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Plasticity and within plant sex-ratio variation in monoecious *Emex spinosa*

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Abstract: Understanding how phenotype trait expression varies at different levels of biological organization is crucial to understanding the fundamental ecological, evolutionary, and developmental issues that contribute to adaptive plasticity. This is particularly important in plants because of their modular organization. Here, we study plasticity in flower production in response to light intensity at 3 levels of biological organization (between populations, among individuals, and within individuals) in *Emex spinosa* (L.) Compd., a Mediterranean amphicarpic annual. Plants exposed to high light intensity grew faster and produced more flowers than plants at low light intensity. Female flower production was the most labile trait. Within individuals, the production of female and male flowers, and the floral sex ratio strongly varied along the stems. Light intensity only significantly affected flower production at central and terminal positions in the inflorescence, while sex ratio was invariable to light intensity in each position, reflecting a sexual specialization independently of light, from initial femaleness towards maleness at the end of flowering. In *Emex spinosa*, the production of selfing fruits seems not only to concern ground fruits, but also early aerial fruits.

Key words: Amphicarpy, flower production, modularity, phenotypic plasticity, sex ratio

1. Introduction

Plants have different strategies to cope with variable environments, which range from adaptation and specialization, to bet-hedging, generalization, and phenotypic plasticity. These strategies are not discrete, but appear combined in nature, forming a general strategy that is variable from one species to another (DeWitt and Langerhans, 2004). Phenotypic plasticity occurs when a genotype produces different phenotypes in response to different environmental conditions (Ghalambor et al., 2007). Phenotypic responses to environmental conditions are fairly common in organisms, and are recognized as major sources of variation in nature (Schlichting, 1986; Thompson, 1991; Kutbay and Uçkan, 1998; Sultan, 2003, 2004). Variation in phenotypic expression can have profound ecological consequences, which have been particularly well studied in plants (Sultan, 2003).

Phenotypic plasticity can be simply a passive consequence of environmental stress (Dorn et al., 2000; Bell and Galloway, 2007) or a result of highly specific developmental, physiological, or reproductive adjustments that enhance survival in response to environmental variation (Bell and Galloway, 2008; Hameed et al., 2013; Molina-Montenegro et al., 2013). In the latter case, the variation can represent adaptive plasticity and is of particular interest because it may promote establishment and persistence in new environments and thus play a major role in both the ecological distribution of organisms and the process of evolutionary diversification (Sultan, 2003; Ghalambor et al., 2007).

Like any trait, phenotypic plasticity is shaped by selective pressures, phylogenetic history, and genetic constraints (Scheiner, 1993; Schlichting and Pigliucci, 1995); thus, species and even populations within a single species may show different patterns of plasticity and different capacities for adaptive environmental response (Sultan, 2003; Ghalambor et al., 2007). Plasticity enhances ecological niche breadth and widespread generalist species usually show adaptive plasticity (Baker, 1974; Oliva et al., 1993). Moreover, adaptive plasticity confers a fitness advantage to invasive plants (Richards et al., 2006). Species with a greater adaptive plasticity are more likely to survive in novel environmental conditions created by human activity, since such changes often occur so rapidly that adaptive variation in particular morphological or physiological traits may be too slow to track the environmental changes (Sultan, 2004). On the other hand, plasticity may alter some traits that directly affect the reproductive success, as reproductive timing, biomass allocation to reproduction, total reproductive output, and

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the size and quality of offspring (Sultan, 2001). In both passive and adaptive plasticity, the type and intensity of the response of these traits to a particular environmental stress may determine the ability of a species to maintain populations in stressful habitats (Sultan, 2001, 2003). The availability to produce different phenotypes in response to environmental changes is a basic strategy in weeds and aggressive invasive species in terms of their adaptation to novel environments (Funk, 2008; Droste et al., 2010; Gupta and Narayan, 2012).

Often, the responses of organisms to environmental changes are complex and consist of several combined responses. As integrated systems, the different responses of organisms to environmental changes are expressed in conjunction, as occurs, for example, in shade-avoidance syndrome (Smith and Whitelam, 1997; Schmitt et al., 2003; Franklin and Whitelam, 2005). However, although studies on shade avoidance are abundant in the literature (Stuefer and Huber, 1998; Weijschede et al., 2006; Bell and Galloway, 2008), little is known about responses to light for taxa inhabiting in heterogeneous environments, such as forest edges (but see Petit and Thompson, 1998; Galloway and Etterson, 2009), or anthropic areas, where individuals can indistinctly experience both full sun or shade situations.

Bet-hedging is defined as the expression of several phenotypes by a single individual in a way that may enhance individual fitness across generations (Cohen, 1966; Guillespie, 1977). Amphicarpic plants follow this strategy, since they produce 2 different types of propagules with contrasting ecological roles: a) ground flowers appear early in the flowering season, are usually self-pollinated, and produce seeds that germinate in situ, ensuring local persistence; and b) aerial flowers develop later in the season, are usually cross-pollinated and produce achenes with enhanced dispersal characteristics (Weiss, 1980; Cheplick, 1987). This strategy is common in short-lived fugitive species whose habitat varies in time and space (Harper, 1977). Moreover, the bet-hedging strategy in amphicarpic plants can be "fine-tuned" by phenotypic plasticity (Sadeh et al., 2009). Organisms are also developmental systems that continually integrate internal and external signals to modulate gene expression (Sultan, 2004). The expression of a plastic response over time is known as *dynamic plasticity* (Sultan, 2004) and includes variation in rates of phenotypic response, patterns of developmental iteration, and ontogenetic trajectories, such as ontogenetic contingency (Diggle, 1994). Thus, phenotypic plasticity in plants can be expressed at sub-individual level. Local environmental conditions can trigger each meristem, leave, branch, or root (Sultan and Stearns, 2005), and the response of a plant to its environment is the sum of all modular responses to their local conditions plus all interaction effects due to module integration (de Kroon et al., 2005).

In this study we analyze flower production and sex ratio in response to light intensity of 2 populations of *Emex spinosa* (L.) Campd., a Mediterranean amphicarpic annual that occurs in habitats with different levels of environmental variation (Weiss, 1980; Ortiz et al., 2009; Sadeh et al., 2009). Architectural effects have been previously found to affect reproductive traits of *Emex spinosa* (Ortiz et al., 2009), and we postulate that architecture may also be affected by environmental conditions; in particular, we could expect a different degree of phenotypic plasticity at different architectural levels. The responses to light in this species were studied at 3 levels of biological organization: among populations, among individuals, and within individuals. Specifically we address the following questions: 1) How does light intensity affect reproductive traits in *Emex spinosa*? 2) Do plastic responses to light differ between individuals or populations? and 3) How does the response to different environmental conditions vary within a plant, i.e. at different architectural levels? We thus address how a plastic response to environmental variation may vary across levels of biological organization.

2. Materials and methods

2.1. Study species

Emex spinosa (Polygonaceae) is an amphicarpic wind-pollinated annual frequent in the Mediterranean basin. It is a colonizer species, mainly monoecious, with sessile female flowers at the base of a stem and male flowers appearing in pedunculate clusters towards the tip of the stem. In *Emex spinosa*, architecture and development are highly correlated. In the rosette stage, both male and female flowers are produced; these flowers are at ground level but not completely buried with stigmas and stamens standing out a few millimeters from the ground (hereafter, we will refer to these as ground flowers; Ortiz et al, 2009). After fecundation, fruits from these flowers are buried by the action of contractile roots. Afterwards, one or several stems develop from the rosette and both female and male flowers are produced at successive nodes of the stem and in lateral branches as these stems develop (aerial flowers hereafter). The first developing stem is usually the largest, and therefore it will be called main stem hereafter. *Emex spinosa* is an auto-compatible species, and in nature, as well as under cultivation, almost all its female flowers are transformed into fruits (Ortiz et al., 2009).

2.2. Experimental design

We selected 2 wild populations: El Gandul (Seville province, SW Spain 37°19′N; 5°47′W) and El Rocío (Huelva Province, SW Spain 37°8′N; 6°29′W). Plants from El Gandul were growing in a field crop abandoned 12 years before, without tree canopy, while plants from El Rocío were growing in waste grounds and road sides within a village.

Newly emerged seedlings at the cotyledon stage were collected from both populations in December 2006 and cultivated outside the greenhouses of Seville University. Each plant was placed in a pot (15 cm in diameter) in a peat–perlite mixture and was left to complete its life cycle; water was added as needed. Plants from each population were separated into 2 sets of 26–29 plants that were assigned to each of 2 light intensity (LI) treatments: high light intensity (HLI hereafter; plants exposed directly to sun; mean photosynthetically active radiation (PAR): 1236 ± 51 μE m^{-2} s^{-1}), and low light intensity (LLI hereafter; plants in the shade; mean PAR: 114 ± 11 μE m^{-2} s^{-1}).

The phenology of each plant was monitored by observations every 10–15 days. The numbers of female and male ground flowers as well as the numbers of female and male flowers produced in each node of the main stem and its lateral branches were recorded. Total number of stems per plant was also recorded. At the end of the flowering of each plant, nodes from aerial stem were assigned to 1 of the 3 following positions: proximal (when produced in the lower third of the stem), central (in the middle third), or terminal (in the upper third). Aerial flowers were assigned to one of these positions. With these data, we constructed the following variables: 'total female flower production' and 'total male flower production' as the total sum of female and male flowers, respectively, produced in the main stem; 'plant sex ratio' as total male to female flower production; 'amphicarpic ratio' as ground to total aerial female flowers; 'female flowers per position' and 'male flowers per position' as the sum of female and male flowers, respectively, of the nodes assigned to each position; and 'sex ratio per position' as the number of male flowers to the number of female flowers of each position.

2.3. Data analyses

At the plant level, the number of stems per plant, the number of nodes per stem, the total female and male flower production, the plant sex ratio and the amphicarpic ratio were compared by means of generalized linear models (GLM), with a gamma distribution and a log link function. Population and light intensity treatment were treated as fixed factors. When necessary, raw data were log-transformed in order to better fit the model. Otherwise, Pearson correlations were performed between the number of nodes and total female, total male, total aerial, and ground flower production.

The production of male and female flowers and the sex ratio in each of the 4 positions of the plant (ground, proximal, central, and terminal) were compared using generalized estimated equations (Liang and Zeger, 1986). In this analysis, 'plant' was the subject effect and the position was the within-subject effect. Response variables (female flowers per position, male flowers per position, and sex ratio per position) were square root-transformed in order to better fit the model. When significant differences were found, pairwise comparison analyses were performed in order to examine differences among positions in light intensity treatments and between light intensity treatments in each position of the stem. All analyses were performed with SPSS version 17.0.

3. Results

3.1. Phenotypic responses to light at population and individual level

Plants of both populations were statistically similar in size and total male flower production (Table 1), but total female flower production was higher in plants from El Rocío than in those from El Gandul (mean ± se: 52 ± 6 flowers vs. 35 ± 3 flowers). This difference was only marginally significant (P = 0.056, Table 1) due to the high dispersion of the El Rocío dataset (female flower production variance = 2350) while the dataset from El Gandul was not so dispersed (female flower production variance = 493). Fruit set was

Table 1. Wald chi square statistics from GLM performed for the variables that describe plant size (number of nodes, number of stems) and those that describe reproductive traits (total female and male flower production per stem, plant sex ratio [male to female flower production], and amphicarpic ratio [ground to aerial female flower production]).

Source of variation	Plant size		Plant flower production		Plant
	No. stems	No. nodes	Female	Male	sex ratio
Intercept	303.39***	3492.24***	434.24	166.28***	142.39***
Population (POP)	2.98	2.13	3.80'	0.56	50.19***
Light intensity (LI)	5.89*	6.66*	13.52***	7.51**	6.80**
POP × LI	0.19	1.15	0.88	0.25	1.82

Asterisks after statistics indicate significant differences 'P = 0.056* P < 0.05 ** P < 0.01 *** P < 0.001.
n = 110; df = 1 for each independent factor.

always very high, and in all plants more than 95% of female flowers transformed into fruits. Significant correlations were found between plant size (measured as the number of nodes in the main stem) and total female and male flower production ($r = 0.71$; $n = 110$; $P < 0.001$, and $r = 0.67$, $n = 110$; $P < 0.001$, respectively). When considering aerial and ground flower production separately, we found that both female and male aerial flower production was correlated with plant size ($r = 0.72$, $n = 110$; $P < 0.001$ and $r = 0.87$, $n = 110$; $P < 0.001$, respectively), while a weaker and nonsignificant effect of size was observed in the number of ground flowers ($r = 0.46$, $n = 110$, $P = 0.634$, and $r = 0.19$, $n = 110$, $P = 0.068$ for female and male ground flowers, respectively).

Plants exposed to HLI produced significantly more stems, more nodes per stem, and more female and male flowers per stem than those exposed to LLI (Figures 1A–D; Table 1). The response of these traits to the 2 light treatments followed the same trend in both populations (interaction population by LI nonsignificant; Table 1). Amphicarpic ratio was also similar in both populations (Table 1). Plants exposed to LLI showed a significantly higher amphicarpic ratio compared to those exposed to a HLI (Table 1; Figure 1E). The variation of amphicarpic

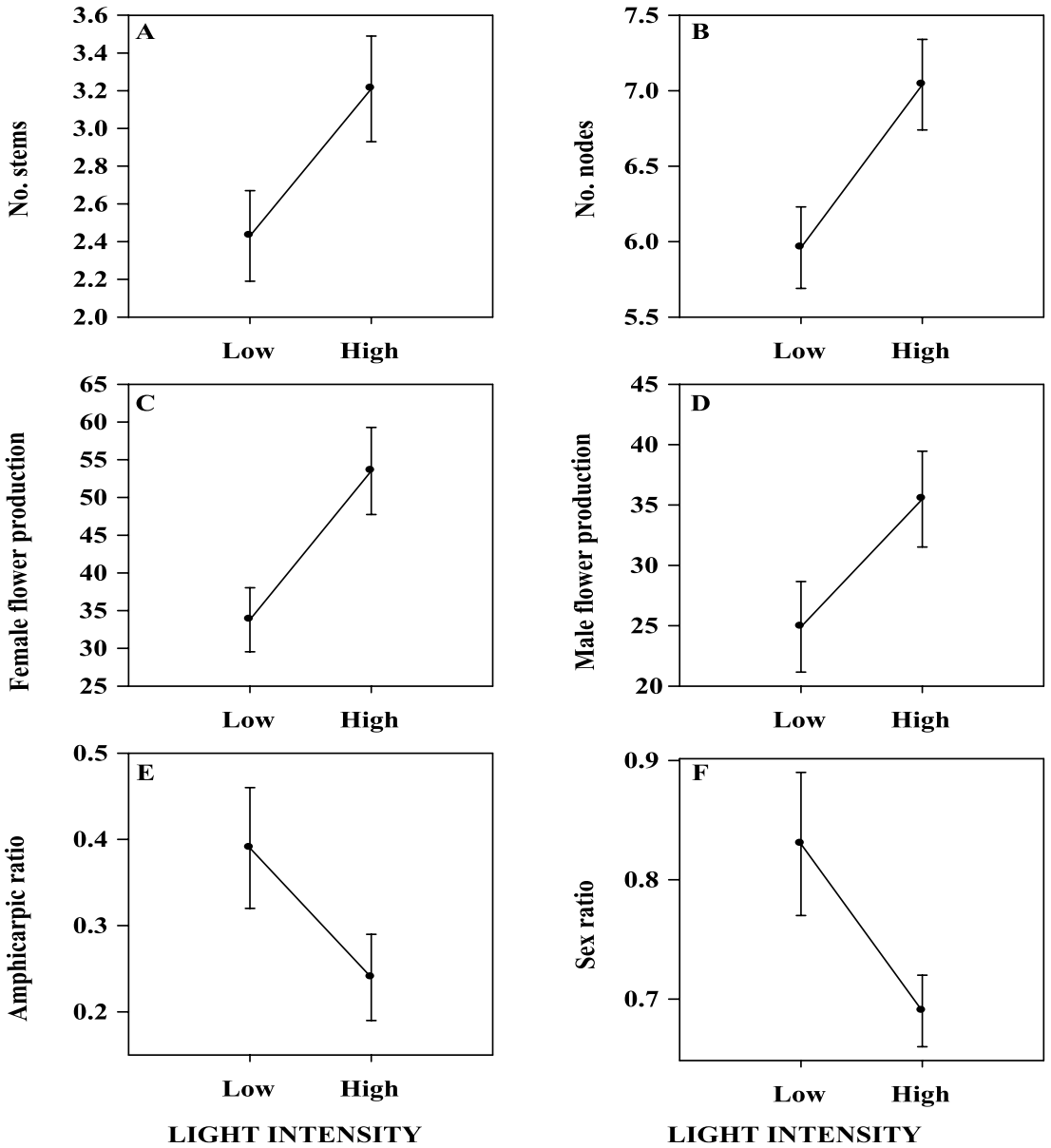

Figure 1. Plastic responses to light intensity in *Emex spinosa.*

ratio depending on light intensity treatment was due to the striking increase in aerial female flower production under HLI (47.7 ± 5.7 flowers) compared to that under LLI (28.5 ± 4.2 flowers; Wald chi square = 13.83; P < 0.001; figure not shown). By contrast, the number of ground female flowers was statistically similar in both treatments (Wald chi square = 0.425; P = 0.114), with a mean of 5.0 ± 0.4 in LLI and 5.8 ± 0.2 in HLI. No significant differences between populations were found when analyzing aerial and ground female flower production separately (Wald chi square = 2.22 and 3.20; P = 0.136 and 0.74, respectively; figure not shown).

Plant sex ratio was in general female-biased, especially in the El Rocío population (0.59 ± 0.02), where 96.5% of the plants produced many more female than male flowers. In the El Gandul population, sex ratio was more variable, with 70% of the plants being female-biased, and a mean sex ratio of 0.92 ± 0.05. This difference in plant sex ratio between populations was statistically significant (Table 1). Light intensity also significantly affected plant sex ratio (Table 1), so that plants exposed to HLI were more female-biased that those exposed to LLI (Figure 1D). Sex ratio responded similarly to the 2 light treatments in both populations (interaction population by LI nonsignificant; Table 1).

3.2. Phenotypic responses at sub-individual level

The production of female and male flowers, and the sex ratio strongly varied along the stems. In fact, the effect of the position was the largest source of variation for all the measured traits (Table 2). With weaker effect size and a lower significance level, the population and the light intensity also affected flower production along the stems (Table 2). In both populations, female and male flower production per position tended to increase along the plant axes, showing a slight fall at terminal positions. However, ground positions showed intermediate values of flower production. The differences among positions were higher in the El Gandul population (interaction population by position significant; Table 2). Plants of both populations responded to light intensity in each position in a similar manner (interaction population by LI by position nonsignificant; Table 2).

Sex ratio per position was strongly female-biased at proximal positions and tended to increase significantly along the stems, being less female-biased at terminal positions (Table 2, pairwise comparisons, P < 0.05). The trend was similar in both populations but the interaction population by position was significant (Table 2) due to the much higher increase in sex ratio towards maleness in the El Gandul population at terminal positions (Figure 2). Each population showed intermediate values of sex ratio at ground positions, being in El Rocío female-biased and in El Gandul slightly male-biased (Figure 2).

LI differentially affected female and male flower production, but did not affect sex ratio in each position (Table 2). Both populations produced more female and male flowers at HLI, but each position responded differentially to light intensity treatments (interaction position by LI significant; Table 2). While light intensity had no significant effect in female flower production at ground and proximal positions, a strong increase in female flower production was detected at central and terminal positions (Figure 3A). In relation to male flower production, no significant effect of light intensity was detected either at ground or at central positions, while at proximal and terminal positions plants under HLI showed higher male flower production (Figure 3B). These trends were similar in both populations (interaction population by LI by position nonsignificant; Table 2).

Table 2. Generalized estimated equations model effects for the variables female flowers, male flowers, and sex ratio. In this analysis, plant was the subject effect and the position was the within-subject effect. Response variables were square root-transformed in order to better fit the model. Wald chi square statistics are presented. n = 110. Asterisks after statistics indicate significant differences * P < 0.05 ** P < 0.01 *** P < 0.001.

	df	Female flowers	Male flowers	Sex ratio
Intercept	1	985.25***	628.60***	1709.38***
Population (POP)	1	9.27**	4.24*	3.20
Light intensity (LI)	1	9.38**	4.80*	1.33
Position (POS)	3	302.35***	368.29***	253.08***
POP × LI	1	0.69	0.30	0.99
POP × POS	3	9.13*	51.43***	55.65***
LI × POS	3	11.60**	9.04*	6.97
POP × LI × POS	3	5.67	5.48	1.88

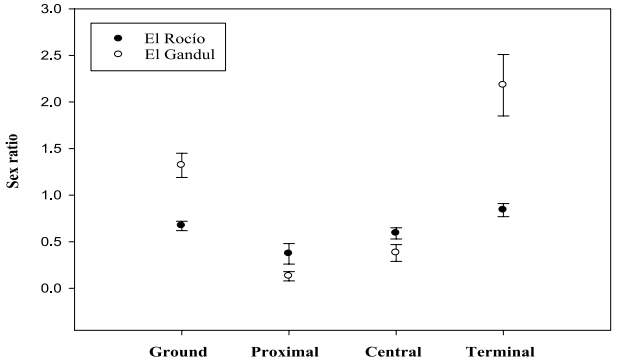

Figure 2. Mean sex ratio variation along plant axes in 2 populations of *Emex spinosa:* El Rocío (closed circles) and El Gandul (open circles). Four positions along plants axes are considered: ground, proximal, central, and terminal. Bars represent standard errors of means.

4. Discussion

Emex spinosa showed contrasting patterns of expression of vegetative and reproductive traits influenced by light treatments that were variable among individuals, but, in general, plants exposed to HLI increased their size and their flower production, with female flower production being the most plastic trait in both populations. Light effects were similar in both populations although significant differences between populations were detected in some traits. Plants from the El Rocío population were female-biased at all positions, while plants from El Gandul were male-biased at ground and terminal positions. Individual genetic components (Friedman and Barrett, 2011) and/or cross generational effects (Talavera et al., 2010) could be affecting the observed patterns in both populations of *Emex spinosa;* however, to test these effects, a further study with controlled linkages will be necessary.

Plant responses to environmental variation include passive limitation of growth under low resource conditions, as well as active developmental plasticity that enhances performance and resource acquisition in each resource environment (Sultan and Bazzaz 1993; Coleman et al., 1994). In our study, the significant effect of light intensity on plant size could be seen as a mere passive plastic effect of resource availability, so that plants exposed to high light intensity have a greater size. However, plasticity is adaptive if the phenotypes produced in response to a change in the environment result in higher average fitness (van Kleunen and Fischer, 2005). A usual estimator of net fitness is plant fruit production (Dorn et al., 2000, Bell and Galloway, 2007, 2008). In our study, fruit set of *Emex spinosa* was always very high, reaching nearly 100%, so that the higher female flower production in plants exposed to light would lead to higher fruit production. This result suggests that this species is able to respond with increased fitness in favorable light conditions showing one possible strategy of an invader that benefits from plasticity as a '*Master-of-some*', that is, by increasing fitness in favorable environments (Richards et al., 2006; Davidson et al., 2011). However, a more complex analysis on the cost and benefits of plasticity and also on the average fitness benefits of plasticity itself under different environmental conditions would be necessary to test whether plasticity is adaptive in *Emex spinosa.*

4.1. Plasticity and plant sex-ratio variation

Monoecious plants have the capacity to allocate resources separately to male and female functions more easily than hermaphrodites, and this flexibility can be advantageous when a shift in an environmental stress occurs during development (Charnov and Bull, 1977; Freeman et al., 1981; Lloyd and Bawa, 1984; Dorken and Barrett, 2004; Narbona and Dirzo, 2010). As reported previously (Ortiz

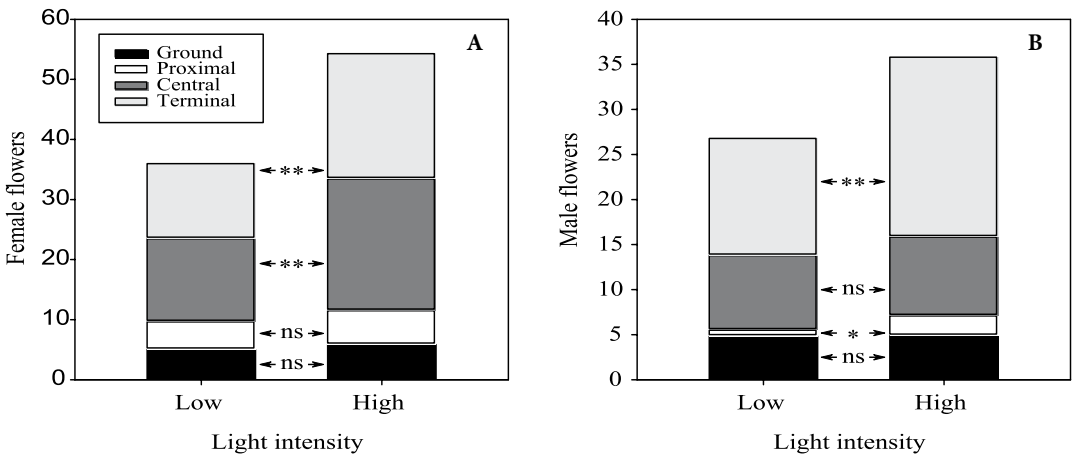

Figure 3. Plastic responses to light intensity at sub-individual level in *Emex spinosa*. In each plant, 4 positions were considered: ground, proximal, central and terminal. Means for each variable in each position are shown. ns, nonsignificant; * $P < 0.05$ ** $P < 0.01$.

et al., 2009), plants of *Emex spinosa* were female-biased, a common strategy of inbreeders (Lloyd, 1979; Lemen, 1980). Inbreeding can be favored in colonizing species as *Emex spinosa* where the importance of high fecundity and the lack of competitors in disturbed habitats partially offset the benefits of outcrossing (Lemen, 1980; Price and Jain, 1981). As predicted by sex allocation theory (Charnov, 1982), female-biased sex allocation could be selected to assure high fecundity in an annual plant living in a highly disturbed place, where mates can be scarce some years.

The cost of reproduction is frequently greater for female than for male reproductive function (Lloyd, 1979; Freeman et al., 1981; Goldman and Willson, 1986; Charlesworth and Morgan, 1991), and thus allocation to female function is more susceptible to vary with environment conditions. Indeed, we observed that female flower production was the most plastic trait of all those we studied. Moreover, sex ratio significantly varied among light treatments, being significantly more female-biased at HLI. This finding is opposite to that stated in *Ambrosia artemisiifolia* L., an annual, wind-pollinated species, in which higher male flower production was found in sun vs. shade treatments (Friedman and Barrett, 2011). Unlike *Emex spinosa*, *Ambrosia artemisiifolia* is a self-incompatible and obligate xenogamous species, and thus the possible fitness benefits of selfing under certain circumstances are not pertinent. Our results, however, fit with the general theory of resource allocation (Charnov, 1982; Lloyd and Bawa, 1984), so that plants produce more female flowers under sunny conditions. Thus, high light environments are commonly associated with femaleness in monoecious (Gregg, 1978; Cid-Benevento, 1987; Menges, 1990; Bertin, 2007) and andromonoecious plants (Solomon, 1985; Bertin and Kerwin, 1998; see Korpelainen, 1998 for a revision). In *Emex spinosa*, this result suggests that when plants are exposed to full sun they have a strong invader strategy, producing a high amount of propagules.

Model predictions and empirical studies reveal that heterocarpic plants tend to allocate more resources into seeds with low dispersal availability under unfavorable conditions (Cheplick, 1989; Venable et al., 1995). If amphicarpic plants, such as *Emex spinosa*, can respond to environmental variation, they could allocate more resources into aerial fruits relative to ground fruits under favorable conditions holding an opportunity to colonize new patches (Sadeh et al., 2009). Our study supports this and although ground achene number was invariable between light treatments, aerial flower production was markedly affected by light, and this plasticity determined the higher allocation of resources to ground flowers at lower light intensities. Similar results have been found in other populations of *Emex spinosa* (Weiss, 1980; Sadeh et al., 2009).

4.2. Phenotypic responses at sub-individual level

The effect of position in every measured trait was the highest source of variation in the performed analyses. This indicates the importance of analyzing plastic responses in plants not only as integrated systems but also as developmental systems constituted by numerous modules. It is well known that sex expression can be related to plant size, age, or position (Armbruster, 1991; Bissell and Diggle, 2008; Mancuso and Peruzzi, 2010; Zhao, 2010). In fact, the variability of reproductive traits along plants axis had been previously studied in *Emex spinosa* (Ortiz et al., 2009), and we will discuss whether this variability is also affected by light intensity.

In *Emex spinosa* aerial flowering is coupled to vegetative growth (Weiss, 1980; Sadeh et al., 2009), as demonstrated by the correlation between plant size and aerial flower production. In relation to flower production, terminal positions were more labile to respond to changes in light intensity whereas ground positions were less variable. A similar situation was found in *Solanum hirtum* Vahl., where distal portions of the inflorescence were the most labile to changes in resource availability (Diggle, 1994). Rather than unitary reactions of whole plants, sex allocation strategies should be considered as the cumulative outcome of numerous consecutive decisions (Lloyd, 1979). Since plant ontogeny is the result of the development of separate meristems, the fate of a flower primordium depends upon where and when it is produced within the architecture of an organism and what events have preceded it during ontogeny. Thus, in *Emex spinosa*, environmental cues determine plant growth and ultimately shape flower and fruit production, affecting plant fitness.

Sex ratio showed significant differences in each position along plant axes independently of light intensity. This contrasts with results of other wind-pollinated species, in which sex allocation is dependent on environmental conditions and can be adjusted plastically (Friedman and Barrett, 2011). We have found in *Emex spinosa* an increase in maleness at terminal positions of the aerial stems independently of environmental conditions. This could reflect a programmed function at each step of the development, which implies higher pollen exportation at terminal positions, where flowers are more exposed to the wind and pollen is more susceptible to be dispersed, since the ability to disperse pollen should increase with plant height in wind-pollinated species (Niklas, 1985; Burd and Allen, 1988; Bickel and Freeman, 1993; but see Shakarishvili and Osishvili, 2013 for a nonwind-pollinated species). In fact, male flowers at terminal positions produce more stamens and pollen than earlier flowers (Ortiz et al., 2009), supporting a male sexual specialization at the end of flowering in *Emex spinosa*. Male flowers at terminal positions are placed optimally for long-distance

pollen dispersal, which is expected to be more effective with increased height because pollen travels further, increasing mating opportunities (Friedman and Barrett, 2011). This sexual specialization could suggest an increase in xenogamy from basal to terminal positions, and so the mating strategy in *Emex spinosa* changes throughout development.

In conclusion, the direction of the plastic responses we observed was towards increasing size and flower production at higher light intensity. Both populations increased flower production and consequently plant fitness at higher light intensity; this could suggest that plasticity is adaptive. At the sub-individual level, terminal positions were the most labile, which highlight that the different modules of a plant are able to respond differentially to light, in order to better fit to the environment. Most plants were female-biased but a decrease in femaleness was observed along plant axis, reflecting a sexual specialization at the end of flowering independently of light. This study suggests that in amphicarpic plants the strategy of producing selfing fruits to assure local persistence (Zeide, 1978) may not only concern ground fruits, but also early aerial fruits.

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