



## Compensatory responses of an arid land crucifer, *Chorispora tenella* (Brassicaceae), to experimental flower removal

José M. Gómez\* & Marcelino Fuentes†

\**Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain*

†*Facultade de Ciencias, Universidade da Coruña, E-15071 A Coruña, Spain*

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We studied experimentally the compensatory ability of an annual arid land crucifer, *Chorispora tenella*, with respect to density of conspecifics. *Chorispora tenella* was able to compensate for flower losses by modulating the rates of abortion of flowers, fruits and ovules. In addition, plants growing at lower density compensated more intensely against losses than plants growing at high density. Nevertheless, as a consequence of compensation, plants in all treatments produced the same quantity of seeds (equal compensation). These results suggest that, from flower production to fruit and ovule maturation, *C. tenella* maintained a number of ovules that exceeded those that it could eventually mature. This could help to colonize arid environments successfully, in which resources are typically scarce and spatio-temporally unpredictable.

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### Introduction

Plants have a flexible system of reproduction. They usually produce more flowers and ovules than they develop into fruits and seeds, this apparently serving as an insurance against possible losses of reproductive structures (Ehrlén, 1991). When flowers are removed, resources that would be allocated to them are subsequently reallocated to adjacent remaining flowers, thus enhancing seed production of the latter (Lee & Bazzaz, 1982; Ho, 1992; Vaughton, 1993). Plants may also replace lost or damaged flowers by producing new ones (Ho, 1992). This compensation allows damaged plants to regain their fitness through extra growth and reproduction (Rosenthal & Kotanen, 1994; Strauss & Agrawal 1999).

Many extrinsic factors influence a plant's ability to compensate for damage (Maschinski & Whitham, 1989; Houle & Simard, 1996). The availability of resources necessary for compensation may be depressed by competition from neighbouring plants (Dirzo, 1984; Price, 1991, Houle & Simard, 1996), thereby restricting plant regrowth and reproductive compensation (Coley *et al.*, 1985; Maschinski & Whitham, 1989;

\* Corresponding author. Fax: + 34 58 243238. E-mail: [jmgreyes@goliat.ugr.es](mailto:jmgreyes@goliat.ugr.es)

Price, 1991; Belsky *et al.*, 1993; Hjältén *et al.*, 1993; Sadras, 1996). Moreover, low-productive habitats, like deserts, constrain the ability of plants to regrow after damage (Rosenthal & Kotanen, 1994; Strauss & Agrawal, 1999). In this paper, we experimentally test the effect of the density of conspecifics on the compensatory ability of an annual weed of Asian origin, *Chorispora tenella* (Pall.) DC. (Brassicaceae) in an arid-land habitat of North America. Our specific objectives are to analyse (1) the effect of flower removal on subsequent patterns of flower survival and fruit and seed production; and (2) the effect of density of conspecifics on the plant's ability for compensation.

## Methods

### *Plant species and study site*

The study area was a livestock pasture located in the Great Basin at Tintic Valley Research Site, 5 km west of Eureka (Juab County, west-central Utah, U.S.A.), 1750 m a.s.l., that was surrounded by extensive Utah juniper (*Juniperus osteosperma*, Cupressaceae) woodlands and sagebrush (mainly *Artemisia tridentata*, Asteraceae) shrub-grasslands. In this area, *C. tenella* typically grows in dense patches near watering places or along roadsides. Our plot was a virtually monospecific stand of *C. tenella*.

*Chorispora tenella* flowers during early spring (April–June), producing on average 5.1 flowers ( $n = 15$  control plants, see below) with 15.6 ovules per flower.

### *Experimental design*

We conducted the experiment during spring 1994. We chose 60 plants of a population and randomly selected 30, each of which was subjected to low density by removing, at the start of the experiment and periodically thereafter, all *C. tenella* plants growing within in a 10-cm radius of the plant. The other 30 plants were subjected to the natural high-density environment with an average of  $28.7 \pm 3.61$  (mean  $\pm 1$  S.E.) individuals per 100 cm<sup>2</sup> ( $n = 10$  quadrats). In each group, we trimmed 15 randomly selected plants, and left the other 15 as controls. Trimming consisted of removing flowers before anthesis with a forceps. We first cut half the flowers already present on the plants (on alternate positions), and then at 3–5-day intervals we cut every other new flower produced. In all, we removed  $51.5 \pm 2.3\%$  of the flowers produced by plants in the two trimming groups. At the start of the study all 60 experimental plants were at the same phenological stage (initiating flowering), and there were no significant differences among groups in plant height, measured to the nearest 1 mm (ANOVA  $p > 0.4$  in all cases; height was log-transformed).

### *Measurements*

We counted the number of flowers produced by each individual plant every 3–5 days until flowering stopped, noting for each flower the position in the inflorescence, numbering them from one to the total number of flowers produced, and working up from the base to the apex of the stalk, since flower opening is strictly basal to apical in this species. When a plant produced lateral stalks, we numbered the flowers according to the opening date. We measured the diameter of each newly-opened flower with a caliper. The measurement was taken consistently at the same phenological stage (beginning of anthesis) of the flower. At the end of the experiment, we collected all surviving plants and took them to the lab. For each plant we noted the number and position of the flowers

that dropped, set aborted fruit, or set ripe to mature fruit. We also measured the length of the mature fruit with a caliper. For each mature fruit, we counted the number of undeveloped ovules and mature seeds with the help of a binocular microscope. In all, we analysed 390 fruits.

We used two groups of estimates of plant reproductive success: fecundity-oriented estimates, which quantify the absolute number of reproductive units produced by plants, and ratio-oriented estimates, which quantify the proportion of reproductive units successfully passing to the next phase. We used four fecundity-oriented estimates: number of flowers produced (including the trimmed ones), number of fruits, number of ovules per fruit and total number of seeds (thereafter called 'seed/plant'). We also used four ratio-oriented estimates: fruit initiation (percentage of flowers initiating fruits), fruit set (percentage of flowers setting ripe fruits), seed/ovule ratio (percentage of ovules setting seed per ripe fruit), and seed set (percentage of ovules setting seed per flower). The ratio-oriented variables included only flowers allowed to open.

### *Statistical analysis*

We analysed the effect of the treatments on the production of lateral stalks by the plants by means of a multi-way analysis of contingency (PROC CATMOD in SAS Institute Inc., 1997), in which presence or absence of lateral stalks was the categorical dependent variable, and the two factors (trimming and density), plus their interaction, were the independent variables. The significance of each factor was tested by means of Wald chi-squares (SAS Institute Inc., 1997). We studied the relationship between the position of the flowers on the stalk and the number of seeds produced per flower by means of linear regression analyses, considering flower position as a continuous variable. For this, we calculated for each treatment the average seed set of the flowers arranged in each position of the stalk. After this, we regressed these figures against flower position. We fitted a different regression equation for each of the four treatments.

We analysed among-treatment variation in reproductive variables with fully crossed two-way ANOVA, with density and trimming as fixed factors, and one-way ANOVA comparing the trimming levels within each density environment (PROC GLM, SAS Institute Inc., 1997). To improve homoscedasticity, we arcsin-transformed ratios and log-transformed the remaining variables. Therefore, we tested whether the variances across groups was homogeneous by means of the one-way Levene test (PROC GLM, SAS Institute Inc., 1997). If this test of equal variances revealed that the group variances were significantly different, we used the Welch ANOVA, which weighs means by the reciprocal of the sample variances of group means (see SAS Institute Inc., 1997 for further details).

We used individual plants as sample units in all above-mentioned analyses. When the same statistical model was performed more than once, we adjusted the  $p$ -values to  $\alpha = 0.05$  using the Bonferroni correction (Rice, 1989). All means are shown  $\pm 1$  S.E.

## **Results**

### *Effect of flower position on the stalk on reproductive success*

Of the plants growing in the low-density environment, 46.1% ( $n = 30$  plants) and only 13.3% of those growing in the high-density environment, produced lateral stalks or secondary modules originating from the main stalk, each of them producing flowers apically. The differences were clearly related to plant density (Wald  $\chi^2 = 6.44$ ,  $p = 0.01$ ) but not to trimming (Wald  $\chi^2 = 0.01$ ,  $p = 0.9$ ) or their interaction (Wald  $\chi^2 = 0.01$ ,  $p = 0.9$ ; Multi-way analysis of contingency). Plants bearing lateral branches

**Table 1.** Summary of the regression analyses of seed set (percentage of ovules setting seeds) in each flower against flower position.  $R^2$  refers to the proportion of the variability in seed set explained by the models. Only  $t$  values in bold were significant according to a sequential Bonferroni correction (Rice, 1989)

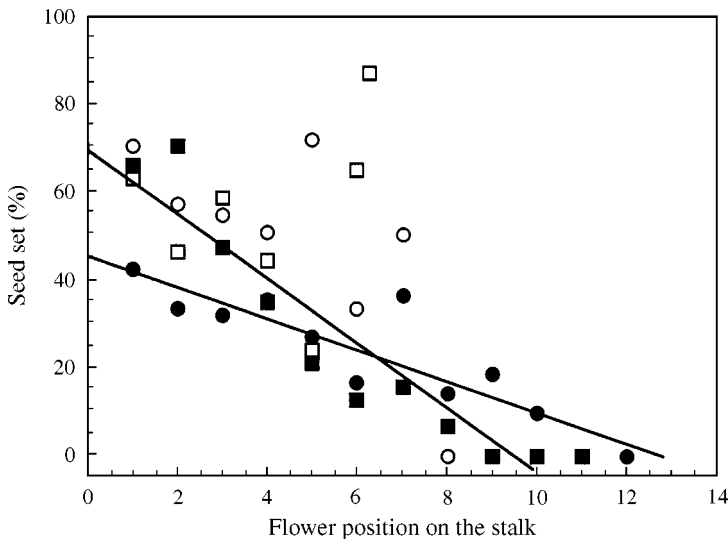
		$R^2$	$\beta \pm 1 \text{ SE}$	$ t $	$p$
Untrimmed	High-density	0.87	$-0.07 \pm 0.01$	<b>8.39</b>	0.0001
	Low-density	0.79	$-0.03 \pm 0.01$	<b>6.48</b>	0.0001
Trimmed	High-density	0.43	$-0.07 \pm 0.02$	2.54	0.04
	Low-density	0.03	$0.04 \pm 0.04$	0.91	0.41

produced significantly more flowers ( $14.3 \pm 1.0$  flowers/plant,  $n = 17$  plants) than plants without lateral branches ( $4.6 \pm 0.6$ ,  $n = 43$  plants; Levene test:  $F_{1,57} = 17.07$ ,  $p < 0.0001$ ; Welch test:  $F_{1,57} = 38.20$ ,  $p < 0.0001$ ).

The probability of an ovule setting seed significantly decreased with the position of the flower in the stalk for untrimmed plants (Table 1, Fig. 1). Thus, 40–70% of the ovules set seeds in the flowers located in the most basal positions (positions numbered as 1 or 2), whereas only 0–9% of the ovules set seeds in the uppermost positions (positions 10–12, Fig. 1). In contrast, the effect of flower position on seeds produced per flower disappeared in trimmed plants (Table 1), with around 50% of the ovules setting seeds in the flowers located both in the basal and apical positions (Fig. 1).

#### *Effect of trimming and plant density on plant reproductive success*

Flower diameter was significantly affected by plant density ( $F_{1,56} = 4.22$ ,  $p = 0.04$ ), but not by trimming ( $F_{1,56} = 0.60$ ,  $p = 0.44$ ), not by their interaction ( $F_{1,56} = 0.06$ ,  $p = 0.79$ , two-way ANOVA). Thus, plants growing in low-density environments had



**Figure 1.** Relationship between flower position in the stalk and seed set, estimated as the percentage of ovules setting seed per flower. Only the regression lines for the two untrimmed treatments are shown, since they were the only treatments having significant relationships (see Table 1 for details). Untrimmed, low density (●), untrimmed, high density (■), trimmed, low density (□), trimmed, high density (○).

larger flowers ( $85.2 \pm 2.1$  mm diameter) than plants growing in high-density environments ( $78.3 \pm 2.6$  mm).

Trimming did not significantly affect any fecundity-oriented estimate of plant reproductive success (Table 2). Plants in low-density environments produced more flowers, fruits and ovules per fruit than plants in high-density environments (Fig. 2), although this difference was not significant (Table 2). Fruit size did not vary significantly among groups (all  $p > 0.1$ , two-way ANOVA), ranging from  $24.8 \pm 1.13$  mm to  $27.3 \pm 1.3$  mm.

In contrast, all ratio-oriented estimates of plant reproductive success except fruit set were affected by trimming (Table 2). However, this effect proved important only in low-density environments (Fig. 2). Trimmed plants abscised significantly fewer flowers before setting fruit than untrimmed plants only when growing in low-density environments. Similarly, fruit set was marginally higher in trimmed than in untrimmed plants (Table 2), and the seed/ovule ratio of the ripe fruits was significantly higher in the trimmed *vs.* untrimmed plants only in low-density environments (Fig. 2). As a consequence, although trimming increased female seed set in both density environments, it was statistically significant only in the low-density environments (Fig. 2).

Finally, there was no statistical difference among treatments in the number of seeds produced by the plants (Table 2), with plants in all groups yielding an average of about 40 mature seeds (Fig. 2).

## Discussion

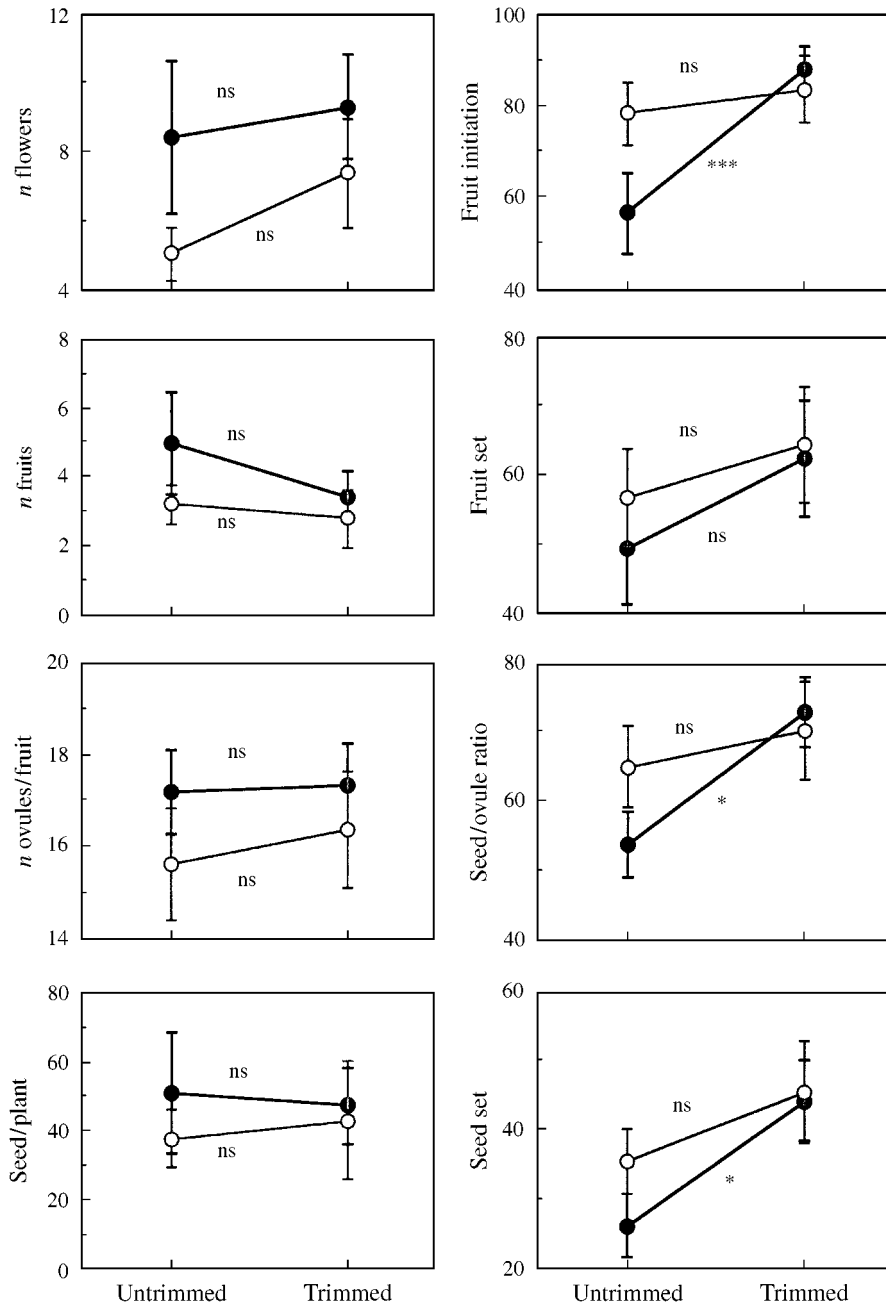
*Chorispora tenella* was able to compensate against flower losses in each reproductive stage by modulating the rates of abortion of flowers, fruits and ovules; as a result, trimmed plants ended up producing roughly the same number of seeds as untrimmed plants (see also Stephenson, 1992; Gedge & Maun, 1994). Flowers produced at a later date were the main target of reproductive modulation (see Vaughton, 1993 for a similar result). Among untrimmed plants, the proportion of ovules setting seed rapidly decreased from basal to apical (later-developed) flowers. Among trimmed plants, however, seed production did not decrease from basal to apical flowers, with the seed set of the latter being significantly higher than in untrimmed plants. Thus, it seems that resources that would be allocated to flowers that we clipped were redirected to later-formed ovaries or fruits that would otherwise abort (Stephenson, 1980; Lee, 1988; Ho, 1992).

Plants modulated flower survival and fruit and seed abortion according not only to artificial flower removal but also to conspecific density. Experimental removal of neighbors resulted in increased flower production following lateral vegetative growth (for similar results in other crucifers, see Pyke, 1989; Matthies, 1990; Yano, 1993; Clauss & Aarssen, 1994; Sans & Masalles, 1994; Kudoh *et al.*, 1995; Lesica & Shelly, 1995). However, it did not result in increased maternal seed production, because these plants suffered higher rates of abortion of flowers, fruits and ovules. It seems that release from the interference of neighbors allows plants to expand laterally and thus produce more flowers, but does not free up enough resources to maintain all of them. Nevertheless, this excess of flowers could enhance fitness through additions to male reproductive success (Sutherland & Delph, 1987).

In sum, our experiment has shown that a number of processes interacted to cancel out initial differences in flower number among treatments, the end result being that plants subjected to contrasting treatments finally produced roughly the same number of seeds ('exact compensation' *sensu* Belsky, 1986). The exact compensation displayed by *C. tenella* suggests that there is an upper threshold for the plant's ability to feed seeds, which may depend on environmental conditions. It seems that this crucifer kept in each life-cycle stage a number of ovules that exceeded those that it could mature. So, in each reproductive stage it could compensate for losses in previous stages. This reserve helps

**Table 2.** Summary of the two-way ANOVAs (overall *df.* = 3,55) testing the effect of trimming (two levels) and plant density (two levels) on several reproductive parameters of *Chorispora tenella*.  $R^2$  refers to the proportion of the variability of each reproductive parameter explained by the overall model. Only F values in bold were significant according to a sequential Bonferroni correction (Rice, 1989)

	$R^2$	SS	Trimming		SS	Density		Trimming $\times$ density		
			<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>	SS	<i>F</i>	<i>p</i>
Number of flowers	0.07	2.24	2.50	0.12	1.56	1.74	0.19	0.00	0.00	0.94
Number of fruits	0.01	0.19	0.27	0.60	0.18	0.28	0.60	0.06	0.09	0.77
Number of ovules/fruit	0.04	0.04	0.14	0.71	0.40	1.48	0.23	0.03	0.10	0.75
Number of seed/plant	0.01	1.53	0.11	0.74	0.40	0.03	0.86	5.00	0.36	0.55
Fruit initiation	0.23	0.65	<b>9.48</b>	0.003	0.18	2.62	0.11	0.36	5.22	0.03
Fruit set	0.08	0.31	3.35	0.07	0.12	1.24	0.29	0.07	0.76	0.39
Seed/ovule ratio	0.13	0.20	<b>4.95</b>	0.03	0.03	0.73	0.40	0.07	1.79	0.19
Seed set	0.16	0.40	<b>8.11</b>	0.006	0.08	1.71	0.19	0.06	1.21	0.27



**Figure 2.** Between-treatment differences in the fecundity-oriented (left panels) and ratio-oriented (right panels) estimates of female reproductive success of *C. tenella*. \* $p < 0.05$ , \*\*\* $p < 0.001$ , in comparisons between trimmed and untrimmed plants within each density environment. High density (—●—), low density (—○—).

the plant to buffer against external losses in reproductive structures and to eliminate ‘excess’ ovules in order to match seed number to available resources. This could partially explain why this annual crucifer can successfully colonize arid habitats, which are characterized by scarce and spatio-temporally unpredictable resources.

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