproductive

258   structures intact. Mass SDI changed across the different density levels, with a tendency

259   to increase when the level of competition for light was relaxed (Fig.3). This was the case

260   especially in pots placed in the center of plots, though these differences were not

261   significantly different (Table 3). It is worth noting that variance was high among pots

262   placed in the center of the less dense plots (Table 3), partially explained by the presence

263   of two extreme outliers with Mass SDI>20 (Fig.3). Mass SDI in central pots was

264   significantly different from 0 for the distance classes 5, 15, 35 and 85 (with $p < 0.03$) and

265   fell short of significance for the distance class 0 and 25 ($p = 0.08$). Pots placed at the

266   edge of plots showed somewhat less variation in mass SDI among densities (Fig.3),

267 though these differences were not statistically different (Table 3). On average, the

268 highest mass SDI was often reached at the interplant distance 35 (Table 3), i.e., not the

269 sparsest plots.

270

271 Height SDI increased significantly when density decreased for pots placed in the center

272 of the plots, but not for pots placed at the edge of plots (Table 4).

273

274 **Discussion**

275 Notwithstanding high variation among lowest-density plots, we found that sexual dimorphism

276 in size tended to be lower in plots with high density than lower density, as well as for plants

277 reared in plot centers compared with their edges. Both these results largely conform to the

278 size-constraint hypothesis, which predicts that competition for access to light represents an

279 ecological component of selection that will strongly constrain responses to sexual selection.

280

281 It is somewhat puzzling that plants at the lowest-density plot (i.e., 85cm) showed lower sexual

282 size dimorphism than the plants at the density level 35cm, hence reversing the trend we

283 observed across the other treatments (i.e. reduced sexual size dimorphism when increasing

284 density levels from 35cm to 0cm). We grew our plants in pots that were perhaps more

285 susceptible to drying out in low-density situations that high-density situations, and this might

286 have affected growth rates at the lowest-density extreme of our experiment. While growing

287 plants in pots may poorly emulate natural conditions, it allowed us in our experiment to

288 ensure that all plants experienced the same belowground competitive situation. Although we

289 watered all pots similarly, differences in desiccation rates among pots might have introduced

290 unintended variation among the treatments we imposed. We can offer no other explanation for

291 the seemingly anomalous finding at the lowest plot densities. As might be expected, the effect

292 of growing at the edge compared to the center of plants was most apparent at high-density

293 plots, where the competitive environment experienced by plants will have been greatest, i.e.,

294 growing at the edge of a plot released plants from competition more in high- than in low-

295 density plots.

296

297 In the case of *M. annua*, male investment in flowering and nitrogen-greedy pollen production

298 leads to a particularly steep trade-off with aboveground growth, so that males that invest in

299 nitrogen-harvesting roots tend to be smaller than females (Harris and Pannell 2008). Our

300 results indicate that, in dense situations, males and females respond plastically by maintaining

301 sizes more consistent with their opposite-sex neighbours. Interestingly, Conn and Blum

302 (1981) also found that differences in the size of males and females of the dioecious annual

303 *Rumex hastatulus* were smaller at high density, though the result was not interpreted in terms

304 of constraints on sexual selection. Similarly, Lovett Doust et al. (1987) noted that the much-

305 described patterns of sexual dimorphism in *Silene latifolia* (e.g., higher number of stems in

306 female and higher number of flowers in males; Delph et al. 2002) disappeared in experimental

307 conditions under high densities.

308

309 The experimental setups of Conn and Blum (1981) and Lovett Doust et al. (1987) affected

310 both below-ground and above-ground competition simultaneously, and the authors discussed

311 their results in terms of the calorific allocation to reproduction by males versus females.

312 Because all plants were exposed to the same level of below-ground competition, our

313 experiment teases apart the two components of competition and focuses on the importance of

314 above-ground competition only. Although competition for resources below ground will often

315 be important, especially where soil nutrients are limiting, above-ground competition for light

316 has the peculiarity of being highly asymmetrical between plants with different sizes

317   (Schwinning and Weiner 1998). Once plants are overtopped by their neighbours, their slower

318   growth will expose them to increasingly low light quality in a process with positive-feedback

319   on performance, ultimately leading to mortality – the cause of 'self-thinning' in dense plant

320   populations (Weller 1987; Lonsdale 1990; Vanderwerf et al. 1995). The essence of the size-

321   constraint hypothesis is that selection will favour phenotypes that maintain similar sizes to

322   their neighbours when competition is intense but that males and females may attain different

323   sizes when released from the competitive constraint at lower densities. It is well known that

324   plants can respond in their growth to the presence of neighbours that they detect through their

325   sensitivity to the R:FR ratio: green neighbours transmit or reflect low R:FR ratios, which

326   induce altered growth patterns, including stem extension, internode elongation and decreased

327   branching (Schmitt and Wulff 1993). Sleeman et al. (2002) documented a phytochrome-

328   mediated shade-avoidance response in androdioecious *M. annua*, which occupies similar open

329   habitat to dioecious populations we studied here. Our results here suggest that dioecious *M.*

330   *annua* also responds to R:FR ratio, and that this response does not differ much between the

331   sexes.

332

333   From the perspective of mating opportunities and reproduction, plant size may experience

334   different selective pressures/constraints in females and males that would explain sexual size

335   dimorphism. The outcome of allocation trade-offs between growth and reproduction would be

336   a good reason to expect males and females to differ in size. The sex with the greater

337   reproductive burden, i.e., the greater marginal cost of reproduction when measured in terms of

338   its negative effect on growth, is expected to be the smaller, particularly after allocation to

339   reproduction has commenced. Lloyd and Webb (1977) suggested that the result of such trade-

340   offs would be evident only in perennial plants with iteroparous reproduction, but the

341   prediction should also apply to annuals with indeterminate reproduction, like *M. annua*,

342   because reproduction early in the season will affect ongoing growth and opportunities for

343   reproduction later in the same season (in this sense, such plants are 'iteroparous' annuals). In

344   iteroparous species, including annuals with indeterminate reproduction, the premium on plant

345   height for maintaining a positive carbon budget should strongly affect density-dependent

346   patterns of allocation, as has indeed been observed for *M. annua* (Pannell 1997). This

347   premium should apply especially in dense stands, so that both males and females will be

348   selected to maintain optimum (and similar) height by adjusting their allocation to

349   reproduction. In sparse stands where height will be less important in maintaining a positive

350   carbon budget, males and females should adopt a gender-dependent strategy in the trade-off

351   between growth and reproduction, leading to greater sexual size dimorphism, as largely

352   observed in our experiment.

353

354   A second reason why we may expect males and females to differ in size could be the selection

355   on male height for pollen dispersal. In wind-pollinated species (especially herbs such as *M.*

356   *annua*), tall males will benefit from an outcross siring advantage over their smaller male

357   competitors by dispersing their pollen to the wind more effectively. This advantage has been

358   labelled a 'direct effect' of size (Klinkhamer et al. 1997). Eppley and Pannell (2007) found

359   that, in *M. annua*, the dispersal of pollen from erect inflorescences held above plants

360   increased siring success per pollen grain by approximately 60%, a result that is consistent

361   with a direct effect of size (though plant height per se was not estimated). In another revealing

362   study, Pickup and Barrett (2012) found that although females were taller than males in wind-

363   pollinated *R. hastatulus* late in the reproductive season, males were the taller sex when pollen

364   was being dispersed. This observation can be interpreted as an outcome of selection on height

365   in males when it matters for mating. Despite the mating advantage for taller males of *M.*

366   *annua* in the context of pollen dispersal, selection on height may be overridden by selection

367   on reproductive investment (Harris and Pannell 2008), which might explain why males are

368   typically smaller than females in this species.

369   Our results illustrate the fact that the high levels of plasticity displayed by plants in their

370   response to the environment (Schlichting 1986; Sultan 2000) affect traits that can be sexually

371   dimorphic in dioecious plants, so that indices of dimorphism themselves become plastic.

372   Indeed, sex-specific plasticity in response to environmental conditions may be responsible for

373   intraspecific variation in sexual dimorphism, as has been hypothesized to explain sexual

374   dimorphism variation in insects (Stillwell et al. 2010). Similarly, sex-specific plasticity

375   probably explains the fact that, in the plant *Simmondsia chinensis*, sexual dimorphism in

376   several vegetative traits was observed only under drier conditions (for further examples, see

377   the review by Delph 1999).

378

379   In discussing the size-constraint hypothesis, we have emphasised the flexibility that plants

380   have in responding to their local conditions, particularly in varying their allocation to growth

381   versus reproduction. The reduced sexual size dimorphism observed for dioecious species at

382   high density, consistent with the size-constraint hypothesis, is likely a response that allows

383   both males and females to compete with one another on a more equal footing than would be

384   the case if their allocation patterns reflected a response to selection on reproduction only. But

385   this buffering effect of plasticity is clearly only partial. There is ample evidence that sex ratios

386   in dioecious plant populations vary widely, often as a result of differential mortality under

387   different conditions (reviewed in Field et al. 2013). Such patterns reflect a kind of niche

388   partitioning between the sexes (Bierzychudek and Eckhart 1988; Eppley 2006), also manifest

389   in observed spatial separation of the sexes in a number of species (Bierzychudek and Eckhart

390   1988; Iglesias and Bell 1989; Korpelainen 1991; Shea et al. 1993; Lokker et al. 1994; Eppley

391   et al. 1998; Bertiller et al. 2002; Stark et al. 2005; Dudley 2006). They are likely due to the

392   fact that males and females ultimately still strike a different balance between the benefits of

393   gender specialisation and the risks of mortality. In the context of the paradigm that

394   phenotypes reflect a tension between ecological and sexual components of natural selection

395   (Lande 1980; Slatkin 1984; Shine 1989; Cornwallis and Uller 2010), it seems clear that

396   plasticity invoked by the size-constraint hypothesis for variation in sexual size dimorphism in

397   dioecious plants only partially resolves the tension: males and females still need to reproduce

398   to maintain a stake in the evolutionary game, and this necessity comes with gender-dependent

399   risks.

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410   **Literature Cited**

411   Ågren J, Danell K., Elmqvist T., Ericson L., Hjältén J. (1999) Sexual dimorphism and biotic

412   interactions. In: Geber MA, Dawson TE, Delph LF (eds) Gender and sexual

413   dimorphism in flowering plants. Springer

414   Andersson M (1994) Sexual selection Princeton, NJ: Princeton University Press

415   Ashman TL, Cole DH, Bradburn M (2004) Sex-differential resistance and tolerance to

416   herbivory in a gynodioecious wild strawberry. Ecology 85:2550-2559

417   Ballare CL (1999) Keeping up with the neighbours: phytochrome sensing and other signalling

418   mechanisms. Trends in Plant Science 4 (3): 97-102

419   Ballare CL, Scopel AL, Sanchez RA (1990) Far-red radiation reflected from adjacent leaves:

420   an early signal of competition in plant canopies. Science 247:329-332

421   Barrett SCH, Hough J (2013) Sexual dimorphism in flowering plants. Journal of

422   Experimental Botany 64:67-82

423   Bertiller MB, Sain CL, Bisigato AJ, Coronato FR, Aries JO, Graff P (2002) Spatial sex

424   segregation in the dioecious grass *Poa ligularis* in northern Patagonia: the role of

425   environmental patchiness. Biodiversity and Conservation 11:69-84

426   Bierzychudek P, Eckhart V (1988) Spatial segregation of the sexes of dioecious plants.

427   American Naturalist 132:34-43

428   Bond WJ, Maze KE (1999) Survival costs and reproductive benefits of floral display in a

429   sexually dimorphic dioecious shrub, *Leucadendron xanthoconus*. Evolutionary

430   Ecology 13: 1-18

431   Bond WJ, Midgley J (1988) Allometry and sexual differences in leaf size. American

432   Naturalist 131: 901-910

433   Brunet J, Charlesworth D (1995) Floral sex allocation in sequentially blooming plants.

434   Evolution 49:70-79

435   Conn JS, Blum U (1981) Differentiation between the sexes of *Rumex hastatulus* in net energy

436   allocation, flowering and height. Bulletin of the Torrey Botanical Club 108:446-455

437   Cornwallis CK, Uller T (2010) Towards an evolutionary ecology of sexual traits. Trends in

438   Ecology & Evolution 25:145-152

439   Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London

440   Dawson TE, Geber MA (1999) Dimorphism in physiology and morphology. In: Geber MA,

441   T.E. D, Delph LF (eds) Gender and sexual dimorphism in flowering plants. Springer

442   Delph LF (1999) Sexual dimorphism in live history In: Geber MA, Dawson TE, Delph LF

443   (eds) Gender and sexual dimorphism in flowering plants. Springer

444   Delph LF, Galloway LF, Stanton ML (1996) Sexual dimorphism in flower size. American

445   Naturalist 148:299-320

446   Delph LF, Knapczyk FN, Taylor DR (2002) Among-population variation and correlations in

447   sexually dimorphic traits of *Silene latifolia*. Journal of Evolutionary Biology 15:1011-

448   1020

449   Delph LF, Bell DL (2008) A test of the differential-plasticity hypothesis for variation in the

450   degree of sexual dimorphism in *Silene latifolia*. Evolutionary Ecology Research

451   10:61-75

452   Delph LF, Frey FM, Steven JC, Gehring JL (2004) Investigating the independent evolution of

453   the size of floral organs via G-matrix estimation and artificial selection. Evolution &

454   Development 6:438-448

455   Dudley LS (2006) Ecological correlates of secondary sexual dimorphism in *Salix glauca*

456   (Salicaceae). American Journal of Botany 93:1775-1783

457   Durand B (1963) Le complexe *Mercurialis annua L.* s.i.: une etude biosystematique. Annales

458   des sciences naturelles botaniques Paris 12:579-736

459   Eppley SM (2006) Females make tough neighbors: sex-specific competitive effects in

460   seedlings of a dioecious grass. Oecologia 146:549-554

461   Eppley SM, Pannell JR (2007) Density-dependent self-fertilization and male versus

462   hermaphrodite siring success in an androdioecious plant. Evolution 61:2349-2359

463   Eppley SM, Stanton ML, Grosberg RK (1998) Intrapopulation sex ratio variation in the salt

464   grass *Distichlis spicata*. American Naturalist 152:659-670

465   Fairbairn DJ (1997) Allometry for sexual size dimorphism: Pattern and process in the

466   coevolution of body size in males and females. Annual Review of Ecology and

467   Systematics 28:659-687

468   Field DL, Pickup M, Barrett SCH (2013) Comparative analyses of sex ratio variation in

469   dioecious flowering plants. Evolution 67:661-672

470   Forrest JRK (2014) Plant size, sexual selection, and the evolution of protandry in dioecious

471   plants. American Naturalist 184:338-351

472   Gleiser G, M. Verdu, JG, Segarra-Moragues, SC, Gonzalez-Martinez, Pannell JR (2008)

473   Disassortative mating, sexual specialization, and the evolution of gender dimorphism

474   in heterodichogamous *Acer opalus*. Evolution 62:1676-1688.

475   Gross KL, Soule JD (1981) Differences in biomass allocation to reproductive and vegetative

476   structures of male and female plants of a dioecious, perennial herb, *Silene alba*

477   *(Miller) Krause*. American Journal of Botany 68:801-807

478   Harper JL (1977) In: Population biology of plants. Academic Press, London UK

479   Harris MS, Pannell JR (2008) Roots, shoots and reproduction: sexual dimorphism in size and

480   costs of reproductive allocation in an annual herb. Proceedings of the Royal Society

481   B-Biological Sciences 275:2595-2602

482 Harris MS, Pannell JR (2010) Canopy seed storage is associated with sexual dimorphism in

483 the woody dioecious genus Leucadendron. Journal of Ecology 98:509-515

484 Hesse E, Pannell JR (2011) Sexual dimorphism in a dioecious population of the wind-

485 pollinated herb *Mercurialis annua*: the interactive effects of resource availability and

486 competition. Annals of Botany 107:1039-1045

487 Iglesias MC, Bell G (1989) The small scale spatial distribution of male and female plants.

488 Oecologia 80:229-235

489 Jing SW, Coley PD (1990) Dioecy and herbivory: the effect of growth rate on plant defense in

490 *Acer negundo*. Oikos 58:369-377

491 Klinkhamer PGL, deJong TJ, Metz H (1997) Sex and size in cosexual plants. Trends in

492 Ecology & Evolution 12:260-265

493 Korpelainen H (1991) Sex ratio variation and spatial segregation of the sexes in populations

494 of *Rumex acetosa* and *R. acetosella* (Polygonaceae). Plant Systematics and Evolution

495 174:183-195

496 Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters.

497 Evolution 34:292-305

498 Lankinen A, Madjidian JA (2011) Enhancing pollen competition by delaying stigma

499 receptivity: pollen deposition schedules affect siring ability, paternal diversity, and

500 seed production in *Collinsia heterophylla* (Plantaginaceae). American Journal of

501 Botany 98:1191-1200

502 Lloyd DG, Webb CJ (1977) Secondary sex characters in plants. Botanical Review 43:177-216

503 Lokker C, Susko D, Lovettdoust L, Lovettdoust J (1994) Population genetic structure of

504 *Vallisneria americana*, a dioecious clonal macrophyte. American Journal of Botany

505 81:1004-1012

506 Lonsdale WM (1990) The self-thinning rule: dead or alive. Ecology 71:1373-1388

507   Lovett- Doust JL, Obrien G, Doust LL (1987) Effect of density on secondary sex

508   characteristics and sex ratio in *Silene alba* (Caryophyllaceae). American Journal of

509   Botany 74:40-46

510   Lovich JE, Gibbons JW (1992) A review of techniques for quantifying sexual size

511   dimorphism. Growth Development and Aging 56:269-281

512   Meagher TR (1992) The quantitative genetics of sexual dimorphism in *Silene latifolia*

513   (Caryophyllaceae) 1. genetic variation. Evolution 46:445-457

514   Moore JC, Pannell JR (2011) Sexual selection in plants. Current Biology 21:R176-R182

515   Obeso JR (2002) The costs of reproduction in plants. New Phytologist 155:321-348

516   Pannell J (1997) Variation in sex ratios and sex allocation in androdioecious *Mercurialis*

517   *annua*. Journal of Ecology 85:57-69

518   Pannell JR, Obbard DJ, Buggs RJA (2004) Polyploidy and the sexual system: what can we

519   learn from *Mercurialis annua*? Biological Journal of the Linnean Society 82:547-560

520   Pannell JR, Ojeda F (2000) Patterns of flowering and sex-ratio variation in the Mediterranean

521   shrub *Phillyrea angustifolia* (Oleaceae): implications for the maintenance of males

522   with hermaphrodites. Ecology Letters 3:495-502

523   Pickup M, Barrett SCH (2012) Reversal of height dimorphism promotes pollen and seed

524   dispersal in a wind-pollinated dioecious plant. Biology Letters 8:245-248

525   R Core Team (2013) R: A language and environment for statistical computing. In, 3.0.2. edn.

526   R Foundation for Statistical Computing, Vienna, Austria

527   Ruberti I, Sessa G, Ciolfi A, Possenti M, Carabelli M, Morelli G (2012) Plant adaptation to

528   dynamically changing environment: The shade avoidance response. Biotechnology

529   Advances 30:1047-1058

530   Sanchez Vilas J, Pannell JR (2011) Sexual dimorphism in resource acquisition and

531   deployment: both size and timing matter. Annals of botany 107:119-126

532   Sanchez-Vilas J, Turner A, Pannell JR (2011) Sexual dimorphism in intra- and interspecific

533   competitive ability of the dioecious herb *Mercurialis annua*. Plant Biology 13:218-

534   222

535   Sangoi L, Gracietti MA, Rampazzo C, Bianchetti P (2002) Response of Brazilian maize

536   hybrids from different eras to changes in plant density. Field Crops Research 79:39-51

537   Schlichting CD (1986) The evolution of phenotypic plasticity in plants. Annual Review of

538   Ecology and Systematics 17:667-693

539   Schmitt J, Wulff RD (1993) Light spectral quality, phytochrome and plant competition.

540   Trends in Ecology & Evolution 8:47-51

541   Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in

542   competition among plants. Oecologia 113:447-455

543   Shea MM, Dixon PM, Sharitz RR (1993) Size differences, sex ratio, and spatial distribution

544   of male and female water tupelo, *Nyssa aquatica* (Nyssaceae). American Journal of

545   Botany 80:26-30

546   Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review of the

547   evidence. Quarterly Review of Biology 64:419-461

548   Shuster SM, Wade MJ (2003) Mating systems and strategies in: Monographs in Behavior and

549   Ecology Princeton, NJ: Princeton University Press

550   Skogsmyr I, Lankinen A (2002) Sexual selection: an evolutionary force in plants. Biological

551   Reviews 77:537-562

552   Slatkin M (1984) Ecological causes of sexual dimorphism. Evolution 38:622-630

553   Sleeman JD, Dudley SA, Pannell JR, Barrett SCH (2002) Responses of carbon acquisition

554   traits to irradiance and light quality in *Mercurialis annua* (Euphorbiaceae): Evidence

555   for weak integration of plastic responses. American Journal of Botany 89:1388-1400

556   Stark LR, McLetchie DN, Mishler BD (2005) Sex expression, plant size, and spatial

557   segregation of the sexes across a stress gradient in the desert moss *Syntrichia*

558   *caninervis*. Bryologist 108:183-193

559   Stillwell RC, Blanckenhorn WU, Teder T, Davidowitz G, Fox CW (2010) Sex differences in

560   phenotypic plasticity affect variation in sexual size dimorphism in insects: from

561   physiology to evolution. Annual Review of Entomology 55: 227-245

562   Sultan SE (2000) Phenotypic plasticity for plant development, function and life history.

563   Trends in Plant Science 5:537-542

564   Tutin TG et al. (1968) Flora Europea. Cambridge University Press, Cambridge

565   Vanderwerf HMG, Wijlhuizen M, Deschutter JAA (1995) Plant density and self thinning

566   affect yield and quality of fiber hemp (*Cannabis sativa* L.). Field Crops Research

567   40:153-164

568   Wallace CS, Rundel PW (1979) Sexual dimorphism and resource allocation in male and

569   female shrubs of *Simmondsia chinensis*. Oecologia 44:34-39

570   Weller DE (1987) A reevaluation of the -3/2 power rule of plant self-thinning. Ecological

571   Monographs 57:23-43

Table 1. Minimal adequate models (LMM; random factors: replicate/pot) for the effects of (a) distance between pots, plant sex and their interaction on plant mass of plant reared in the centre and at the edge of the population, and (b) distance between pots, position in the population and their interaction on the mass of female and male plants. Effect sizes given are untransformed. We present model comparisons (log likelihood ratio tests) by comparing the full model (for a: III: distance + sex + distance × sex; for b: III: distance + position + distance × position), and simplified models II (for a: position + distance; for b: sex + distance), I (for a: sex; for b: position), I' (for a and b: distance).

(a) By position

Explanatory variables	Centre y= plant mass; $\lambda = 0.22$				Edge y= plant mass; $\lambda = 0.34$			
	Effect size	SE	t	LLRT	Effect size	SE	t	LLRT
(Intercept: female at distance 0)	1.53	0.04	35.37		2.28	0.048	48.02	**I-II (Distance):**
Distance 5	0.06	0.06	0.97		0.05	0.062	0.78	**Ip(χ^2_5>42.25)<0.0001**
Distance 15	0.10	0.06	1.71		0.08	0.062	1.25	
Distance 25	0.20	0.06	3.23		0.28	0.062	4.57	
Distance 35	0.37	0.06	6.22		0.28	0.062	4.52	
Distance 85	0.37	0.06	6.11		0.26	0.062	4.15	**I'-II (Sex) :**
Sex (M)	-0.05	0.06	-0.75		-0.23	0.036	-6.37	**p(χ^2_1>39.21)<0.0001**
Dist. 5 : sex M	-0.02	0.09	-0.23	**II-III (Distance x Sex):**				
Dist. 15 : sex M	-0.01	0.08	-0.12	**p(χ^2_5>12.8)=0.03**				
Dist. 25 : sex M	0.08	0.09	0.99					
Dist. 35 : sex M	-0.19	0.09	-2.25					II-III: p(χ^2_5>7.75)=0.17
Dist. 85 : sex M	-0.11	0.08	-1.26					

(b) By sex

Explanatory variables	Female y= plant mass; $\lambda = 0.26$				Male y= plant mass; $\lambda = 0.30$			
	Effect size	SE	t	LLRT	Effect size	SE	t	LLRT
(Intercept: Centre at distance 0)	1.65	0.05	31.13		1.79	0.05	37.37	**I-II (Distance):**
Distance 5	0.07	0.07	1.00		0.00	0.06	0.00	**p(χ^2_5>64.84)<0.0001**
Distance 15	0.13	0.07	1.83		0.05	0.06	0.85	
Distance 25	0.25	0.07	3.41		0.32	0.06	5.37	
Distance 35	0.49	0.07	6.61		0.27	0.06	4.55	
Distance 85	0.48	0.07	6.52		0.30	0.06	5.10	**I'-II (Position):**
Position (E)	0.22	0.07	3.29		0.06	0.04	1.84	**p(χ^2_1>3.38)=0.07**
Dist. 5 : Pos. (E)	0.01	0.09	0.15	**II-III (Distance x Position):**				
Dist. 15 : Pos. (E)	-0.04	0.09	-0.40	**p(χ^2_5>31.53)<0.001**				
Dist. 25 : Pos. (E)	-0.08	0.09	-0.90					
Dist. 35 : Pos. (E)	-0.33	0.09	-3.66					II-III: p(χ^2_5>5.08)=0.41
Dist. 85 : Pos. (E)	-0.34	0.09	-3.73					

Table 2. Minimal adequate models (LMM; random factors: Replicate/pot) for the effects of (a) distance between pots, plant sex and their interaction on plant height of plant reared in the centre and at the edge of the plots and (b) distance between pots, position in the plot and their interaction on plant mass of female and male plants. We present model comparisons (log likelihood ratio tests), comparing full model (for a: III: distance + sex + distance × sex; for b: III: distance + position + distance × position), and simplified models II (for a: sex + distance; for b: position + distance), I (for a: sex; for b: position), I' (for a and b: distance).

(a) By position

Explanatory variables	Centre				Edge			
	y= plant height				y= plant height			
	Effect size	SE	t	LLRT	Effect size	SE	t	LLRT
(Intercept: female at distance 0)	4146.2	123.49	33.57		437.14	8.57	51.01	
Distance 5	-875.3	139.41	-6.28	I-II (Distance):	-71.75	10.25	-7	I-II(Distance):
Distance 15	-1524.7	139.41	-10.94	$p(\chi^2{}_5>76.9)<0.0001$	-93.3	10.25	-9.1	$p(\chi^2{}_5>138.07)<0.0001$
Distance 25	-1403.0	139.79	-10.04		-110.65	10.27	-10.78	
Distance 35	-1330.8	139.79	-9.52		-88.58	10.25	-8.64	
Distance 85	-1595.0	139.41	-11.44	I'-II (Sex):	-121.52	10.25	-11.85	I'-II (Sex):
Sex (M)	-385.0	52.46	-7.34	$p(\chi^2{}_1>46.3)<0.0001$	-39.36	3.85	-10.22	$p(\chi^2{}_1>89.08)<0.0001$
Dist. 5 : sex M								
Dist. 15 : sex M								
Dist. 25 : sex M				II-III: $p(\chi^2{}_5>8.19)=0.15$				II-III: $p(\chi^2{}_5>3.16)=0.67$
Dist. 35 : sex M								
Dist. 85 : sex M								

(b) By sex

Explanatory variables	Female				Male			
	y= plant height				y= plant height			
	Effect size	SE	t	LLRT	Effect size	SE	t	LLRT
(Intercept: Centre at distance 0)	2387.24	54.50	43.80		513.683	14.91	34.44	
Distance 5	-483.71	62.76	-7.71	I-II (Distance):	-93.84	18.83	-4.98	I-II (Distance):
Distance 15	-708.07	62.76	-11.28	$p(\chi^2{}_5>192.2)<0.0001$	-161.75	18.83	-8.59	$p(\chi^2{}_5>193.84)<0.0001$
Distance 25	-754.10	62.97	-11.98		-157.20	18.83	-8.35	
Distance 35	-612.04	62.76	-9.75		-166.47	19.01	-8.76	
Distance 85	-866.52	62.76	-13.81		-177.72	18.83	-9.44	I-II (Position):
Position (E)				I'-II: $p(\chi^2{}_1>2.60)=0.11$	-46.366	16.75	-2.77	$p(\chi^2{}_1>5.60)=0.02$
Dist. 5 : Pos. (E)					7.207	23.51	0.31	
Dist. 15 : Pos. (E)					46.758	23.51	1.99	
Dist. 25 : Pos. (E)				II-III: $p(\chi^2{}_5>7.83)=0.17$	25.258	23.55	1.07	II-III: $p(\chi^2{}_5>9.80)=0.08$
Dist. 35 : Pos. (E)					59.805	23.65	2.53	
Dist. 85 : Pos. (E)					41.468	23.51	1.76	

Table 3. Variation in mass SDI (a) with increasing distance between adjacent pots across the three replicates (A, B and C); mean ± SD and for all pots grouped per distance level (Mean ± SE and Mean ± SD). We separated the data for pots placed either in the center of the plot or at the edge since this reflects differences in competition degree within plot. We present sexual dimorphism in mass without the two extreme outliers (SDI > 20) at the distances 35 and 85 cm (b). We performed a non-parametric Fligner Killeen test for homogeneity of variances, with 5 df for each test. We used non-parametric Kruskal-Wallis test to compare mean SDI when variances were homogeneous (5 df in each test) and Welch's ANOVA (one way) when variances were heterogeneous (df numerator: 5; df denominator: 69.2 and 68.5 for Mass SDI with outliers included and excluded, respectively).

(a) **Mass SDI (Center)** | | | | | | **All replicates together** | | |

Distance	A		B		C		Mean	SE	SD
0	0.27	± 0.72	0.34	± 0.82	0.97	± 1.80	0.52	± 0.24	± 1.19
5	0.23	± 0.96	1.06	± 1.29	0.41	± 0.48	0.57	± 0.20	± 1.01
15	0.55	± 1.37	0.71	± 1.50	0.81	± 1.00	0.69	± 0.24	± 1.26
25	0.81	± 1.13	0.53	± 1.25	0.30	± 1.06	0.54	± 0.22	± 1.12
35	0.54	± 1.48	7.05	± 14.61	3.19	± 3.23	3.71	± 1.75	± 8.92
85	5.79	± 11.80	1.36	± 2.82	0.75	± 1.72	2.63	± 1.38	± 7.17
					Fligner Killeen test		$\chi 2$=18.9; p=0.002		
					Welch's ANOVA		F=1.09; p=0.37		

Mass SDI (Edge)

Distance	A		B		C		Mean	SE	SD
0	0.46	± 1.02	0.78	± 1.17	1.05	± 1.28	0.77	± 0.17	± 1.16
5	1.02	± 1.17	1.80	± 2.11	0.81	± 1.36	1.20	± 0.23	± 1.61
15	1.21	± 1.66	0.94	± 1.49	1.37	± 2.49	1.18	± 0.28	± 1.90
25	0.53	± 0.69	0.90	± 1.44	1.20	± 3.04	0.88	± 0.29	± 1.97
35	1.07	± 2.67	2.43	± 7.28	2.16	± 5.60	1.88	± 0.79	± 5.39
85	0.43	± 1.03	1.16	± 2.07	1.14	± 2.16	0.91	± 0.26	± 1.81
					Fligner Killeen test		$\chi 2$=4.2; p=0.44		
					Kruskal test		$\chi 2$=6.68; p=0.24		

(b) **Mass SDI (without outliers; Center)**

Distance	A		B		C		Mean	SE	SD
0	0.27	± 0.72	0.34	± 0.82	0.97	± 1.80	0.52	± 0.24	± 1.19
5	0.23	± 0.96	1.06	± 1.29	0.41	± 0.48	0.57	± 0.20	± 1.01
15	0.55	± 1.37	0.71	± 1.50	0.81	± 1.00	0.69	± 0.24	± 1.26
25	0.81	± 1.13	0.53	± 1.25	0.30	± 1.06	0.54	± 0.22	± 1.12
35	0.54	± 1.48	2.31	± 3.65	3.19	± 3.23	2.06	± 0.61	± 3.04
85	1.94	± 2.61	1.36	± 2.82	0.75	± 1.72	1.33	± 0.47	± 2.37
					Fligner Killeen test		$\chi 2$=16; p=0.006		
					Welch's ANOVA		F=1.58; p=0.18		

Mass SDI (without outliers; Edge)

Distance	A		B		C		Mean	SE	SD
0	0.46	± 1.02	0.78	± 1.17	1.05	± 1.28	0.77	± 0.17	± 1.16
5	1.02	± 1.17	1.80	± 2.11	0.81	± 1.36	1.20	± 0.23	± 1.61
15	1.21	± 1.66	0.94	± 1.49	1.37	± 2.49	1.18	± 0.28	± 1.90
25	0.53	± 0.69	0.90	± 1.44	1.20	± 3.04	0.88	± 0.29	± 1.97
35	1.07	± 2.67	0.58	± 1.30	0.83	± 1.83	0.84	± 0.30	± 2.01
85	0.43	± 1.03	1.16	± 2.07	1.14	± 2.16	0.91	± 0.26	± 1.81
					Fligner Killeen test		$\chi 2$=2.1; p=0.83		
					Kruskal test		$\chi 2$=8.02; p=0.15		

Table 4. Variation in height SDI with increasing distance between adjacent pots across the three replicates (A, B and C); Mean ± SD and for all pots grouped per distance level (mean ± SE and mean ± SD). We separated the data for pots placed either in the center of the plot or at the edge, since this reflects differences in competition degree within plot. We performed a non-parametric Fligner Killeen test for homogeneity of variances with 5 df for each test. We used a non-parametric Kruskal-Wallis test to compare mean SDI when variances were homogeneous (5 df in each test), and Welch's ANOVA (one way) when variances were heterogeneoius (df numerator: 5; df denominator: 69.5)

Height SDI (Center)						All replicates together		
Distance	A		B		C	Mean	SE	SD
0	0.03 ±	0.08	0.05 ±	0.08	0.05 ± 0.06	0.04	± 0.01	± 0.07
5	0.02 ±	0.07	0.07 ±	0.10	0.07 ± 0.09	0.06	± 0.02	± 0.09
15	0.03 ±	0.26	0.08 ±	0.14	0.06 ± 0.17	0.06	± 0.04	± 0.19
25	0.06 ±	0.15	0.09 ±	0.16	0.13 ± 0.14	0.09	± 0.03	± 0.15
35	0.07 ±	0.20	0.23 ±	0.21	0.18 ± 0.12	0.17	± 0.04	± 0.19
85	0.13 ±	0.23	0.07 ±	0.14	0.09 ± 0.11	0.10	± 0.03	± 0.16
				Fligner Killeen test		$\chi 2$=18; p=0.003		
				Welch's ANOVA		F=2.45; p=0.04		

Height SDI (Edge)						All replicates together		
Distance	A		B		C	Mean	SE	SD
0	0.10 ±	0.13	0.10 ±	0.15	0.05 ± 0.15	0.08	± 0.02	± 0.14
5	0.11 ±	0.14	0.14 ±	0.14	0.06 ± 0.14	0.10	± 0.02	± 0.14
15	0.16 ±	0.14	0.06 ±	0.25	0.10 ± 0.12	0.11	± 0.03	± 0.18
25	0.10 ±	0.16	0.08 ±	0.12	0.11 ± 0.17	0.10	± 0.02	± 0.15
35	0.09 ±	0.15	0.14 ±	0.21	0.10 ± 0.16	0.11	± 0.03	± 0.17
85	0.04 ±	0.14	0.09 ±	0.15	0.08 ± 0.13	0.07	± 0.02	± 0.14
				Fligner Killeen test		$\chi 2$=4.7; p=0.45		
				Kruskal test		$\chi 2$=3.05; p=0.7		

Figure 1. (a) Effect of interplant competition (distance between pots) on dry vegetative mass (g) of male and female *Mercurialis annua*; subsample of all male and female plants reared in the centre of the plot, N = 27 individuals per sex per distance between pots. (b) Effect of position in the plot (center vs. edge) and distance between pots (i.e. interplant competition levels) on plant dry mass separately for male and female plants. Data present mean ± SE.

Figure 2. (a) Effect of interplant competition (distance between pots) on plant height after eight weeks growth (cm) of male and female *Mercurialis annua*; subsample of all male and female plants reared in the centre of the plot, N = 27 individuals per sex per distance between pots. (b) Effect of position in the plot (center vs. edge) and distance between pots (i.e. interplant competition levels) on plant height separately for male and female plants. Data present mean ± SE.

Figure 3. Sexual dimorphism in mass (a) and height (b) within pot, for plants reared at the edge or in the centre of the plots. The index of sexual dimorphism (SDI) was calculated as follows: (female trait –male trait)/(male trait9. For mass SDI (a), we present mean ± SE for both data with (left panel) and without (right panel) four extreme outliers occurring at the distance between pots of 35 cm (1 central pot, 2 edge pots) and 85 cm (1 central pot).
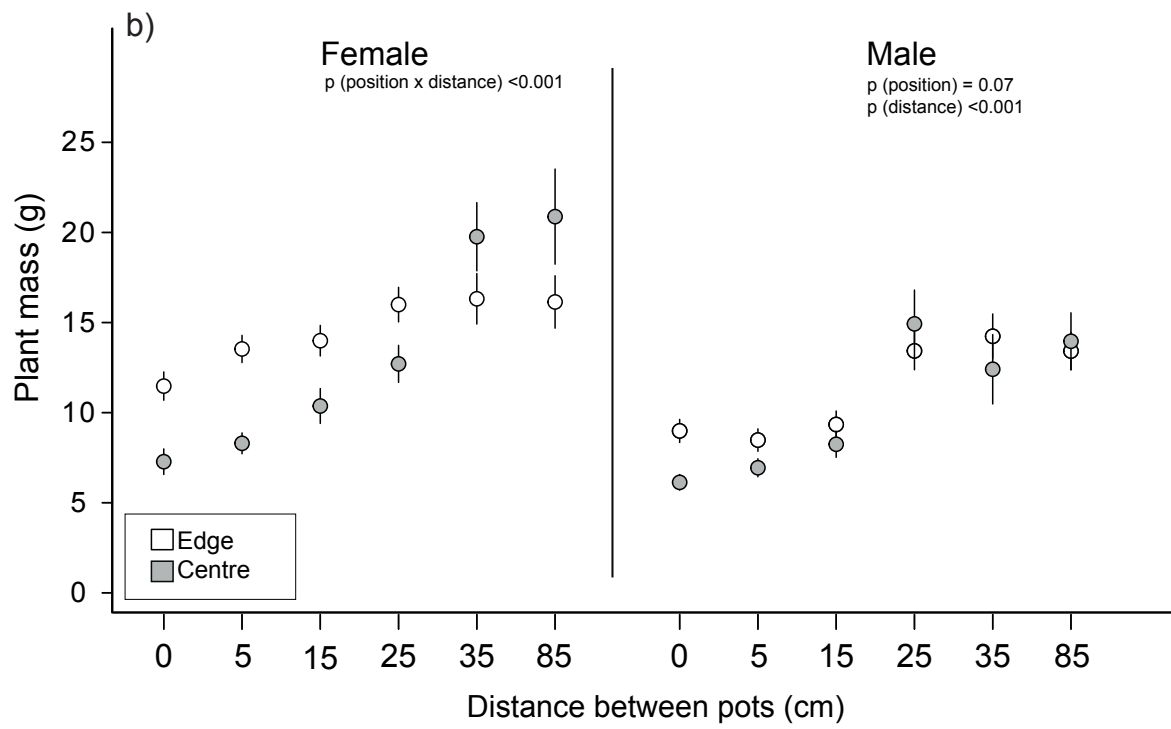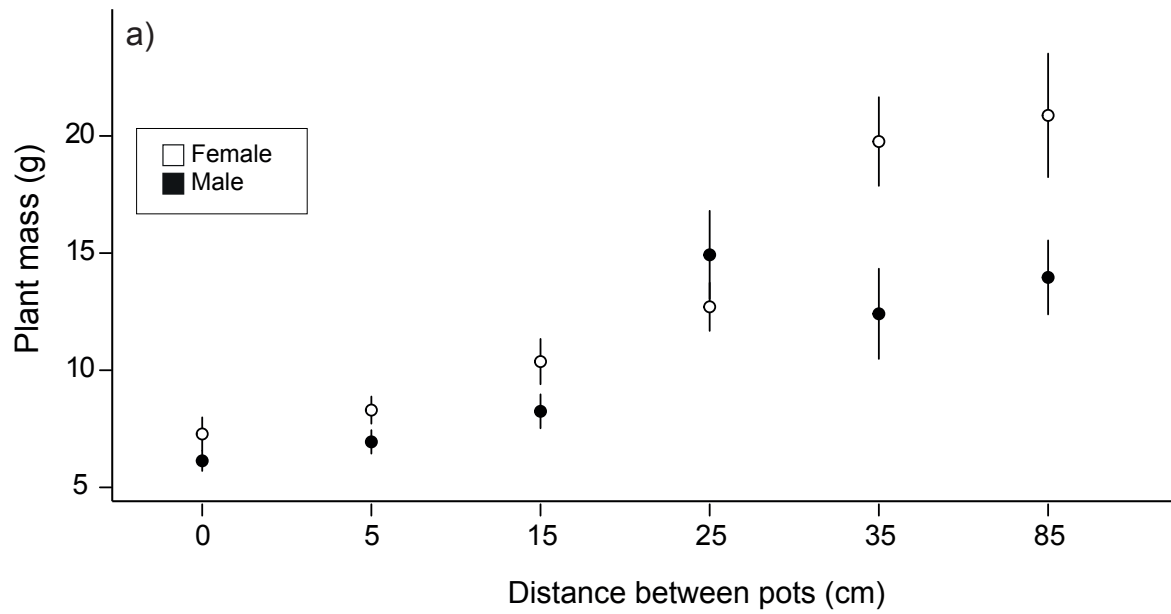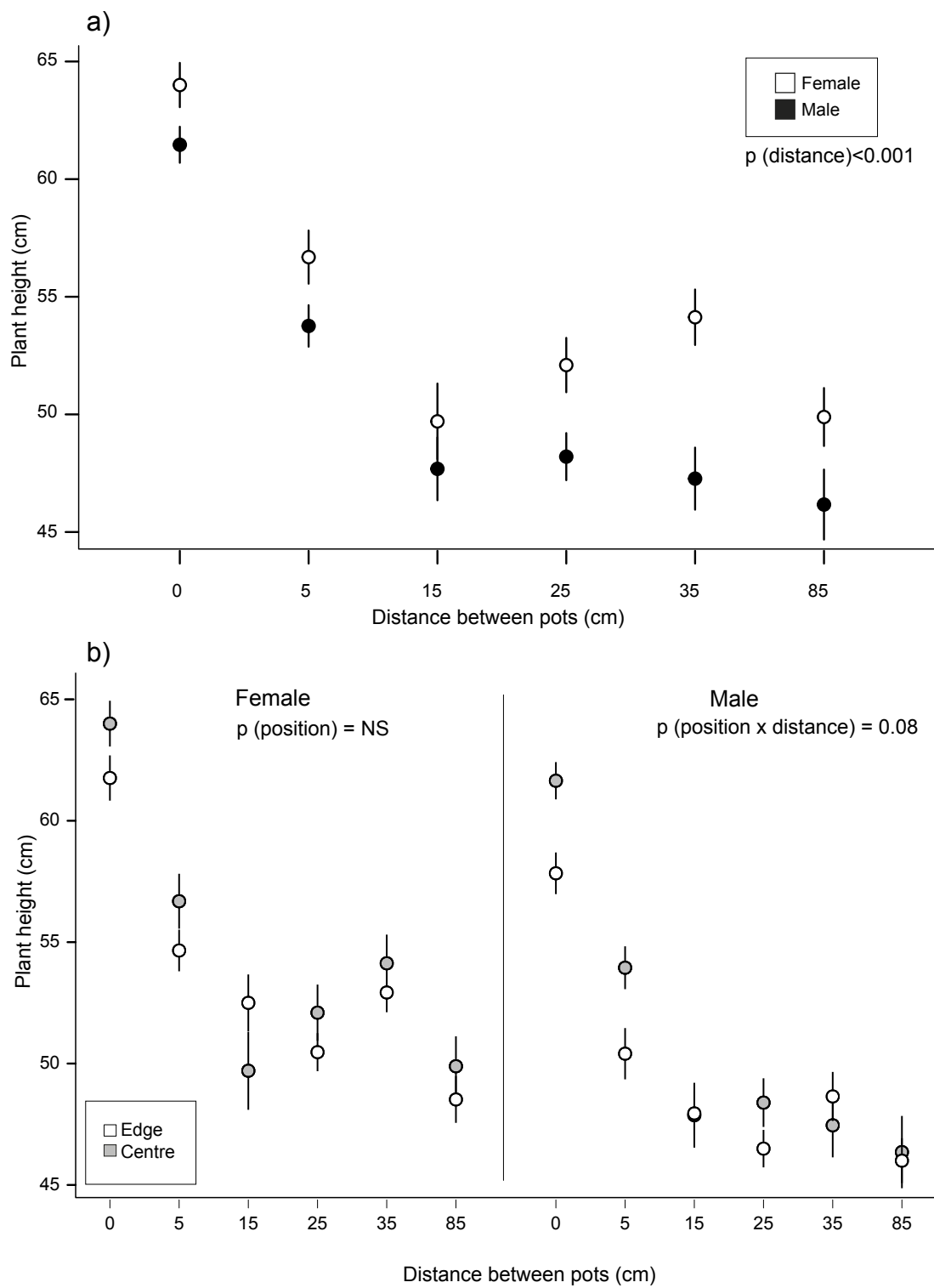
Figure 1.

Figure 2.

Figure 3.