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## Sex expression variation in response to shade in gynodioecious-gynomonoecious species: *Silene littorea* decreases flower production and increases female flower proportion

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### ABSTRACT

Sexual expression can vary at different levels in diclinous sexual systems. To measure total phenotypic variation, it is necessary to consider the genetic component, the effect of environment, and interaction (i.e. the heritable component of plasticity). *Silene littorea* has a gynodioecious-gynomonoecious sexual system, with a high proportion of gynomonocious individuals in populations, making this species a good system for studying how male and female sexual functions vary within and among individuals in response to a depletion of resources. In the current study, we experimentally assigned sibs from different maternal genotypes to sun vs. shade treatments for three populations and measured their effect on sex expression, onset of flowering, total flower production, and aboveground and belowground biomass. We found significant differences between genotypes and light environments in total flower number, with shaded plants producing fewer total flowers and a higher proportion of female flowers. Throughout the season, shaded plants produced a higher ratio of female to hermaphroditic flowers, with an increase at the end of the flowering period. Shaded plants produced less significant aboveground and belowground biomass as well as fewer flowers per plant, and flowering started later. Sexes of *S. littorea* differed in their first flowering day, with male-sterile plants starting to flower later than male-fertile plants. We found among population differences in relative distance plasticity index (RDPI) for total number of flowers and aboveground biomass. The plasticity in sexual expression found in *S. littorea* agrees with the bet-hedging strategy proposed for gynomonocous: gynomonocous plants may adjust for the resources available, producing a variable amount of small and less costly female flowers, which in addition could have lower selfing rates.

### 1. Introduction

Phenotypic plasticity is defined as the ability of a genotype to express different phenotypes in response to environmental variation (Pigliucci, 2001; Forsman, 2015), and it may play a critical role in the adaptation of plants to their local environments. The understanding of plastic phenotypic expression in plants is important since it facilitates adaptation to unpredictable environments and response to rapid environmental change (e.g. climate change) (Valladares et al., 2007). It is expected that phenotypic plasticity plays a relevant role in plant species evolution given that it is genetically controlled, heritable and may be adaptive (Schlichting and Pigliucci, 1993; Sultan, 2000). Therefore, to have a clear picture of how natural selection influences phenotypic variation, we must know the levels of genetic variation, the plastic

components, and the heritable component of plasticity (Vogler et al., 1999; Ashman and Majetic, 2006; Koski and Ashman 2013).

Plasticity in sexual expression has been proposed as an important mechanism to deal with harsh environments (Ashman, 2006). Species exhibiting differences in flower gender at the individual level (i.e. monoecy, andro- and gynomonocous) are expected to show sexual plasticity in response to environmental changes (Bertin, 2007). One hypothesis for the evolution and maintenance of these sexual systems posits that the existence of two flower types allows flexibility in allocation of resources to female and male functions in variable environments (Charlesworth and Morgan, 1991; Bertin and Kerwin, 1998). Specifically, sex-allocation theory predicts an increase in female function in response to elevated resource levels, and a female cost when plants are exposed to a depletion of resources (Charnov, 1982; Bishop

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et al., 2010). Although several studies support this prediction (e.g. Solomon, 1985), an increasing body of literature indicates that more complex patterns can be found in monoecious species (Bertin and Kerwin, 1998; Arceo-Gómez et al., 2009; Narbona and Dirzo, 2010).

Light is a critical environmental factor, whose plastic responses have been well studied for several traits (Valladares et al., 2006; and references therein; Bell and Galloway, 2007, 2008), although its effects on sexual expression have scarcely been investigated (Van Etten et al., 2008; Van Etten and Chang, 2009; but see Varga et al., 2015). The few available studies for diclinous sexual systems support an increase in femaleness in high light environments (Bertin, 2007 and references therein). Conversely, in shade conditions plants invest more resources in vegetative growth and reduce allocation for sexual reproduction (Jacquemyn et al., 2010). This effect on plant allocation is expected to be greater in plants bearing hermaphrodite flowers in comparison with plants that bear male or female flowers, because the former must invest in two sexual functions at once.

*Silene littorea* Brot. is a gynodioecious-gynomonoecious (hereafter Gd-Gm) species that exhibits a low proportion of female plants, and a variable proportion of hermaphrodites and gynomonoecious individuals (n and Medrano 2000; Casimiro-Soriguer et al., 2013, 2015). In other species of *Silene*, gynomonoecious plants can exhibit flexibility in sexual expression by changing the proportion of hermaphroditic and female flowers (Folke and Delph 1997; Maurice, 1999; Dufay et al., 2010). On the other hand, light is expected to play an important role in *S. littorea*, given that plants live in coastal dunes differing in tree and scrub cover, with also latitudinal changes (Lomba et al., 2008; Del Valle et al., 2015), thus leading to substantial variations in shading of plants. High inter-population variability was described for this species in the number of flowers/plant when comparing populations established on dunes with or without tree cover (Casimiro-Soriguer et al., 2013). This within- and among-population shading variation may select for differentiation in plasticity (Bell and Galloway, 2008).

Here, we perform a shade experiment with *S. littorea* from three populations. We predict that total flower production and proportion of female flowers are plastic traits in gynomonoecious individuals, with a reduction in the former and an increase in the latter in response to shade. These plastic responses may increase plant resource availability to produce seeds in less costly female flowers when resources diminish, because in *S. littorea* female flowers are smaller than hermaphrodite flowers (Casimiro-Soriguer, 2015), as has also been described for other gynomonoecious and gynodioecious species of *Silene* (revised in Casimiro-Soriguer et al., 2016). We also expect the proportion of female flowers to increase at the end of the flowering period, when resources are scarce and temperatures higher. To compare differences in plastic responses among populations, we used the Relative Distance Plasticity Index (RDPI), which allows for statistical comparisons of phenotypic plasticity between populations of a given species (Valladares et al., 2006). The specific aims of this study are to discover: 1) what percentage of phenotypic variance of total flower number and proportion of female flowers is attributable to genotype, plasticity and to the heritable component of plasticity, 2) how the proportion of female flowers changes throughout the season, 3) if the change throughout the season differs between the two light environments, 4) if there are differences among male-sterile vs. male-fertile plants and light environment in terms of aboveground biomass, belowground biomass, total flower production and first flowering day, and 5) if there are differences in RDPI among populations.

## 2. Materials & methods

### 2.1. Study species

*Silene littorea* is a self-compatible, annual plant extending from the northwestern to the southeastern region of the Iberian Peninsula (Talavera, 1990). Flowering takes place between March and June, and

its main pollinators are bees, butterflies and moths (Del Valle, unpublished data). In two populations of southern Spain, plants exhibited large variations in flower production, from three to ca. 300 flowers per plant, and phenotypic femaleness fluctuated throughout the flowering period (Casimiro-Soriguer et al., 2013).

### 2.2. Experimental design

Seeds were collected from 15 individual plants at each of two locations in the Northwest of Spain (Barra, Pontevedra, 42°15'35" N, 8°50'25" W and Furnas, A Coruña 42°38'15" N 9°02'21" W) in the spring of 2012. Seeds were scarified and maintained at 45 °C for a month to break dormancy, and afterwards they were germinated in a germination chamber at 22 °C/15 °C (12 h light/12 h dark). The seedlings were planted in pots of 20 cm upper diameter and 15 cm height, filled with around 2.5L of a mixture of standard substrate (Sisanflor, S.L., 80–90% organic material, pH = 6.5) and beach sand (v 50:50) and maintained in the University Pablo de Olavide greenhouse. In the spring of 2013, flowers of the surviving maternal plants were cross-pollinated using pollen from another individual of the same population. However, we considered the seeds of each marked fruit as half-siblings because some of them may be the result of autonomous self-fertilization. Given that *S. littorea* cannot be vegetatively propagated, half-sibs were assigned to each treatment (shade or sun) instead of clones. The resulting seeds were germinated in September 2013, and seedlings planted in November 2013, as previously described. In February 2014, pots were put outside on two benches in the experimental garden. For each experimental garden bench, photosynthetic photon flux was measured in three moments of the day: early morning (0900), noon (1200) and afternoon (1500) (Table 1). The bench assigned to shade treatment was covered with 95% shade cloth, which reduced the photosynthetic photon flux in 189  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at early morning, 975 at noon and 680 at afternoon (Table 1); the second bench was left uncovered and received natural sunlight. After excluding those maternal genotypes with less than two replicates per treatment, we finally obtained 14 maternal genotypes with 67 plants for the sun and 52 for the shade treatment (Table S1). In addition, seeds from a location in the Southwest of Portugal (Sines, Setúbal, 37°55'17" N, 8°48'17" W), separated by 500 km from the other populations, were also collected in the spring of 2013. These seeds were treated exactly as those previously described for Barra and Furnas and at the same time. For Sines, we obtained 29 plants for sun and 19 plants for shade treatment, from 6 maternal genotypes (Table S1). Results for Sines were excluded for estimates of heritability because the different procedure to obtain maternal genotypes. The northwestern locations (Barra and Furnas) differ from Sines in UV radiation (30.3 kJ/m<sup>2</sup> vs 34.8 kJ/m<sup>2</sup>), mean annual precipitation (138.5 mm vs 63.3 mm), and mean temperature (12.6 °C vs 15.1 °C; see more details in Del Valle et al., 2015).

We monitored the production of female and hermaphroditic flowers for both environments (sun and shade) during the entire flowering period from March 7th to May 29th, for a total of 13 collection dates. At the end of the flowering period, plants were dried and biomass was measured. We excluded from the analysis plants that did not flower later than 11th April.

**Table 1**  
Photosynthetic photon flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measures during the censuses day. Values represent mean (max, min, n).

Light treatment	9:00–10:00	12:00–13:00	15:00–16:00
shade	15.86 (36,1,22)	36.10 (56,11,22)	39.45 (98, 9, 22)
sun	205 (701,18,22)	1011.45 (1731,128,22)	719.81 (1984,89,22)

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