



Intraspecific sexual competition in the clonal gynodioecious herb *Glechoma hederacea* in response to patchy nutrient distribution

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Abstract Plants have developed numerous strategies to maximise resource uptake in response to the highly heterogeneous resource distribution in soils. Clonal growth enables plants to scavenge larger surfaces, potentially maximising nutrient acquisition by selectively growing in nutrient-rich patches. However, the production of clonal units put plants into higher intraspecific competition. In gynodioecious clonal plants, genders usually exhibit sexual dimorphism in several growth and life history traits, but whether the genders have different competitive abilities and whether these are affected by nutrient distribution is underexplored. Here, we investigated whether the genders of *Glechoma hederacea* have different competitive abilities and whether these are affected by soil nutrient distribution using a greenhouse pot experiment. Female and hermaphrodite ramets were grown either alone or in competition with the same or the opposite gender in two different soil nutrient distributions for four months. Our results show that competition was the strongest factor affecting biomass accumulation and allocation. Females and hermaphrodites showed little sexual dimorphism in

total biomass accumulation, but they differed in how they allocated this biomass between roots and shoots and in their clonal growth strategies in response to soil nutrient distribution. Taken together, our results indicate that soil nutrient distribution affects the competitive abilities of *G. hederacea* in a gender-specific manner. In the field, these differences would determine the structure and the dynamics of the two genders within the populations.

Keywords Clonality · gynodioecy · Intersexual competition · Intrasexual competition · Soil nutrient distribution

Introduction

Soils are crucial key components of all land ecosystems, sustaining plant growth in addition of housing the largest biodiversity reservoir on Earth (Bardgett and van der Putten 2014). From a plant point of view, soils are highly heterogeneous environments regarding the distribution of its inhabitants, its physical and chemical components and the amount of light that the soil surface receives (Hutchings 1997; Farley and Fitter 2001). In this regard, the distribution of nutrients in the soils is usually highly heterogeneous as a result of the original parent material, weathering and the biological activity of microorganisms and plants

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(Jobbagy and Jackson 2001), forcing plants to develop life history strategies that maximises resource uptake.

One adaptation to heterogeneous resource environments is clonality (Fischer and van Kleunen 2001; Bitterbiere et al. 2020), the production of genetically identical units or ramets that are physically connected to the initial parental unit but growing at some distance from each other. Clonal growth allows the individual plant or genet to scavenge wider surfaces, potentially maximising nutrient acquisition by selectively growing in nutrient-rich patches (e.g. Fischer and van Kleunen 2001; Hutchings and Wijesinghe 2008). Indeed, numerous studies have shown that clonality may confer interspecific competitive advantage over plants with no clonal growth for two reasons (reviewed in Bitterbiere et al. 2020). First, if physiological integration between ramets occurs (i.e. the sharing of resources between connected ramets), ramets growing in resource-rich patches may be able to support the rest of the genet (Hutchings and Wijesinghe 2008) and references there). It is well known that plasticity and physiological integration between connected ramets enhances the performance of the whole genet, and this is especially true when resources (light and nutrients) or enemies (pathogens or herbivores) are present in only certain parts of the habitat (Wijesinghe and Handel 1994). And second, the production of ramets may allow the genet to escape unfavourable conditions and simply grow into more favourable patches (Bazzaz 1991).

Clonal plants may exhibit two different clonal growth strategies regarding the spatial distribution of their ramets in the horizontal space: phalanx plants produce numerous closely aggregated ramets with small spacer lengths, thus excluding other genets, whilst guerrilla plants produce ramets with bigger spacer lengths, allowing spreading through the habitat (Lovett-Doust 1981; Bitterbiere et al. 2020). The spatial distribution of the ramets will strongly influence competition not only with other plant species (i.e. interspecific) but also within other individuals of the same species (i.e. intraspecific).

An interesting case of intraspecific competition occurs in sexually dimorphic plants, where in addition to competing with the same species, individual plants may also need to compete both with plants of the same gender (intrasexual competition) and the opposite (intersexual competition). In sexually dimorphic plants, genders usually have different resource needs

and allocation patterns as a result of the different costs associated with each sexual function (Case and Ashman 2005). For example, seed production is generally more costly than pollen production (Obeso 2002), which may result in sexual dimorphism in growth, physiology or life history traits (Geber et al. 1999). In this case, the gender with superior growth will have a competitive advantage over the other gender. As pointed out by Agren et al. (1999; p 220), 'if there is a sexual difference in competitive ability, then the relative growth and survival of the sex with the greater competitive ability should increase with increasing plant density, and competitive interference should be asymmetrical when the sexes compete with each other'.

One example of sexually dimorphic breeding system is gynodioecy, a relatively rare breeding system where female plants coexist with hermaphrodites within the same population. It is estimated that about 2% of angiosperm genera contain gynodioecious species (Renner 2014). In gynodioecious plants, genders may possess sexual dimorphism in several life history traits, including growth traits related to competitive abilities. A model species in such studies is *Glechoma hederacea* (ground ivy), a gynodioecious clonal plant with remarkable sexual dimorphism in floral size and reproductive output (Widén 1992). In this species, the genders are reported to differ in height, flowering frequency, and flower and seed production (Slade and Hutchings 1989; Widén and Widén 1990). Even though previous studies indicate that genets are able to actively grow into better sites by producing ramets and rooting, showing growth adaptations to resource availability in addition of physiological integration (Birch and Hutchings 1992; Hutchings 1997, 1999; Price and Hutchings 1992; Hutchings and Wijesinghe 2008; Hutchings and John 2004; Price et al. 1992; Slade and Hutchings 1987), no study has evaluated whether the competitive abilities of the genders differ when growing together. As far as we know, only one study has previously tested whether the genders differ in their functional clonal traits under nutrient heterogeneity (Song et al. 2016). By growing the closely related species *G. longituba* in two different nutrient distributions, Song et al. (2016) found that the two genders did not differ in any vegetative trait investigated except for root to shoot ratio that was higher in females. Unfortunately, the plants were not grown together in competition.

Therefore, in this study we forced female and hermaphrodite genets to compete with each other in homogeneous or heterogeneous nutrient soil distributions. Understanding whether the two genders possess different competitive abilities will further our understanding of whether genders may exhibit different strategies when growing in natural communities that could explain their spatial distribution.

Material and methods

Study plant

Glechoma hederacea (Lamiaceae) is a clonal gynodioecious herb widely distributed within temperate latitudes and found widely across the UK (Hutchings and Price 1999). The frequency of female genets has not been estimated in the field due to the difficulties in identifying different genets, but ramet female frequency ranges from 0 to 100% depending on the population (Widén and Widén 1990, 1999). It reproduces both through seed production and with the production of monopodial stolons and in the UK, flowering takes places from March to June (Hutchings and Price 1999).

Propagation

To obtain enough number of ramets, several individuals naturally growing in the University of Lincoln Riseholme Campus (53.2647 N, 0.5371 W) were excavated in July 2017 and planted in 10 × 10 × 10 cm pots with John Innes all-purpose compost. Plants were grown for 2 months in a glasshouse (average 19 °C, no artificial light provided) until September 2017. Plants were sexed in the field by looking at the flowers. Hermaphroditic flowers usually have larger perianths and bear four stamens. Further ramets spreading from the initial plant were tied down with gardening wire into adjacent pots to stimulate rooting. Pots were given 100 ml of tap water three days a week. New spreading ramets had the stolons cut after they were successfully rooted in the new pot.

Experimental design

We performed a fully factorial experiment where each plant gender was grown either alone or in competition

with the same or the opposite gender under two different soil nutrient distributions (Fig. 1). We had seven replicates per gender, totalling 70 pots with 112 individuals. Plants were potted in 19 cm in diameter pots and filled with a 1:1 sand (washed gardening sand) and soil mix (Westland Multi-Purpose Compost). The potting mix was prepared so that both the homogeneous and heterogeneous pot treatments would have the same total nutrient content. For the homogeneous treatment, 12 ml of Miracle Grow All Purpose fertiliser was added to 4.5 L of the potting mix. The heterogeneous pots were made using separators which divided the pot into four equal sections: into two opposite portions, 24 ml of the same fertiliser was added to 4.5 of soil mix, whereas the other two were filled with the potting mix containing no added nutrients (Fig. 1). After filling the pots, the physical separators were carefully removed.

At the start of the experiment, plants were weighed and the number of leaves counted. For plants growing in competition pots, individuals of similar size were allocated to the same pot and planted opposite to each other (Fig. 1). For the heterogeneous pots, individuals were planted on the dividing line between the non-fertilised and fertilised sections.

Plants were grown for four months in the same glasshouse under a 12:12 h light:dark regime, with diurnal temperatures around 22 °C and watered with 100 ml of tap water every three days. To force competition between individuals within the pots, stolons growing outside the pots were threaded back and guided around the inside of their own pots.

At harvesting, individual plants were identified and separated from competitors if necessary. Plants were washed free of soil and the total number of leaves and stolons were counted. Spacer length was measured for each segment. Masses were put in paper bags and dried at 80 °C for three days before obtaining the dry mass.

Statistical analyses

All analyses were carried out with R v.3.6.2 (R Core team 2019). We fit linear mixed-effects models with plant genotype and pot included as random factors, initial plant mass as a covariate and the three-way interaction between gender, nutrient distribution and competition treatment as a fixed factor. Shoot/root ratio data were squared-root transformed to fit model assumptions, and a Poisson distribution was used to

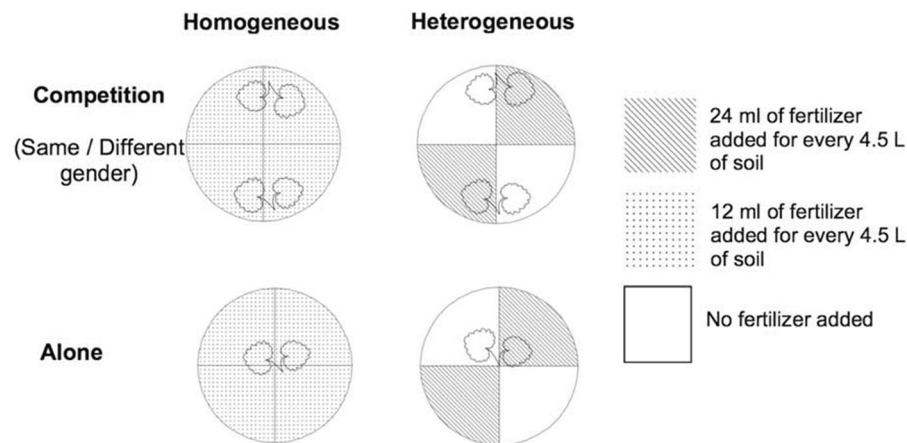


Fig. 1 Experimental layout showing the nutrient distribution and the position of the plants in the experimental pots. Ramets (not drawn to scale) were grown either alone (Alone) or in competition with the same (Same) or opposite gender (Different)

analyse differences in the number of stolons and rooting units produced. If significant interactions were found, pairwise comparisons were performed with the emmeans package (Lenth 2019), using Tukey's correction for multiple comparisons. One plant died during the experiment, and therefore, that pot was excluded from all analyses.

Results

After 4 months, both genders accumulated a similar amount of total mass (3.7 ± 0.3 g and 3.6 ± 0.2 g in female and hermaphrodite plants, respectively) regardless of the soil nutrient distribution (Table 1). Competition treatment had a significant effect on total

mass accumulation (Table 1; Fig. 2). As expected, all plants growing in competition showed a reduction in total mass accumulation compared to plants growing alone whether with the same gender ($t_{105} = 3.690$, $p = 0.001$) or the opposite ($t_{84.9} = 4.583$, $p < 0.001$; Fig. 2). No statistically significant interactions between factors were detected (Table 1). All plants accumulated at least two times more mass above-ground than belowground as shown by the positive values of the shoot/root ratios (range: 2.5–109.5, average 17.7 ± 1.2). None of the parameters of the model explained shoot/root ratios (Table 1).

All but one plant produced stolons during the experiment. On average, plants produced 1.3 ± 0.5 stolons (range: 0–2 stolons) and we could not detect any statistically significant difference between sexes

Table 1 Statistical results for the effects of plant gender, soil nutrient content, competition treatment and their interactions on several plant traits in *Glechoma hederacea* plants

	df	Final plant mass		Shoot/root ratio		# Stolons		# Rooting units		Spacer length	
		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Gender (G)	1	0.015	0.90	0.750	0.39	0.098	0.75	0.988	0.32	0.419	0.52
Nutrient (N)	1	0.002	0.95	0.017	0.90	0.044	0.83	2.524	0.11	0.631	0.42
Competition (C)	2	26.617	< 0.01	0.693	0.71	0.121	0.94	32.106	< 0.01	6.753	0.03
G × N	1	1.619	0.20	0.579	0.98	0.018	0.89	9.767	< 0.01	0.002	0.95
G × C	2	0.008	0.99	2.897	0.45	0.001	0.99	3.359	0.18	9.561	< 0.001
N × C	2	5.715	0.06	3.471	0.23	0.325	0.84	4.750	0.09	2.086	0.35
G × N × C	2	3.657	0.16	4.671	0.09	0.300	0.86	12.147	< 0.01	2.982	0.22

Significant results are shown in bold

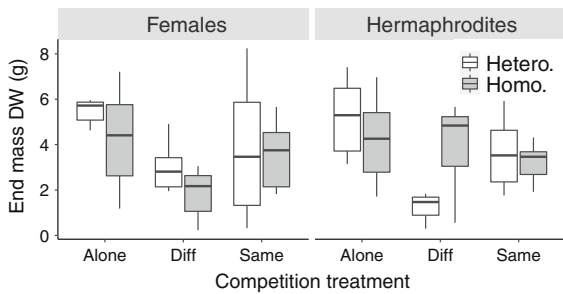


Fig. 2 Boxplot of total final plant dry mass (g) of *Glechoma hederacea* plants growing in heterogeneous (white boxes) or homogeneous (grey boxes) soil nutrient distributions alone or in competition with another *G. hederacea* plant from the opposite gender (Diff.) or the same

and nutrient distribution of competition treatment (Table 1). The average total length of these stolons was 230.7 ± 17.7 cm and they had, on average, 8.3 ± 0.5 rooting units per plant (Fig. 3), which made an average spacer length of 7.8 ± 0.5 cm (Fig. 4). There was a statistically significant 3-way interaction explaining the number of rooting units per plant (Table 1; Fig. 3). In females, differences in the number of rooting units between soil nutrients were only statistically significant in plants grown alone, with 1.4 times more rooting units formed in heterogeneous vs. homogeneous pots ($z = 3.761$, $p < 0.01$; Fig. 3), whilst in males, significant differences were only found when grown in competition with female plants, and in this case, less rooting units were formed in heterogeneous pots ($z = 2.071$, $p = 0.03$; Fig. 3).

Even though spacer length was not statistically affected by nutrient distribution, there was a significant interaction between gender and competition

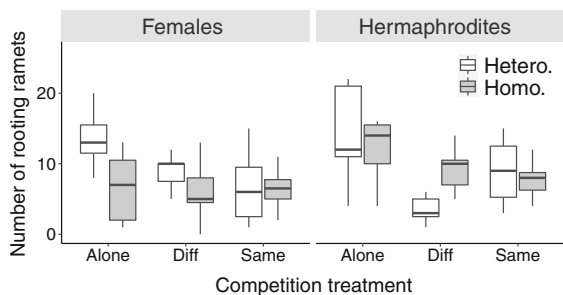


Fig. 3 Boxplot of the number of rooting ramets in *Glechoma hederacea* plants growing in heterogeneous (white boxes) or homogeneous (grey boxes) soil nutrient distributions alone or in competition with another *G. hederacea* plant from the opposite gender (Diff.) or the same gender

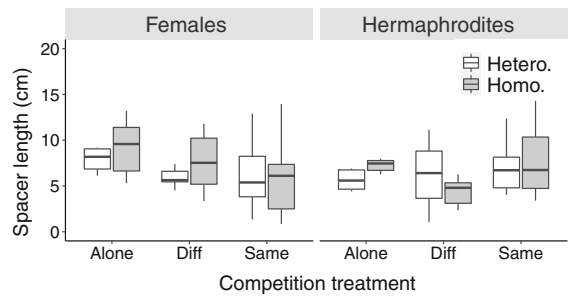


Fig. 4 Boxplot of the average spacer length (cm) in *Glechoma hederacea* plants growing in heterogeneous (white boxes) or homogeneous (grey boxes) soil nutrient distributions alone or in competition with another *G. hederacea* plant from the opposite gender (Diff.) or the same gender

(Table 1; Fig. 4). Genders had similar spacer length when growing alone or in competition with the opposite gender (both Tukey's $p \geq 0.22$), but hermaphrodite plants produced significantly longer internodes when growing in competition with another hermaphrodite plant compared to females growing with another female ($p = 0.01$; Fig. 4).

Discussion

In this study we investigated whether the genders of *G. hederacea* have different competitive abilities and whether this competition is affected by nutrient distribution in the soil. Our results suggest that females and hermaphrodites of this clonal species possess little sexual dimorphism in total biomass accumulation and allocation, but they differ in their clonal growth strategies when grown in different soil nutrient contents, with significant effects detected by the gender identity of the competitors found. These results indicate that not only soil nutrient distribution affects the competitive abilities of *G. hederacea* in a gender-specific manner but also whether plants are experiencing intrasexual or intersexual competition, with implications at the population level.

Competition and gender

Even though gynodioecious plant populations are relatively frequent in nature, no previous study has investigated whether different genders differ in their competitive abilities when grown in close proximity. Differences in competitive ability are expected in

sexually dimorphic plants due to the widely reported sexual differences in morphology, physiology and life history traits (Geber et al. 1999). In our study, after four months of growth we did not find differences in total biomass accumulation and allocation between the two genders of *G. hederacea*, even though size sexual dimorphism is predicted in species showing different reproductive costs between the genders as reported in *G. hederacea* (e.g. Slade and Hutchings 1989; Widén and Widén 1990). The lack of sexual plant size dimorphism found in our study might be due to the fact that the clonal fragments were regenerated from clonal fragments collected from the field and were not flowering during the duration of the experiment. Nevertheless, detailed comparisons between the genders should be carried out, as all previous studies have only reported sexual dimorphism in reproductive allocation (i.e. flower and seed production; Slade and Hutchings 1989; Widén and Widén 1990; Widén 1992), not mass acquisition and growth (but see Slade and Hutchings 1989 for differences reported in ramets height).

In this study, competition strongly reduced mass accumulation similarly in both genders as plants grown alone accumulated more biomass than plants grown in competition, confirming our aim to limit the available pot surface and volume available for plants, and thus forcing them to compete for resources. Here, we show that for total plant mass acquisition, the effects of intraspecific competition did not depend on whether plants were competing with the same gender or the opposite one, as both sexes suffered similarly from competition. We did detect strong sexual differences in the clonal architecture of our study plant, with significant differences in the number of rooting units and internode lengths between these. As far as we are aware of, few studies have investigated the effects of rooting frequency in clonal plants (but see Roiloa and Hutchings 2011).

Even though evidence is lacking for gynodioecious plants, previous studies in dioecious species have reported significant differences in mass acquisition depending on whether plants were competing with the same gender or the opposite one (Hesse and Pannell 2011; Varga and Kytöviita 2012; Mercer and Eppley 2014). The present study suggests that more pronounced differences in the costs of reproduction between the genders might be needed in *G. hederacea* to create differential competitive abilities. In this

species, hermaphrodites have been reported to produce more flowering ramets than females, and also more and larger flowers (Slade and Hutchings 1989), with a significant higher total seed production which should translate in a significant larger cost of reproduction for hermaphrodites. In the absence of demographic (i.e. differences in survival and/or flowering frequency) or physiological mechanisms (i.e. differences in photosynthetic rates) that mitigate these costs (reviewed in Obeso 2002), hermaphrodites could be expected to be smaller than female plants, and thus, one could expect to see different competitive abilities between the genders. The available limited evidence suggests a lack of physiological differences between genders in gynodioecious plants (reviewed in Varga and Kytöviita 2017). Moreover, long-term studies would be needed to fully evaluate the existence and magnitude of demographic costs in perennial clonal plants.

Competition and soil nutrient distribution

We observed that competition was a significant factor affecting biomass accumulation but did not affect how biomass was allocated to above- and belowground organs, and this was not related to the spatial distribution of nutrients in the soil. This was perhaps not surprising because total nutrient availability per pot was kept similar (as we only modified the distribution of the nutrients) in a similar way as the study by Song et al. (2016) working with the close species *G. longituba*. In their study, Song et al. (2016) also did not find any significant effect of soil nutrient distribution on total plant mass. However, an earlier study by Birch and Hutchings (1994) using *G. hederacea* reported greater growth in plants grown in patchy vs. uniform distribution, demonstrating for the first time that *G. hederacea* is able to exploit environmental heterogeneity by modifying clonal traits. The present study confirms this but also indicates that soil nutrient distribution affects the plants in a gender-specific manner. When growing alone, we observed that females produced more rooting ramets when grown in heterogeneous soils than when nutrients were homogeneously distributed, but this response was not seen when grown in competition with another plant. It is well known in this and other clonal species that higher nutrient contents in the soil translate into more ramets per

clone and shorter internode lengths (e.g. Slade and Hutchings 1987), and our study shows for the first time that the genders of a gynodioecious plant have sex-specific responses to not only soil nutrient content but also competition.

As far as we are aware of, investigations into the clonal strategy of gynodioecious plants have not been performed. Clonal expansion greatly affects mating patterns and how fitness is achieved in plants with separate genders (see van Drunen et al. 2015, and references therein).

In dioecious plants, females are hypothesised to follow a more phalanx-like strategy (i.e. short internode lengths and more rooting units than males), which should confer them an advantage to exclude other plants especially in highly competitive environments. On the other hand, males are thought to follow a guerrilla strategy, which should be advantageous to improve pollen dispersal (van Drunen et al. 2015). This seems to be the case also in our study species, even though our experimental set-up was not designed to evaluate clonal expansion.

To conclude, this study shows that even though the genders of *G. hederacea* may show little dimorphism in total mass accumulation, they do differ in mass allocation and in their clonal growth strategy in response to soil nutrient distribution. In the field, these differences will probably have important consequences for the structure and the dynamics of the populations. To gain a full understanding of the effects of intraspecific sexual competition in this and other perennial species, longer studies should be performed in the field, including measurements of the reproductive success (see e.g. Varga and Kytöviita 2012).

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Author contributions Both authors designed the experiment. NH carried out the experiment and collected the data; SV analysed the data. Both authors wrote the manuscript.

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Data availability Data are available at <https://doi.org/10.6084/m9.figshare.13176935.v1>.

Compliance with ethical standards

Conflict of interest The authors have no conflict of interest to declare.

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