DIFFERENTIAL COMPETITIVE ABILITY BETWEEN SEXES IN THE DIOECIOUS

**Antennaria dioica** (Asteraceae)

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**Key Results**

- **Background and Aims** Differences in competitive ability between the sexes of dioecious plants are expected as a result of allocation trade-offs associated with sex-differential reproductive costs. However, the available data on competitive ability in dioecious plants are scarce and contradictory. In this study sexual competition was evaluated using the dioecious plant *Antennaria dioica* in a common garden transplantation experiment.

- **Methods** Male and female plants were grown for 3 years either in isolation, or in competition with a plant of the same sex or the opposite sex. Flowering phenology, sexual and asexual reproduction, plant growth, nutrient content and arbuscular mycorrhizal colonization in the roots were assessed.

- **Key Results** Our results showed little evidence of sexual differences in competitive ability. Both sexes suffered similarly from competition, and competitive effects were manifested in some traits related to fitness but not in others. Survival was unaffected by competition, but competing plants reduced their vegetative growth and reproductive investment compared with non-competing plants. In addition, differences in sexual competitive ability were observed in relation to flowering frequency, an important life history trait not reported in previous studies.

- **Conclusions** The findings indicate that female and male *A. dioica* plants possess similar intersexual competitive abilities which may be related to the similar costs of reproduction between sexes in this species. Nevertheless, intrasexual competition is higher in females, giving support for asymmetric niche segregation between the sexes.

**Key words:** *Antennaria dioica*, competition, dioecy, niche segregation, sexual dimorphism.

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**INTRODUCTION**

In most environments, plants experience competition with other individuals for access to limited resources. Individuals typically compete both with conspecifics and with other species, and both types of competition play an important role in determining the composition and functioning of plant communities (Tilman, 1982, 1988; Goldberg and Barton, 1992; Callaway and Walker, 1997). Competition can occur above- and below-ground. Whilst above-ground competition takes place when plants decrease the survival, growth or fecundity of a neighbour by reducing access to light or pollinators, below-ground competition occurs in response to limited soil resources (Casper and Jackson, 1997). Plants may alter their competitive ability by adjusting morphologically and physiologically to the resource levels and the neighbour densities they encounter (Weiner and Thomas, 1992). However, the increased ability to compete for above-ground resources by changes in allocation patterns may reduce below-ground competitive ability, or vice versa, resulting in a negative interaction between root and shoot competitive ability. Interactions between root and shoot competition vary among species (Cahill, 2002) and have been shown to influence individual plants (Cahill, 1999, 2002), with consequences at the community level (Lamb and Cahill, 2008).

In sexually dimorphic plants, where more than one type of individual can be recognized regarding their gender, the two sexes may differ in resource requirements even though they may also compete for the same limiting resources.
that male and female plants differ in competitive ability (reviewed in Ágren et al., 1999). Secondly, inconclusive results are also reported by examining whether the relationship between growth and distance to the nearest neighbour depends on the sex of the neighbour. For example, Herrera (1988) proved that the competitive inference was asymmetric in the hemiparasitic shrub Osyris quadriripartita (Santalaceae), and the growth of males was reduced more when the nearest neighbour was a female than when it was another male. However, Zhang et al. (2009) showed that sexual competition had a negative influence on stem growth for both genders in Fraxinus mandshurica (Oleaceae) trees. In addition, Vasiliasukas and Aarssen (1992) noted that although the presence of neighbours decreased plant size in Juniperus virginiana (Cupressaceae), the reduction in growth was independent of the sex of the nearest neighbour. Thirdly, differences in competitive ability between sexes of sexually dimorphic plants have been examined by growing female and male plants in a confined space, forcing them to compete for the same resources. This approach was adopted by Bertiller et al. (2002), Eppley (2006), Hawkins et al. (2009), Mercer and Eppley (2010), Sánchez-Vilas et al. (2011) and Hesse and Pannell (2011). Bertiller et al. (2002) grew dioecious Poa ligularis (Poaceae) in a greenhouse experiment under two different plant densities. They demonstrated that density was the main factor affecting total biomass in both sexes, and females had higher competitive ability than males. However, Hawkins et al. (2009) showed in a similar experiment with Lindera melissifolia (Lauraceae) that although density influenced competition, male and female plants had similar competitive ability. Eppley (2006) and Mercer and Eppley (2010) observed gender-specific competitive differences at the seedling stage in Distichlis spicata (Poaceae), with female seedlings exhibiting a stronger competitive effect than male seedlings. Sánchez-Vilas et al. (2011) also reported Mercurialis annua (Euphorbiaceae) females to be more aggressive intra- and interspecific competitors than males. Also, recently, Hesse and Pannell (2011) found that competition affected the reproductive allocation of females, but not that of males even though competition did not affect plant size. Altogether, these results indicate that females may be generally more competitive than males, at least when considering herbaceous species.

Most plants take up nutrients through arbuscular mycorrhizal (AM) symbiosis (Smith and Read, 1997; Wang and Qiu, 2006). Since AM fungi mediate resource acquisition, AM fungi have the potential to affect competitive interactions among plants (reviewed in Smith et al., 2010). AM fungi may favour inferior competitors (Zobel and Moora, 1995; Moora and Zobel, 1996) or contribute to competitive exclusion if AM fungi favour a superior competitor (Allen and Allen, 1990). Moreover, in sexually dimorphic plants, AM fungi may have sex-specific effects on survival, growth and reproduction (reviewed in Varga, 2010). These sex-specific differences have been linked to differences in resource requirements and allocation patterns within the sexes (e.g. Varga et al., 2009; Vega-Frutis and Guevara, 2009) and they could theoretically influence the outcome of sexual interactions among plants. For example, AM inoculation increased plant mortality in females in a greenhouse experiment manipulating soil pH, suggesting that the cost of AM formation was higher in female than in male plants (Varga and Kytöviita, 2010).

In the present study, we examined sexual competition using the dioecious clonal plant Antennaria dioica (Asteraceae) in a common garden transplantation experiment. Specifically, we compared the performance of females and males growing alone or with a competitor of the same or different sex during 3 years. Our main aim was to determine whether the sexes differ in competitive ability when growing with the same or different sex. Sexual dimorphism in secondary sex characters in this species is subtle, with both sexes showing equal flowering frequency, similar costs of reproduction (Varga and Kytöviita, 2011) and similar growth under experimental conditions (Varga and Kytöviita, 2008, 2010), even though sexual differences in performance have been observed in response to abiotic factors and mycorrhizal fungi (Varga and Kytöviita, 2008, 2010). Nevertheless, A. dioica exhibits a female-biased sex ratio in the field (Öster and Eriksson, 2007; Varga and Kytöviita, 2011) which cannot be explained by SSS or sex lability (Varga and Kytöviita, 2011). Therefore, we investigated whether the sexes differ in their competitive ability.

MATERIALS AND METHODS

Plant species

Antennaria dioica Gaertn. (Asteraceae) is a dioecious, perennial, clonal plant that grows in heaths, dry grasslands and sandy or stony places. In addition, A. dioica sometimes occurs in semi-open forests. It is widely distributed in temperate regions of the northern hemisphere (Tutin et al., 1976) and is normally colonized by AM fungi in the field (Wang and Qiu, 2006). Each genet may produce one to several ramets by clonal growth of surface-creeping stolons. Genets flower, producing up to one flowering shoot per ramet, and both sexes have similar annual flowering probability (Varga and Kytöviita, 2011). In Finland, flowering takes place between June and July and the species is pollinated by generalist insects from several orders including Lepidoptera, Hymenoptera, Diptera and Coleoptera (Willis and Burkill, 1903).

Experimental set-up

In July 2005 we randomly selected 20 male (referred as M) and 20 female (referred as F) A. dioica genets of similar size growing at Oulanka National Park (66°22′32″N, 29°20′19″E). The plants were excavated and the soil adhered to the roots was removed and mixed. From each individual, four clonal fragments were selected to allow representation of the same plant genotype in each treatment. The clonal fragments had a similar number of ramets (4.4 ± 0.1; sex, $F_{1,38} = 2.39$, $P = 0.13$; genotype, $F_{3,120} = 1.55$, $P = 0.04$) and biomass (2.04 ± 0.06 g; sex, $F_{1,38} = 0.90$, $P = 0.35$; genotype, $F_{3,120} = 2.99$, $P < 0.01$) to ensure we did not obtain any sex-specific effect due to initial differences in plant size. In addition, in the competition treatments (see below) clonal fragments of similar size were chosen.

The experimental area was set up in the close vicinity of the Oulanka Research Station in a fenced plot within a pine forest.
To limit the available soil space and force competition among plants, the clonal fragments were planted in plastic boxes (27 × 23 × 8 cm) so that the soil available for roots was 4970 cm³ and the surface area for clonal growth was 620 cm². The boxes were randomly placed along four rows (Fig. 1) and pierced through the bottom to allow water movement. The four clonal fragments from each M and F plant were randomly assigned to one of the three following treatments or boxes: ‘none’, plants growing with no competitor; ‘same’, plants growing with a competitor of the same sex; and ‘different’, plants growing with a competitor of the opposite sex. ‘None’ boxes contained one clonal fragment from either an M or an F plant (M and F boxes, 20 + 20 clonal fragments, 20 + 20 boxes, Fig. 1); ‘same’ boxes contained two clonal fragments of the same sex but from different genotypes (M + M and F + F boxes, 40 + 40 clonal fragments, 20 + 20 boxes, Fig. 1); ‘different’ boxes contained two clonal fragments of a different sex, one from an M and the other from an F plant (M + F and F + M boxes, 20 + 20 clonal fragments, 20 boxes, Fig. 1). Thus, the experimental design was made up of n = 160 clonal fragments distributed in n = 100 boxes. Plants in the ‘none’ treatment were placed in the centre of the box, and plants in the ‘same’ and ‘different’ treatments were planted 9 cm away from the box border and from the other plant. The experimental plants were watered with tap water after transplantation and left without any care, just removing seedlings which eventually germinated in the boxes. The soil used in the present experiment was sandy pine forest soil with pH<sub>1/10</sub> 4.96 ± 0.07, and the soluble nutrients levels were 1.49 ± 0.03 μg P g⁻¹, 11.25 ± 0.13 μg K g⁻¹, 13.71 ± 0.28 μg Ca g⁻¹ and 27.34 ± 0.26 μg Mg g⁻¹.

**Plant analyses**

From 2006 to 2008, plant survival, plant sex, number of ramets and number of floral shoots and inflorescences (if any) were noted. Because floral shoots and inflorescences remain for a long time after seed dispersal, plants were only checked once per year when they were already fruiting. The experiment was terminated on August 2008, 3 years after it had started. A picture of each box was taken to calculate the experiment was terminated on August 2008, 3 years after it had started. A picture of each box was taken to calculate the above-ground mass excluding the floral shoots and inflorescences was used. Plant material was acid digested using the Paar001H program in the Paar Physica multiwave sample preparation system (Perkin Elmer, Waltham, MA, USA). The P concentration (%, w/w) was determined following the procedure described in John (1970). The P concentrations were measured colorimetrically using a UV-160A Shimadzu analyser from two sub-samples and the readings were then averaged. The Ca, Mg and K were measured using a VARIAN SpectrAA 220 Fast Sequential (Mulgrave, Victoria, Australia) atomic absorption spectrophotometer. The N and C concentrations from the same tissue were analysed using the dynamic flash combustion technique (CE Instruments EA 1110 Elemental Analyzers, Wigan, UK).

**Mycorrhizal analysis**

Roots from each individual were stained after clearing by incubation in 10 % KOH for 4 d at room temperature and additional incubation in 1.5 % alkaline H₂O₂ for 2 h at room temperature. After 2 h in 1 % HCl, we incubated the roots at 80 °C with 0.02 % trypan blue staining solution for 2 h. The AM fungal root colonization was measured at ×100 magnification from 30 root segments of 1 cm length according to Trouvelot et al. (1986).

**Statistical analyses**

To determine whether the proportion of plants flowering differed between sexes and competition treatments, we used a...
RESULTS

Survival

Plant mortality during the experiment was very low, and only five plants (two F and three M) died during the experiment. These plants and their neighbours were excluded from further analyses. Therefore, the final sample size was 155 plants and 95 boxes.

Fifteen plants (eight F and seven M) changed their sexual expression during the experiment. No statistically significant effects of gender, treatment or plant genotype were responsible for the pattern of changing sex observed (all cases P > 0.08). These plants were included in all following analyses with their original sex recorded in 2005 since running the analyses with or without these plants did not change the significance of the results.

Growth

The number of ramets produced by plants was similar in females and males, but differed between the three study years with a significant interaction between year and treatment (Table 1; Fig. 2A). The increase in number of ramets produced by plants was affected by competition only in 2008 (Fig. 2A). In 2006, plant growth (defined as the number of ramets) was positive, and the plants had on average 6.4 ± 2 ramets instead of the 4.4 ± 0.2 ramets they had when the experiment was started in 2005. No statistically significant differences due to gender or treatment were detected explaining the number of ramets that year (sex, $F_{1,45} = 1.59$, $P = 0.21$; treatment, $F_{2,113} = 1.29$, $P = 0.28$; interaction, $F_{2,113} = 0.03$, $P = 0.97$; Fig. 2A). At that point, the number of ramets per box was larger in the ‘same’ and ‘different’ treatments since there were two plants growing per box instead of one growing in the ‘none’ treatment. In 2007, the plants averaged 16.1 ± 1.0 ramets, again with no statistically significant differences due to gender or treatment (sex, $F_{1,49} = 0.14$, $P = 0.71$; treatment, $F_{2,112} = 1.47$, $P = 0.24$; interaction, $F_{2,112} = 1.64$, $P = 0.20$; Fig. 2A). Finally, in 2008, plants growing alone had more ramets (46.4 ± 4.5) than plants growing with a competitor (29.8 ± 1.9 and 31.9 ± 2.2 ramets in the ‘same’ and ‘different’ treatments, respectively), irrespective of the sex of the plant (sex, $F_{1,46} = 0.00$, $P = 0.99$; treatment, $F_{2,111} = 9.19$, $P < 0.01$; interaction, $F_{2,111} = 0.63$, $P = 0.54$; Fig. 2A). At that point, the total surface occupied per box did not differ among the treatments (29.5% of the box was occupied on average $F_{4,94} = 1.16$, $P = 0.33$), even though differences in the number of ramets produced per box were detected ($F_{4,94} = 3.73$, $P < 0.01$; Fig. 2B). Even though there were two plants growing in the ‘same’ and ‘different’ boxes (and therefore the

Table 1. Repeated-measures ANOVA for differences in the number of ramets, floral shoots and inflorescences between sexes, among competition treatments and among years

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Ramets</th>
<th></th>
<th>Floral shoots</th>
<th></th>
<th>Inflorescences</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>d.f.</td>
<td>$F$</td>
<td>$P$</td>
<td>d.f.</td>
<td>$F$</td>
<td>$P$</td>
</tr>
<tr>
<td>Between</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant sex</td>
<td>1</td>
<td>0.50</td>
<td>0.48</td>
<td>1</td>
<td>1-49</td>
<td>0.23</td>
</tr>
<tr>
<td>Competition type</td>
<td>1</td>
<td>4.82</td>
<td><strong>0.01</strong></td>
<td>2</td>
<td>10.26</td>
<td><strong>&lt;0.01</strong></td>
</tr>
<tr>
<td>Genotype (plant sex)</td>
<td>38</td>
<td>0.97</td>
<td>0.55</td>
<td>37</td>
<td>1-38</td>
<td>0.12</td>
</tr>
<tr>
<td>Plant sex × competition type</td>
<td>2</td>
<td>0.95</td>
<td>0.39</td>
<td>2</td>
<td>0.29</td>
<td>0.75</td>
</tr>
<tr>
<td>Error</td>
<td>108</td>
<td></td>
<td></td>
<td>75</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Years</td>
<td>1-6</td>
<td>473.44</td>
<td><strong>0.01</strong></td>
<td>1</td>
<td>106.20</td>
<td><strong>&lt;0.01</strong></td>
</tr>
<tr>
<td>Years × plant sex</td>
<td>1-6</td>
<td>0.312</td>
<td>0.68</td>
<td>1</td>
<td>1-16</td>
<td>0.29</td>
</tr>
<tr>
<td>Years × competition type</td>
<td>3-2</td>
<td>2.83</td>
<td><strong>0.04</strong></td>
<td>2</td>
<td>7.33</td>
<td><strong>&lt;0.01</strong></td>
</tr>
<tr>
<td>Years × genotype (plant sex)</td>
<td>60.3</td>
<td>1.19</td>
<td>0.19</td>
<td>37</td>
<td>0.73</td>
<td>0.85</td>
</tr>
<tr>
<td>Years × plant sex × competition type</td>
<td>3-2</td>
<td>0.91</td>
<td>0.44</td>
<td>2</td>
<td>1.17</td>
<td>0.32</td>
</tr>
</tbody>
</table>

Analysis was conducted on log-transformed data. Greenhouse–Geisser correction was applied due to the lack of sphericity of data. Statistically significant results are indicated in bold.
The RGR of the plants was highest in the absence of competitors \( (F_{2,111}=7.42, P < 0.01; \text{Fig. 3}) \). Post-hoc comparisons indicated that, although competition did not significantly affect RGR in the ‘different’ treatment, it did affect RGR in the ‘same’ treatment: competing with the same sex resulted in the lowest RGR, with plants in the ‘same’ treatment with a competitor of the same sex, or ‘Differ.’ with a competitor of a different sex. For each year, different letters indicate statistically significant differences \( (P < 0.05) \) among treatments based on the Ryan–Einot–Gabriel–Welsch (REGW-F) procedure.

The number of ramets (these boxes should be double compared with the ‘none’ boxes assuming no effect of competition on the number of ramets produced), we detected a statistically significant difference between ‘different’ boxes and females growing alone (Fig. 2B). The RGR of the plants was highest in the absence of competitors \( (F_{2,111}=7.42, P < 0.01; \text{Fig. 3}) \). Post-hoc comparisons indicated that, although competition did not significantly affect RGR in the ‘different’ treatment, it did affect RGR in the ‘same’ treatment: competing with the same sex resulted in the lowest RGR, with plants in the ‘same’ treatment with a competitor of the same sex, or ‘Differ.’ with a competitor of a different sex. For each year, different letters indicate statistically significant differences \( (P < 0.05) \) among treatments based on the Ryan–Einot–Gabriel–Welsch (REGW-F) procedure.

FIG. 2. Number of ramets (mean ± s.e.) for each year for female and male Antennaria dioica (A) plants and (B) boxes grown in the three competition treatments: ‘None’ without competitor, ‘Same’ with a competitor of the same sex, or ‘Different’ with a competitor of a different sex. Different letters indicate statistically significant differences \( (P < 0.05) \) among treatments based on the Ryan–Einot–Gabriel–Welsch (REGW-F) procedure.

FIG. 3. Relative growth rate (RGR, mean ± s.e.) for female and male Antennaria dioica plants grown in the three competition treatments: ‘None’ without competitor, ‘Same’ with a competitor of the same sex, or ‘Different’ with a competitor of a different sex. Different letters indicate statistically significant differences \( (P < 0.05) \) among treatments based on the Ryan–Einot–Gabriel–Welsch (REGW-F) procedure.

In 2006, only 3 % of the plants flowered, probably due to the proximity of genet fragmentation and transplantation, and these data were not statistically analysed (Table 2). In the following years, 41 and 86 % of the plants flowered (Table 2). No statistically significant effects of gender, genotype or treatment were detected in 2007 (Table 2). In 2008, both plant genotype and the treatment × gender interaction explained the proportion of flowering plants: >97 % of females flowered in the ‘none’ and ‘different’ treatments, but only 74 % of females flowered when growing with the same sex (Table 2). Males flowered irrespective of the competition treatment (Table 2).

As the plants grew larger with the years, the number of floral shoots produced increased 5-fold from 2007 to 2008 (1.03 ± 0.15 times vs. 5.03 ± 0.33, respectively). In 2007, there were no statistically significant differences between sexes \( (F_{1,52}=0.37, P=0.55) \), competition treatment \( (F_{2,30}=0.14, P=0.99) \) or interaction between these two factors \( (F_{2,30}=0.93, P=0.47) \).
In 2008, competition reduced the number of floral shoots \( F_{2,89} = 6.64, P = 0.01 \) independently of the sex \( sex, F_{1,53} = 1.86, P = 0.18; \) interaction, \( F_{2,89} = 1.27, P = 0.29 \). Regarding the number of inflorescences produced, no differences were detected in 2007 (Table 2), but in 2008 males produced 1.4 times more inflorescences than females and competing plants reduced the number of inflorescences produced regardless of the sex of the competitor (Table 2).

**Arbuscular mycorrhizal status of the plants**

The roots of both male and female *A. dioica* were intensively colonized by AM fungi. The sexes did not differ in the proportion of root length colonized by AM hyphae \( 53.3 \pm 1.1 \% ; F_{1,7} = 0.003, P = 0.96 \), by AM fungal storage organ vesicles \( 19.4 \pm 0.9 \% ; F_{1,8} = 0.018, P = 0.90 \) or by the specific arbuscule structures where symbiotic exchanges is supposedly most active \( 4.5 \pm 0.4 \% ; F_{1,7} = 0.23, P = 0.65 \). Likewise, competition treatment had no statistically significant effect on the three fungal structures considered (hyphae, \( F_{2,130} = 0.19, P = 0.82 \); vesicles, \( F_{2,130} = 0.61, P = 0.55 \); arbuscules, \( F_{2,130} = 1.22, P = 0.30 \)) and there were no interactions (statistics not shown). Root density in the experimental boxes did not differ among the treatments \( F_{4,98} = 0.456, P = 0.77 \); ‘none’, 1.34 \pm 0.25, ‘same’, 0.95 \pm 0.18 and ‘different’, 1.17 \pm 0.24 mg root g\(^{-1}\) of soil, respectively) and was similar to that measured from natural *A. dioica* habitats \( 0.89 \pm 0.22 mg root g\(^{-1}\) of soil; S. Varga, unpubl. res.).

**Plant nutrient concentrations**

The concentrations of the main nutrients analysed in the plants are shown in Table 3. The sexes did not differ in the concentration of Mg, Ca or carbon. However, males possessed more K, N and P than females. Competition treatment only affected the amount of K in the plants, and plants growing alone had higher concentration of K than plants growing with a competitor (Table 3). The frequency of mycorrhizal structures did not correlate with any plant nutrient concentration analysed (the significances of Spearman’s \( \rho \) correlation tests were >0.09). However, RGR was positively correlated with K concentration \( \rho_{155} = 0.24, P < 0.01 \) whilst no statistically significant correlation was found for the other nutrients analysed (all \( P > 0.12 \)).

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**Fig. 4.** Above-ground and below-ground mass (mean \( \pm \) s.e., in g) at the end of the experiment for female and male *Antennaria dioica* (A) plants and (B) boxes grown in the three competition treatments: ‘None’ without competitor, ‘Same’ with a competitor of the same sex, or ‘Different’ with a competitor of a different sex. Different letters indicate statistically significant differences \( P < 0.05 \) among treatments based on the Ryan–Einot–Gabriel–Welsch (REGW-F) procedure.

**Fig. 5.** Root/shoot ratio (mean \( \pm \) s.e.) for female and male *Antennaria dioica* plants grown in the three competition treatments: ‘None’ without competitor, ‘Same’ with a competitor of the same sex, or ‘Different’ with a competitor of a different sex. Different letters indicate statistically significant differences \( P < 0.05 \) among treatments based on the Ryan–Einot–Gabriel–Welsch procedure.
Differences in competitive ability are expected due to sexual differences in morphology, physiology and life history traits reported for a large number of dioecious species. While our results agree with those of Mercer and Eppley (2010), Sánchez-Vilas et al. (2011) and Hesse and Pannell (2011) in demonstrating that plants can respond differentially to intrasexual competition from conspecifics. Although the relative competitive indices (measure for final plant biomass and number of inflorescences produced) were similar for females and males regardless of the sex of their neighbouring plant, the sex of the neighbouring plant affected the RGR, root mass allocation and probability of flowering in females. In competition, both sexes reduced allocation to roots when grown with the same sex. Generally, in clonal dioecious plants, mass allocation patterns may differ between the sexes: males usually allocate more resources to clonal structures than females (Hancock and Bringhurst, 1980; Meagher, 1984; Garcia and Antor, 1995). However, we did not observe any significant differences in Antennaria dioica resource allocation between the sexes in the absence of competition. The significance of sexual differences in shoot/root allocation in response to competition in A. dioica is difficult to evaluate. Harris and Pannell (2008) proposed that females might pay a high cost for seed and fruit production in terms of carbon allocation, whereas males must invest heavily in terms of other currencies, particularly nitrogen. However, we did not observe this sexual size dimorphism in root:shoot allocation probably due to the similar costs of reproduction in this species (Varga and Kytöviita, 2011; see below). Moreover, the interaction between above- and below-ground competition is not completely understood and it has been shown that these forms of competition may have non-additive reductions in plant growth (Casper and Jackson, 1997).

As far as we are aware of, all comparisons of competitive abilities in dioecious plants have been focused on plant

The means ± s.e. are indicated. Within a column, different letters indicate statistically significant differences at \( P < 0.05 \) (no significant differences were detected in inflorescences/plant in 2007).

### Competition intensity indexes

The CII for plant mass was on average 0.81 ± 0.06 (range: 0.06 and 3.24) and CII for the number of inflorescences produced averaged 0.91 ± 0.13 (0.09 and 8.75). Neither CII was statistically affected by the gender of the target plant considered \((F_{1,106}=0.79, P=0.38\) and \(F_{1,84}=2.21, P=0.14\) for plant mass and flower production, respectively), the gender of the competing pair \((F_{1,106}=2.47, P=0.12\) and \(F_{1,84}=0.00, P=0.97\)) or the interaction \((F_{1,106}=0.28, P=0.60\) and \(F_{1,84}=0.39, P=0.53\), indicating similar CII between the sexes and independence from the gender of the neighbour.

### DISCUSSION

Differences in competitive ability are expected due to sexual differences in morphology, physiology and life history traits reported for a large number of dioecious species (Geber et al., 1999, and references therein) including Antennaria dioica (Varga and Kytöviita, 2008, 2010). We could partially corroborate this expectation in A. dioica. While our results agree with many previous studies reporting no difference in competitive ability between the sexes of dioecious plants in terms of plant growth (e.g. Vasiliauskas and Aarseen, 1992; Hawkins et al., 2009; Mercer and Eppley, 2010), we discovered that the sexual competitive abilities did differ in relation to probability of flowering, an important life history trait not reported in previous studies. Therefore, the effects of competition were complex and difficult to evaluate fully, since competition affected some traits related to fitness but not others. Survival was unaffected by competition in our study, but competing plants reduced their sexual reproduction and vegetative growth compared with non-competing plants, a widely reported result in competition experiments. Competing plants increased relative resource allocation to roots as shown by the larger root/shoot ratios, whilst nutrient concentration in the plants did not change. Taken together, this suggests that the plants competed more for nutrients, not over space, and this is further confirmed by the fact that most of the available space in the boxes was not occupied.

Our study agrees with those of Mercer and Eppley (2010), Sánchez-Vilas et al. (2011) and Hesse and Pannell (2011) in demonstrating that plants can respond differentially to intrasexual competition from conspecifics. Although the relative competitive indices (measure for final plant biomass and number of inflorescences produced) were similar for females and males regardless of the sex of their neighbouring plant, the sex of the neighbouring plant affected the RGR, root mass allocation and probability of flowering in females. In competition, both sexes reduced allocation to roots when grown with the same sex. Generally, in clonal dioecious plants, mass allocation patterns may differ between the sexes: males usually allocate more resources to clonal structures than females (Hancock and Bringhurst, 1980; Meagher, 1984; Garcia and Antor, 1995). However, we did not observe any significant differences in Antennaria dioica resource allocation between the sexes in the absence of competition. The significance of sexual differences in shoot/root allocation in response to competition in A. dioica is difficult to evaluate. Harris and Pannell (2008) proposed that females might pay a high cost for seed and fruit production in terms of carbon allocation, whereas males must invest heavily in terms of other currencies, particularly nitrogen. However, we did not observe this sexual size dimorphism in root:shoot allocation probably due to the similar costs of reproduction in this species (Varga and Kytöviita, 2011; see below). Moreover, the interaction between above- and below-ground competition is not completely understood and it has been shown that these forms of competition may have non-additive reductions in plant growth (Casper and Jackson, 1997).
Lack of sexual dimorphism in reproductive costs may explain the similar competitive abilities found for \( A. \) dioica. In agreement with that, the sexes did not differ in AM fungal colonization or root density, but N and P concentrations were significantly lower in female than optimal conditions for nutrients or water often favours maleness (reviewed in Korpelainen, 1998). Sex lability was displayed in only 3% of these plants without a clear whole-plant N and P content, and females could have higher N and P concentrations in roots and flowering structures. Lastly, potassium concentrations were reduced in both sexes as a response to competition, indicating that this nutrient was limiting growth in the present experiment. Next to nitrogen, potassium is the mineral nutrient required in the largest amount by plants and, when deficient, growth is retarded even though it does not play a direct role in flowering regulation (Marschner, 1995).

Competition has important consequences for the structure and dynamics of dioecious plant populations. When sexual differences occurred in our experiment due to competition, females seemed to suffer more than males. However, lack of sexual differences in competitive ability could be considered adaptive in dioecious species, as differences in competitive ability could result in exclusion of the other sex from the neighbourhood, a result that would certainly reduce sexual reproduction or result in SSS. However, the sexes of \( A. \) dioica are not spatially segregated in the field (Varga and Kytöviita, 2011). In addition, increasing distance between individuals of the opposite sex has been shown to reduce the likelihood that pollen reaches ovules in \( A. \) dioica (Öster and Eriksson, 2007) and therefore it seems unlikely that this trait could be strongly selected in our study species.

Sex change in plants has been linked to several environmental factors which can also be linked to competition, since less than optimal conditions for nutrients or water often favours maleness (reviewed in Kor pelainen, 1998). Sex lability was displayed in almost 10% of plants in the present experiment, and, even though not statistically significant, more females showed sex lability when growing alone compared with plants from the other treatments. Our previous observations both in the field and in the greenhouse indicate that sex lability occurs in \( A. \) dioica but with low frequency. After monitoring 274 plants for five consecutive years, we observed that sex lability was displayed in only 3% of these plants without a clear pattern (Varga and Kytöviita, 2011). Sex lability in long-lived perennials clearly requires further studies before its importance can be fully evaluated.

A comprehensive theory of coexistence should cover both niche differences and relative competitive abilities of the

### Table 3.

<table>
<thead>
<tr>
<th>Factors</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
<th>Ca</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.74</td>
<td>0.76</td>
<td>0.65</td>
</tr>
<tr>
<td>Treatment</td>
<td>0.38</td>
<td>0.08</td>
<td>&lt;0.01</td>
<td>0.34</td>
<td>0.21</td>
<td>0.50</td>
</tr>
<tr>
<td>Sex × treatment</td>
<td>0.26</td>
<td>0.21</td>
<td>0.69</td>
<td>0.78</td>
<td>0.31</td>
<td>0.58</td>
</tr>
<tr>
<td>Genotype (sex)</td>
<td>&lt;0.05</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

Mean values are expressed as percentage dry weight with the s.e. in parentheses. Within a column, different letters indicate statistically significant differences at \( P < 0.05 \).

(b) Results of the statistical analyses of variance

Survival and growth in relatively short-term experiments, neglecting the effect on the frequency of flowering which, when it results in reproduction, is probably the most important plant life history trait determining fitness in perennial plants. In our study, the proportion of flowering females decreased only when growing in competition with another female. This response was asymmetric, and competition decreased the probability of flowering in males irrespective of the sex of the neighbour. For females, this is somehow expected if we assume that competition between two females should be stronger in order to achieve a larger number of mates and the resources available to produce seeds. For females, having a male nearby could ensure access to pollen and reduce competition for resources later in the season when seeds are produced (since at that point males had finished flowering). Males produced more inflorescences than females and these inflorescences were heavier (Varga and Kytöviita, 2011), but females seemed to suffer more than males. However, lack of sexual differences in competitive ability could be considered adaptive in dioecious species, as differences in competitive ability could result in exclusion of the other sex from the neighbourhood, a result that would certainly reduce sexual reproduction or result in SSS. However, the sexes of \( A. \) dioica are not spatially segregated in the field (Varga and Kytöviita, 2011). In addition, increasing distance between individuals of the opposite sex has been shown to reduce the likelihood that pollen reaches ovules in \( A. \) dioica (Öster and Eriksson, 2007) and therefore it seems unlikely that this trait could be strongly selected in our study species.
potential competitors. Our study suggests that the two sexes of *A. dioica* are largely similar in terms of competitive ability, but intrasexual competition is higher in females, giving support to asymmetric niche segregation between the sexes. The reduced growth rate of plants when grown with the same sex together with the observed different nutrient levels of the two sexes suggests that the two sexes are segregated in terms of nutrient requirements. Our study did not provide an explanation for the female-biased sex ratios in this species, and we suggest that in future studies heterospecific competitive abilities and early life history events are explored. Ideally, studies encompassing several years to account for environmental variation and including reproductive success should be performed to evaluate fully the differences in competitive abilities related to flowering in perennial plants.

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