POPULATION ECOLOGY - ORIGINAL PAPER

Fruit size decline from the margin to the center of capitula is the result of resource competition and architectural constraints

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Abstract Plants produce repeated structures, such as leaves, flowers, and fruits, which differ in size and shape. One example of this is fruit size, which is commonly observed to decrease from proximal to distal positions within an inflorescence. The resource limitation hypothesis proposes that because proximal fruits usually develop first, they have temporal priority on access to resources over distal fruits. The non-mutually exclusive architectural effects hypothesis suggests that these position effects in fruit size may also be due to inherent architectural variation along infructescence axes. We separated out the effects of resource competition and inflorescence architecture by removing the outer or the inner flowers within capitula of *Tragopogon porrifolius*. We also studied if fruit position influenced germination and seedling performance in order to assess fitness consequences of position effects. Inner fruits were significantly heavier when outer flowers were removed. However, outer fruits did not significantly increase when inner flowers were removed, suggesting later fruits were limited by the development of early fruits. Our findings also suggest that architectural constraints restricted the size of inner fruits in comparison with outer ones. We found that both resource competition and inflorescence architecture affected the fruit size of *T. porrifolius*, even though this species does not have linear, indeterminate inflorescences. We advance the hypothesis that, when such effects on fitness occur, resource competition-mediated position effects could turn, in evolutionary time, into architectural position effects.

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Introduction

The modular nature of flowering plants has consequences for their phenotypes because plants are constructed of iterated—but not identical—structures, such as leaves, flower, and fruits. This kind of phenotypic variation at the intra-individual scale is critical to any understanding of plant morphology and morphological diversification, such as the great diversity of plant reproductive phenotypes (Diggle 2003). In addition, intra-individual variation may also have profound ecological implications; for example, plants which exhibit a broad range of fruit sizes would be dispersed by a greater diversity of fruit consumers than plants which produce a narrow variety of fruit sizes (Herrera 2009). The intra-individual phenotypic variation sometimes follows a positional pattern because each structure is produced in a distinct positional and ontogenetic context. An example of positional patterning is flower and fruit size, which usually decreases from the proximal (earliest produced) to distal (latest) flower positions within inflorescences (see Stephenson 1981; Wyatt 1982; Diggle 1995, 2003).

These so called 'position effects' (Lee 1988) have been explained by two, non-mutually exclusive mechanisms. First, there can be competition for resources between flowers and/or fruits. Proximal flowers or fruits usually develop first and thus take temporal priority on access to resources. This reduces the potential for fruit and/or seed maturation at later or distal positions within the same inflorescence (Stephenson 1981; Lee 1988). Second, some authors have proposed that proximal-to-distal declines in fruit size may also be due to inherent architectural constraints along plant axes (Wolfe 1992; see Diggle 1995, 2003 for reviews). This 'architectural effect' (Diggle 1995) might be mediated by developmental constraints, such as the amount of vascular tissue supplying the organs (Wyatt 1982; Wolfe 1992; Diggle 2003). The relative importance of resource competition versus architectural effects differs widely among species and may even vary among different floral organs (Ashman and Hitchens 2000; Diggle 2003; Kliber and Eckert 2004). Nevertheless, few experimental studies have considered both mechanisms (Kliber and Eckert 2004).

The investment decline in flowers and fruits has most often been described for linear inflorescences, such as racemes (Byrne and Mazer 1990; Susko and Lovett-Doust 1999; Vallius 2000; Kudo et al. 2001; Wolfe and Denton 2001; Hiraga and Sakai 2007; Zeng et al. 2008). Although position effects are also known in plants having other inflorescence architectures, such as umbels (Wyatt 1980) and capitula (Zohary 1950; Burtt 1977), these structures have been studied much less. The capitulum is basically a flattened raceme, where external flowers are equivalent to proximal ones in a linear inflorescence and are the first to develop, whereas the innermost flowers are equivalent to distal ones and develop later (Burtt 1977). Many species show a large variation in fruit size within capitula, with the outermost fruits usually being larger than the innermost (Rai and Tripathi 1982; Kigel 1992; Imbert et al. 1997; Ruíz de Clavijo 2000; El-Keblawy 2003; Picó and Koubek 2003; but see Ruíz de Clavijo 1995; Chmielewski 1999). Nevertheless, there is currently no experimental evidence supporting the relative importance of resource competition and/or architectural effects on this positional variation within capitula. An examination of positional patterns in several inflorescence architectures would likely confirm whether positional patterns are specific to linear indeterminate inflorescences or whether they represent a general pattern in flowering plants irrespective of inflorescence arquitecture.

In addition to evaluating proximate mechanisms (resource competition and/or architectural constraints) that cause this positional variation, it is also important to assess whether these positional patterns have fitness consequences. Early flowers have the greatest likelihood of producing outcrossed seed, and it will be advantageous to

preferentially allocate more resources to early over later fruits (Brunet and Charlesworth 1995). If the disproportionate allocation to early seeds and fruits would be advantageous, we also expect that these heavier seeds will produce larger seedlings.

In the study reported here, we combined experimental and observational studies in a natural population to identify the proximate mechanisms underlying the positional decline in fruit size within the capitulum of *Tragopogon porrifolius* L. (Asteraceae). We separated out the effects of resource competition from those of inflorescence architecture by removing the outer or the inner flowers within the capitulum. We also studied if fruit position would influence germination and seedling growth and survival. The specific questions addressed are the following: (1) Is there positional variation in fruit size within the capitulum? (2) Is this effect determined by resource competition or by architectural constraints? (3) Does the fruit position within the capitulum influence germination, seedling survival, and seedling size?.

Material and methods

The species

Tragopogon porrifolius L. (Asteraceae), or common salsify, is a monocarpic perennial herb (Qi et al. 1996; Clements et al. 1999) native to Eurasia. It usually occupies disturbed sites in slightly moist habitats, although once established, plants can withstand drought (Clements et al. 1999). This species produces a rosette of long narrow grasslike leaves. Inflorescences are terminal and bear purple flowers, with an elongated ray and centripetal development (Lack 2007). Flowering in Spain occurs in April–May. The plant is self-compatible (Cook and Soltis 1999). Fruits are one-seeded and indehiscent and bear a pappus with many plumose bristles (Anderberg et al. 2007).

Positional variation in fruit mass in a natural population

To confirm position effects on fruit mass within capitula in this species, we studied the variation in fruit size by collecting infructescences at all of the positions from the border to the center of the capitulum. In the spring of 2007, we sampled 20 infructescences from different individuals (genets) in one population in central Spain within the campus of the University Rey Juan Carlos (Móstoles-Madrid: 40°19′40.7″N, 2°54′6.95″W; 661 m a.s.l.). Within capitula, flowers are packaged in series of long and short spirals (parastichies: Leppik 1977) intersecting each other. We assigned fruit positions following long spirals (Fig. 1). The outermost fruit was assigned to position 1, the next fruit in
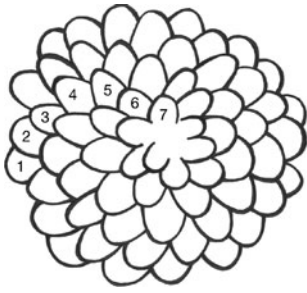
Fig. 1 *Tragopogon porrifolius* receptacle. The *numbers* show how fruits were sampled to describe positional variation in fruit size

Fig. 2 Picture representing the three treatments 'inner flowers removed', 'outer flowers removed', and 'control', applied to capitula of *T. porrifolius* in the experimental manipulation of flower competition. Flowers removed are represented in *gray*. In the control treatment, the remaining fruits were separated in the laboratory into outer and inner

the spiral towards the center of the capitulum was assigned to 2, and so on (Fig. 1). Where possible, we sampled five long spirals per inflorescence. We selected 13 inflorescences of different plants with three to five replicates per fruit position in the analysis, including up to seven positions; inflorescences with more than seven positions were too infrequent to analyze. We weighed all the fruits with their pappus to the nearest 0.1 mg.

We also performed Phytotron and experimental garden tests to study whether fruit position within the inflorescence influenced germination, seedling survival, and seedling size. We conducted the test in the Phytotron of the University of Rey Juan Carlos between July and September 2007 under conditions of a 16:8-h (light/20°C:dark/15°C) photoperiod and 50% humidity. A total of 152 seeds from nine plants, with two replicates per position, were used in the Phytotron experiments, in a completely randomized block design with two trays as blocks. Each tray had 76 fruits, representing one fruit per plant and position. In the experimental garden, we randomly selected one of the long spirals of ten plants without replication by position and plant, giving a total of 79 seeds. We put the seeds in separate pots (1.4 dm³) with standard soil, consisting of a substrate of 28% sand, 15% perlite, and 56% commercial peat. We established this experiment in November 2007. Germination was recorded weekly. Seeds were considered to have germinated as soon as the cotyledons emerged. We measured the longest leaf and the number of leaves 60 days after germination and used the longest leaf length times the number of leaves as a seedling size index.

Experimental manipulation of flower competition: resource limitation versus architectural effects

A flower removal experiment was performed to test whether resource limitation and/or architectural effects influenced fruit size in *T. porrifolius*. The experiment was carried out from April to May 2007 at the same site as the observational study (see above). Three treatments were performed on 99 plants, 33 per treatment (Fig. 2): (1) 'outer
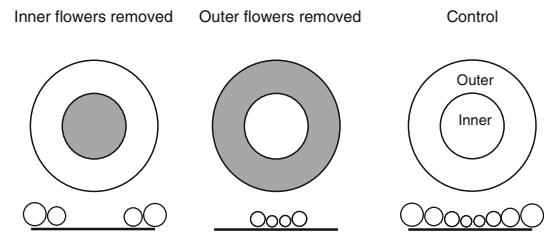
flowers removed', in which the outer half of the flowers was removed in one capitulum per plant prior to anthesis; (2) 'inner flowers removed', in which the inner half of flowers was removed in one capitulum per plant prior to anthesis; (3) 'control', in which inflorescences were not manipulated. One inflorescence was treated per plant, and triplets of plants were always processed together each day to avoid phenological effects, i.e. potential differences in fruit production between earlier and later inflorescences during the blooming season. Inflorescences were hand pollinated to ensure fruit production. Flower number prior to flower removal and fruit set (measured as the number of fruits divided by the number of initial available ovules in the inflorescence) did not significantly differ among treatments (Table 1). The number of flowers removed in the treatment where outer flowers were removed was higher than that in the treatment where inner flowers were removed (Table 1). After ripening, we collected the infructescences. In the laboratory, we separated fruits of control inflorescences into an outer and an inner portion (Fig. 2), and we separated the outermost ring of fruits of each inflorescence. All of the fruits, including their pappus, were weighed to the nearest 0.1 mg.

In each plant we also measured plant height as an estimate of plant size, the number of inflorescences produced as an estimate of the reproductive investment of each plant, and the receptacle diameter as a measurement of inflorescence size. The number of inflorescences might also be a good estimate of plant size since the former has been shown to be correlated with the root crown diameter in *T. pratensis* (Qi et al. 1996) and the root crown diameter was in turn highly correlated with the total plant mass in *T. dubius* (Gross 1981).

We tested three hypotheses. Firstly, resource competition mediated by floral initiation order, i.e., by the earlier access to resources, would mean that fruits from the inflorescences where outer flowers were removed should be heavier than inner fruits of control inflorescences. Secondly, resource competition among fruits, independently of floral initiation order, would mean that fruits produced later

Table 1 Mean of inflorescence traits by treatment level for the flower removal experiment

Trait	Treatment			Test value[a]	P
	OR	Control	IR		
Fruit set ($\times 100$)	84.37 ± 19.64	83.70 ± 15.53	93.32 ± 6.40	$\chi^2 = 4.591$	0.101
Number of flowers prior to flower removal	96 ± 30	81 ± 32	84 ± 28	$\chi^2 = 2.304$	0.316
Number of removed flowers	58 ± 17	–	35 ± 11	$U = 85.000$	0.000
Percentage of flowers removed	61.07 ± 13.17	–	43.72 ± 11.06	$U = 72.000$	0.000
Sample size	22	24	24		

Values in table are given as the mean $\pm$ standard deviation (SD)

OR Outer flowers removed, *IR* inner flowers removed

[a] Fruit set and the number of flowers prior to flower removal were compared using the Kruskal–Wallis test, whereas the number and the percentage of removed flowers were tested using the Mann–Whitney *U* test

affect the size of fruits produced earlier, so fruits from the 'inner flowers removed' treatment should be heavier than outer fruits in control inflorescences. Thirdly, architectural effects where position also affects fruit size means that the outermost fruits from the 'inner flowers removed' treatment should be heavier than the outermost fruits from the 'outer flowers removed' treatment, as the latter are in a relative inner position compared to the 'inner flowers removed' ones.

To determine whether the experimental treatments and fruit positions had effects on germination, we carried out two germination tests, one in a Phytotron and another in an experimental garden. In the experimental garden experiment, seedling survival and growth were also assessed. We selected 15 inflorescences per treatment to carry out a germination test in the Phytotron, with the test conducted in the same Phytotron and on the same dates and under the same conditions as described above. The experiment was arranged in a completely randomized block design with five trays as blocks and 90 fruits per tray. One fruit per inflorescence and position was represented in each tray. Germination was recorded weekly. Seeds were considered to have germinated as soon as the cotyledons emerged. The experiment was concluded 3 weeks after germination was recorded.

For the experimental garden test, we randomly selected eight seeds (four from the outer positions and four from the inner positions) from 36 plants, 12 per treatment. We placed the 288 seeds in separate pots (1.4 dm^3) containing the same standard soil as described above. The experiment was arranged in a randomized complete block design with two plots of 19.7×0.80 m as blocks. In each block, we used two pots per inflorescence, treatment, and position. We established this experiment in November 2007. Germination was recorded weekly. Seeds were considered to have germinated as soon as the cotyledons emerged. We measured the longest leaf and the number of leaves 60 days

after germination and used the longest leaf length times the number of leaves as an index of seedling size.

Statistical analyses

Positional variation in fruit mass in a natural population

We evaluated if position affected fruit mass, germination, and seedling size by fitting Generalized Linear Mixed Models (GLMMs) via restricted maximum likelihood (Patterson and Thompson 1971). GLMMs provide a flexible method to model traits which do not meet the assumptions of a standard linear modeling while simultaneously allowing fixed and random factors to be distinguished in the model. Effects of random factors were tested using Wald *Z*-statistic tests, which are appropriate for large samples, and those of fixed factors were tested with *F* tests, which are preferable when the structure of the variance–covariance matrix depends on an unknown scale parameter (Littell et al. 1996). We used Satterthwaite's method to determine the approximate denominator degrees of freedom for these tests (Verbeke and Molenberghs 1997).

We modeled fruit mass using a normal distribution with an identity link function. The explanatory variables included in the model were fruit position, plant height, number of inflorescences, and receptacle diameter; plant and its interaction with position were included as random factors. Germination in the Phytotron was modeled using a binomial distribution with a logit link function and the following explanatory variables: fruit position (only up to the eighth position because the innermost ones included a very low number of seeds), fruit mass, plant height, receptacle diameter, and tray. The number of inflorescences was not included in this analysis because plants in this test showed very low variation in the number of inflorescences (range: 2–4 per plant). Again, plant and its interaction with position were included as random factors, whereas tray was considered

as a fixed factor because treating it as random led to problems in algorithm convergence. Finally, germination and seedling size in the experimental garden were modeled using a binomial distribution with a logit link function and a Poisson distribution with a log link function, respectively. The explanatory variables fitted in this model included fruit position, fruit mass, plant height, number of inflorescences, and receptacle size as fixed variables and plant and the interaction among plant and position as random factors. There was no seedling mortality; therefore, there was no variation in seedling survival to model.

Experimental manipulation of flower competition: resource competition versus architectural effects

We assessed the effect of removing flowers in different positions within each inflorescence on fruit mass, germination, seedling survival, and seedling size of *T. porrifolius* by fitting GLMMs. We modeled fruit mass using a gamma distribution with an identity link function. The explanatory variables included in the model were treatment (outer fruits of control inflorescences, inner fruits of control inflorescences, 'outer flowers removed', and 'inner flowers removed'), plant height (as a surrogate of plant size), number of inflorescences produced (a surrogate of the reproductive output of the maternal plant), and receptacle diameter (a measure of inflorescence size). Plant was included as a random factor. To test whether fruits from the outermost ring of each treatment (control, 'outer flowers removed', and 'inner flowers removed') were significatively different, we utilized the same model but using only data from the outermost fruits of each inflorescence.

We modeled seed germination in the Phytotron with the same approach as the previous GLMMs but with a binomial distribution with a logit link function. We included the same explanatory variables plus the average fruit mass of each experimental unit (i.e., the mean fruit mass per treatment, position, and plant); plant and tray were included as random factors. Seed germination, seedling survival, and seedling size in the experimental garden were modeled assuming a binomial error with logit link function for the two first variables and a Poisson distribution with a log link function for the last one. We included the same explanatory variables as in the previous model, but in these latter models a block (plot) factor was included. We considered plot and plant as random factors. However, in the germination model, the estimated variance for the random factor plant was very low, and the GLMM analysis produced incorrect degrees of freedom; consequently, we removed plant from this model. All models were fitted using the GLIMMIX procedure of SAS 1990 (SAS Institute, Cary, NC) with the DIFF option in the LSMEANS statement of the GLIMMIX procedure.

Results

Positional variation in fruit mass in a natural population

Fruit mass significantly decreased from outer to inner positions within the infructescences of *T. porrifolius* (Fig. 3a; Table 2). Maternal plant also influenced fruit mass (Table 2); fruit mass was higher in plants with more inflorescences (Table 2). However, germination was not affected by position in either the Phytotron experiments or in the experimental garden (Fig. 3b; Table 2). There was no seedling mortality, and seedling size was influenced by the interaction between maternal plant and position (Fig. 3c; Table 2). Fruit mass did not significantly affect seedling size (Table 2).
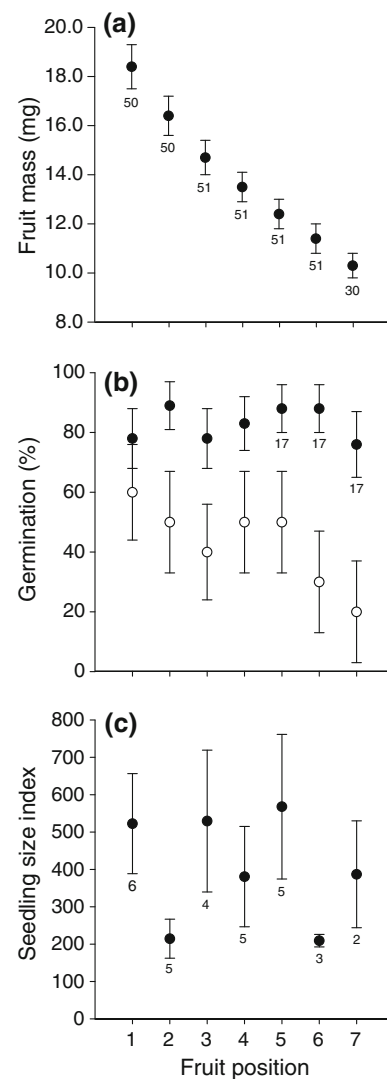

Fig. 3 Least-square means [± standard error (SE)] of fruit mass (**a**), germination in the Phytotron (*black dots*, n = 18) and in the experimental garden (*white dots*, n = 10) (**b**), and seedling size in the experimental garden per position (**c**). Sample size is shown *under each dot* when it differs among positions

Table 2 Effects of flower position and maternal plant traits on fruit mass, seed germination, and seedling size

Explanatory variables	Fruit mass		Germination in Pytotron		Germination in garden		Seedling size	
Fixed factors	F	P	F	P	F	P	F	P
Position	$47.76_{6,6704}$	<0.001	$0.53_{7,1548}$	0.798	$0.47_{6,59}$	0.827	$1.28_{6,1736}$	0.316
Plant height	$-1.03_{1,892}$	0.338	$+4.38_{1,291}$	0.130	$-2.06_{1,662}$	0.196	$+0.10_{1,433}$	0.762
No inflorescences	$+10.35_{1,899}$	0.011	–		$+1.20_{1,574}$	0.318	$+0.61_{1,364}$	0.483
Receptacle size	$+3.89_{1,890}$	0.083	$-4.45_{1,424}$	0.098	$+0.01_{1,740}$	0.921	$+1.39_{1,1261}$	0.260
Fruit mass			$+1.64_{1,123}$	0.203	$+0.00_{1,1917}$	0.988	$-0.29_{1,1502}$	0.599
Tray	–		$8.35_{1,123}$	0.005	–		–	
Random factors	Z	P	Z	P	Z	P	Z	P
Plant	2.06	0.020	0.62	0.268	0.54	0.295	0.21	0.417
Plant x position	3.34	<0.001	1.26	0.103	0.81	0.209	2.67	0.004
Sample size	334		135		70		30	

The Wald-type F statistic (Wald Z-statistic for random factors) is given with the degrees of freedom as a subscript and the sign indicating the direction of the effects
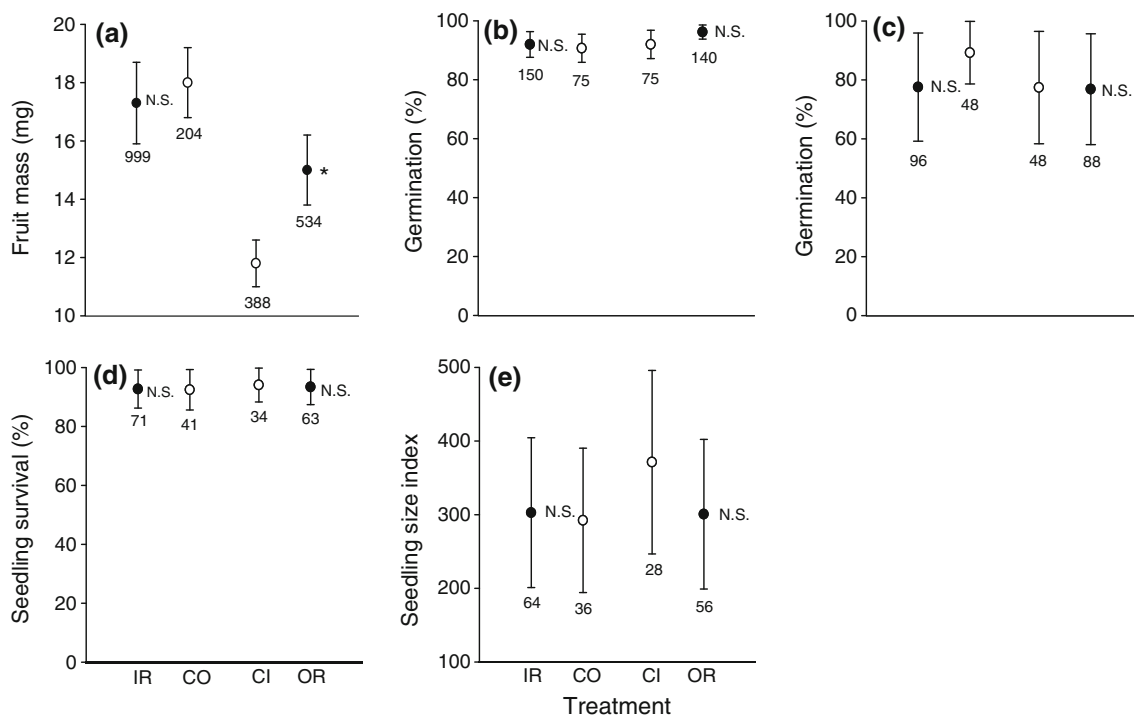

Fig. 4 Least-square means (± SE) of fruit mass (**a**), germination in Phytotron (**a**), germination in the experimental garden (**c**), seedling survival (**d**), and seedling size (**e**) by treatment. *Filled circles* Treatments where flowers were removed (*IR* inner flowers removed, *OR* outer flowers removed), *open circles* control flowers (*CO* outer fruits of control inflorescences, *CI* inner fruits of control inflorescences). Significant differences among IR and CO fruits, and among OR and CI are shown to the *right of IR and OR dots*, respectively (*N.S.* not significant, *$*P < 0.05$*). Sample size is shown *under each dot*

Resource competition versus architectural effect

Flower removal affected fruit mass in *T. porrifolius* (Fig. 4a; Table 3). Fruits were heavier in those treatments in which some flowers were removed in comparison with control ones (Fig. 4a). Nevertheless, only fruits of inflorescences where outer flowers were removed were significantly heavier than inner fruits of control inflorescences (Fig. 4a). Maternal plant significantly influenced fruit mass (Table 3); in particular, fruit mass was positively related with receptacle size (Table 3). In addition, the outermost fruits of inflorescences where outer flowers were

Table 3 Effects of flower removal treatments and maternal plant traits on fruit mass, seed germination, seedling survival, and seedling size

Explanatory variables	Fruit mass		Germination in Pytotron		Germination in Pytotron[b]		Seedling survival in the experimental garden		Seedling size in the experimental garden	
Fixed factors	F	P	F	P	F	P	F	P	F	P
Treatment	$266.00_{3,80.9}$	<0.001	$0.49_{3,60.2}$	0.689	$1.24_{3,272}$	0.294	$0.05_{3,34.0}$	0.984	$49.65_{3,44.7}$	<0.001
Plant height	$-1.27_{1,55.0}$	0.265	$+0.48_{1,46.5}$	0.494	$-0.24_{1,272}$	0.626	$-1.22_{1,17.5}$	0.285	$0.00_{1,29.0}$	0.987
No inflorescences	$+2.35_{1,55.2}$	0.131	$+6.08_{1,56.2}$	0.017	$-0.02_{1,272}$	0.896	$+0.62_{1,37.9}$	0.436	$-0.88_{1,29.0}$	0.355
Receptacle size	$+9.22_{1,55.2}$	0.004	$+0.03_{1,28.9}$	0.870	$+0.00_{1,272}$	0.983	$-0.00_{1,24.9}$	0.994	$-2.69_{1,30.0}$	0.112
Mean fruit mass	–		$-1.53_{1,101.1}$	0.220	$+0.63_{1,272}$	0.428	$+6.50_{1,28.3}$	0.016	$+39.21_{1,176}$	<0.001
Random factors	Z	P	Z	P	Z	P	Z	P	Z	P
Plant	5.19	<0.001	2.39	0.008	–		0.11	0.432	3.76	<0.001
Tray	–		0.72	0.236	–		–		–	
Plot					0.69	0.245	0.62	0.267	0.71	0.221
Sample size	2,124		440		280		209		184	

The Wald-type F statistic (Wald Z-statistic for random factors) is given with the degrees of freedom as a subscript and the sign indicating the direction of the effects

removed [16.1 mg $\pm$ 1.3 (least-squares mean $\pm$ SE), $n = 274$] were significantly lighter than the outermost fruits of inflorescences where inner flowers were removed (19.8 mg $\pm$ 1.3, $n = 373$; $P = 0.048$), but they were not significantly different than control fruits (17.9 mg $\pm$ 1.2, $n = 204$; $P = 0.294$).

Germination in the Phytotron was positively influenced by the number of inflorescences of maternal plants (Table 3) but not by treatment (Fig. 4b; Table 3). Germination in the experimental garden was not significantly influenced by treatment (Fig. 4c; Table 3). Maternal traits, such as plant height, number of inflorescences, and receptacle size, did not influence germination in the experimental garden (Table 3).

Seedling survival was positively influenced only by mean fruit mass (Table 3), but not by flower removal treatment or by maternal traits (Fig. 4d; Table 3). The seedling size index was affected by the flower removal treatment (Fig. 4e; Table 3) and by maternal plant (Table 3). Control seedlings from inner seeds tended to be larger than those from outer seeds (Fig. 4e). In addition, the seedling size index was positively influenced by mean fruit mass and negatively by receptacle size (Table 3). The plot did not affect response variables in the experimental garden (Table 3).

Discussion

Resource competition versus architectural effect

Flower removal produced an increase in the size of the remaining fruits, suggesting that competition for resources is one of the causes of the observed position effect.

The mechanism underlying resource competition within capitula of *T. porrifolius* probably is associated with the centripetal pattern of floral initiation, which gives outer flowers earlier access to resources. Previous studies provide sound evidence for resource preemption by the earlier, outer flowers in capitula (Steer et al. 1988; Charlet and Miller 1993; Alkio et al. 2003). In addition, experimental manipulations of the source–sink ratio conclude that resource limitation is a major determinant of fruit mass in all parts of the capitula (Steer et al. 1988; Alkio et al. 2003).

Our comparison of the outermost fruits in the 'inner flowers removed' and 'outer flowers removed' treatments further indicated an architectural effect. First, these fruits differed in size (inner flowers removed > outer flowers removed) despite being in the same relative outermost position, which strongly suggests an influence of absolute position on fruit mass. Second, support for the insufficiency of resource competition as the only factor influencing fruit size comes from the fact that the number and proportion of removed flowers in the 'outer flowers removed' treatment were significantly larger than those in the 'inner flowers removed' treatment (Table 1), i.e., there was a higher flower/fruit competition in the 'inner flowers removed' than in the 'outer flowers removed' treatment. It has been suggested that the vasculature of inflorescences may regulate intra-inflorescence variation in fruit size (Wyatt 1982; Wolfe 1992; Diggle 2003). Vascular bundles originating from the stem run radially towards the periphery of the capitulum and back, and the central part of the receptacle is almost devoid of vascular bundles (Goffner et al. 1988). However, empty central fruits are structurally and functionally connected to the vascular system of the receptacle (Alkio and Grimm 2003), although generally deprived of

photoassimilate import (Alkio et al. 2002). Hence, some physiological constraint could restrict fruit size in the inner positions, but the proximate mechanism of architectural effects remains uncertain.

To the best of our knowledge, our results represent the first *experimental* evidence supporting both resource competition and architectural effects on fruit size decline within an inflorescence. Although fruit size and/or fruit set declines have been shown in several species in earlier studies (reviewed in Diggle 2003), these were attributed either to competition for resources (Medrano et al. 2000; Vallius 2000; Kliber and Eckert 2004) or to architectural constraints (Byrne and Mazer 1990; Wolfe and Denton 2001; Guitián et al. 2001). Very likely, the relative importance of architectural constraints and resource competition is species- or even trait-specific (Ashman 1992; Wolfe 1992; Diggle 1997; Ashman and Hitchens 2000; Kliber and Eckert 2004).

Our study adds generality to the effects of flower position on fruit size by experimentally confirming it for a kind of inflorescence that is developmentally equivalent (Burtt 1977), but with a 'flat' architecture. Most previous studies on positional effects have focused on linear inflorescences with indeterminate growth (Byrne and Mazer 1990; Vaughton 1993; Vallius 2000; Guitián et al. 2001; Kudo et al. 2001; Wolfe and Denton 2001; Zeng et al. 2008). Nevertheless, a note of caution is needed concerning the generality of a bottom-up/outer-inner position effect. Wesselingh and Arnold (2003) showed a top-down position effect in a linear inflorescence with determinate growth. Apical dominance could cause position effects in inflorescences with determinate growth (Wesselingh and Arnold 2003). Exploration of position effects on a diversity of inflorescence architectures promises to be rewarding in broadening our current understanding of position effects on fruit set and size.

Fitness consequences of position effects

We found inconsistent effects of flower position on different fitness components. Our study showed a positive influence of flower position on fruit size, although it failed to show a relationship between flower position and seedling emergence and growth. We suggest two different reasons for this unexpected lack of match between position, fruit mass, and seedling emergence and growth: (1) the experimental conditions and (2) a lack of direct causal relationship between position and seedling traits. In terms of experimental conditions, the growth conditions in our Phytotron and experimental garden could have not been harsh enough to produce differences in seedling traits despite the large differences in fruit size (Gross 1984; Stanton 1984; Imbert et al. 1997). For example initial differences between fruits may disappear when plants are growing without competition (e.g., *Galinsoga parviflora*, Rai and Tripathi 1987; *Crepis sancta*, Imbert et al. 1997; *Catanache lutea*, Ruiz de Clavijo and Jiménez 1998). This aspect could have been particularly important in the Phytotron test because germination in the experimental garden showed a trend in the expected direction.

The lack of relationship between flower position and seedling traits can also be understood by distinguishing direct from indirect effects of flower position. In our experiments, flower position influenced fruit mass, whereas fruit mass showed a positive influence on seedling survival and seedling size in one of our two tests (Tables 2, 3). Similar results have been found for other species when position and seed size were considered explicitly (*Tragopogon pratensis*, Van Mölken et al. 2005; *Alliaria petiolata*, Susko and Lovett-Doust 2000). Thus, a lack of significance of the factor 'flower position' (i.e., lack of *direct* effects) does not deny *indirect* fitness consequences of position effects (interflower competition and/or architectural constraints). This indirect effect is brought about through their influence on fruit size, since commonly larger seeds produce more vigorous seedlings than smaller ones (Allsop and Stock 1995; Leishman et al. 2000), particularly in harsher growing conditions (Rai and Tripathi 1987; Imbert et al. 1997).

Accumulated evidence indicates that position effects are rather common in plants and not only influence fitness components at the fruiting stage (fruit size or fruit set), but also at earlier stages (ovule and/or pollen number) (Ashman and Hitchens 2000; Kliber and Eckert 2004; Hiraga and Sakai 2007; Zeng et al. 2008; Diggle 2003 for a review). We suggest that these effects on fitness can have evolutionary consequences. If flowers in some positions are consistently prevented from producing fruits, optimal resource allocation could permanently switch off female function and lead to the evolution of andromonoecy (Primack and Lloyd 1980; Emms 1993). More interestingly, resource competition-mediated position effects could turn, in evolutionary time, into architectural position effects if optimization diverts resources from vascular bundles at flower positions where fruiting probability is too low. This would offer a novel view of the relationship between resource-based and architecture-based position effects. Evolution of andromonoecy in *Solanum* (Miller and Diggle 2003) gives tentative support to this intriguing possibility.

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