Allocation of reproductive resources within inflorescences of *Petrocoptis grandiflora* (Caryophyllaceae)

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Abstract: Patterns of fruit set were studied in *Petrocoptis grandiflora*, a species endemic to the northwestern Iberian Peninsula. This plant has a dichasial inflorescence in which the central flower opens first, followed by first-order lateral flowers and then second-order lateral flowers. We investigated whether flowers at different positions in the inflorescence differ in duration, ovule number, nectar production, or probability of fruit set. Our results indicate that mean duration, ovule number, nectar volume, and probability of fruit set are higher for central than for lateral flowers. Fruit set was higher for central than for first-order lateral flowers, and higher for first- than for second-order lateral flowers. To investigate the effects of loss of the central flower, selected inflorescences were manually "decentred." For lateral flowers, analysis of variance indicated that fruit set was affected both by flower position in the inflorescence and by decentring. However, neither total inflorescence fruit set nor mean duration of flowers in the inflorescence differed significantly between decentred and untreated inflorescences. These results suggest that the observed pattern of fruit set in this species is a result of within-inflorescence competition for the limited amount of resources available for fruit production, and that these resources may be redistributed in response to damage to flowers within the inflorescence. Inflorescences of *P. grandiflora* can thus be considered to act as semi-autonomous units with regard to resource allocation.

Key words: inflorescences, fruit set, resource allocation, *Petrocoptis grandiflora*.

Résumé : Les auteurs ont étudié les patrons de mise à fruit chez le *Petrocoptis grandiflora*, une espèce endémique du nord-ouest de la péninsule ibérique. Cette plante possède une inflorescence dichasiale dans laquelle la fleur centrale s'ouvre en premier, suivie par les fleurs latérales de premier ordre, et ensuite des fleurs latérales de second ordre. Les auteurs ont cherché à déterminer si les fleurs occupant différentes positions dans l'inflorescence sont différentes quant à la durée, le nombre d'ovules, la production de nectar et la probabilité de formation d'un fruit. Les résultats montrent que la durée moyenne, le nombre d'ovules, le volume de nectar et la probabilité de mise à fruit sont plus élevés chez les fleurs centrales que chez les fleurs latérales. La mise à fruit est plus importante chez les fleurs centrales que chez les fleurs latérales de premier ordre, et plus élevée chez des dernières que chez les fleurs latérales de second ordre. Afin d'étudier l'influence de la perte des fleurs centrales, les auteurs ont manuellement "décentré" des inflorescences sélectionnées. L'analyse de variance montre que chez les fleurs latérales, la mise à fruit est affectée à la fois par la position florale dans l'inflorescence et par le décentrage. Cependant, ni la mise à fruit totale de l'inflorescence ni la durée moyenne des fleurs de l'inflorescence ne montrent de différences significatives entre les fleurs décentrées ou non traitées. Ces résultats suggèrent que le patron de mise à fruit observé chez cette espèce résulte d'une compétition à l'intérieur de l'inflorescence pour une quantité limité de ressources disponibles pour la production de fruits, et que ces ressources peuvent être redistribuées en réaction aux dommages causés aux fleurs de l'inflorescence. On peut ainsi considérer les inflorescences du *Petrocoptis grandiflora* comme des unités semi-autonomes pour ce qui est de l'allocation des ressources.

Mots clés : inflorescences, mise à fruit, allocation des ressources, *Petrocoptis grandiflora*.
[Traduit par la rédaction]

Introduction

The aggregation of flowers into inflorescences is a common characteristic of plants and has important functional implications (Wilson and Price 1977; Stephenson 1979, 1980, 1981; Pyke 1981; Wyatt 1980, 1982; Watson and Casper 1984; Holtsford 1985; Stephenson and Winsor 1986; Cruzan et al. 1988; Schoen and Dubuc 1990). In particular, the role played by a flower may differ according to its position within the inflorescence, and flowers within the same inflorescence may have different probabilities of reproductive success (Stephenson 1981; Lee 1988). In many species, early-opening flowers have a higher probability of setting fruit than late-opening flowers (but see Goldingay and Whelan 1993), which implies that the plant allocates more resources to early flowers (see Ashman and Baker 1992 and references therein). In addition to such temporal advantages, there may also be spatial advantages: in some species, proximal flowers have

a higher probability of setting fruit than more distal flowers, and this may be related to preferential access to nutrients. Alternatively, flowers at different positions may show clear morphological differences: in a number of species, for example, distal flowers have more ovules than proximal flowers (see Lloyd 1980; Lloyd et al. 1980; Vaughton 1993; Diggle 1995). Spatial and temporal advantages of this type may be relevant among flowers in the same inflorescence or among inflorescences (Lee 1988; Solomon 1988; Devlin 1989; Herrera 1991; Stephenson 1992; Ehrlén 1993; Guitián 1993; Vaughton 1993). It should be stressed that the two types of advantage are often difficult to disentangle, in that the most proximal flowers in the inflorescences of many plant species are also the earliest to open.

In a classic study, Watson and Casper (1984) suggested the term "Integrated Physiological Units" (IPUs) for those plant structures within which resource allocation is to some extent autonomously controlled. On this model, inflorescences that act as reproductive IPUs would be expected to modify their pattern of fruit set (i.e., redistribute resources) in response to extrinsic disturbances such as floral herbivory.

The aim of the present study was to investigate patterns of fruit production in inflorescences of *Petrocoptis grandiflora* (Caryophyllaceae), and to answer three specific questions. First, is fruit set (and thus resource capture) affected by the position of the flower within the inflorescence? Second, are such patterns of fruit set affected by disturbance as removal of that inflorescence's central flower? Third, do inflorescences that open at different times in the flowering season differ in the amount of resources received? To investigate these questions, we monitored duration, nectar production, fruit set, and seed set of flowers of inflorescences subjected to different treatments and of inflorescences opening at different times in the flowering season. We assumed that fruit set at the inflorescence level is a reliable measure of the amount of resources invested by the plant in that inflorescence (see Stephenson 1981; Stephenson and Winsor 1986; Herrera 1991; Ashman and Baker 1992; Guitián 1994).

Plant and study area

Petrocoptis grandiflora Rothmaler (Caryophyllaceae) is a perennial herb with opposite leaves and pentamerous flowers in terminal dichotomous cymes (dichasia: see Weberling 1965 for details of inflorescence typology). These dichasia may be compound (i.e., a central flower, two first-order lateral flowers, and four second-order lateral flowers) or simple (i.e., a central flower and two lateral flowers). A continuum of simple–compound intermediates also occurs; mean number of flowers per inflorescence is 5 (n = 329; standard deviation = 2). The calyx is approximately 10–14 mm long. The corolla consists of five entire, bright purple petals 5–15 mm long. The principal pollinator is the long-tongued bee *Anthophora acervorum* L. (Anthophoridae, Hymenoptera). Mean floral duration is 4 days, and mean fruit set in the study populations in 1992 was 55%. Supplementary pollination does not increase fruit-set (Guitián et al. 1994).

Petrocoptis grandiflora is of particular interest as a model for studies of inflorescence level fruit set control, since it bears inflorescences in which distal flowers open earlier than proximal flowers. Furthermore, plants in our study populations are often severely affected by floral herbivory (largely by juveniles of the snail *Helix aspersa*).

The study was carried out in the El Bierzo region of north-western Spain, in an area with a mosaic of habitats including cultivated land, small villages, limestone crags, holm oak woodland (*Quercus rotundifolia*, *Arbutus unedo*, and *Quercus suber*) and Mediterranean-type scrub communities dominated by *Cistus ladanifer* on siliceous soils or *Cytisus* and spiny Rosaceae on calcareous soils. Two populations of *P. grandiflora*, both situated on limestone rockfaces, were selected for study. For additional information about the study area see Guitián and Sánchez (1992).

Methods

All experiments were carried out in 1992. A total of 107 flowers (n = 22 inflorescences; 22 plants) at different positions within the inflorescence were marked with plastic labels and subsequently monitored every day for 70 days to determine possible variations in flower duration caused by position within the inflorescence. Simultaneously, we extracted and measured nectar with a capillary micropipette from central and first- and second-order lateral flowers, before the onset of pollinator activity (06:00 GMT), and determined sugar concentration immediately with a portable refractometer. To determine whether there were differences in fruit set depending on the positon of the flower within the inflorescence, we marked 319 flowers (n = 69 inflorescences) at different positions within the inflorescence and monitored these flowers until fruiting. To investigate variation in ovule number, flowers (10 from each position) were cut just before anthesis, and ovules were counted under a dissecting microscope.

To investigate the effect of removal of the central flower on fruit set by first- and second-order lateral flowers of that inflorescence, we manually removed the central flowers from 15 inflorescences on 15 plants. Another 15 inflorescences on 15 different plants were monitored as controls. For both groups of inflorescences (decentred and controls), duration and fruit set of flowers at different positions were compared. Fruit set in decentred inflorescences was calculated with respect to number of flowers remaining after removal of the central flower.

Possible effects of inflorescence phenology on flower duration, fruit set and seed set were investigated following definition of three opening subperiods (early, week 1 or 2; intermediate, week 3 or 4; late, week 5 or 6; note that the plants used in this part of the study had synchronous flowering phenology, so that the subperiods defined are of the plant, not the population, flowering period. Note also that second-order lateral flowers were not observed on any of the inflorescences which opened in the early subperiod.

The effects of position in the inflorescence (position) and decentring (treatment) on flower duration and fruit set were investigated by two-way analysis of variance (ANOVA). The effects of position and of inflorescence phenology (opening subperiod) on fruit set and seed set were investigated by analysis of covariance with opening subperiod as covariate. Fruit set percentage data were subjected to an arcsine transformation before analysis of variance. All analyses were carried out with the statistical package SYSTAT (SYSTAT 1992).
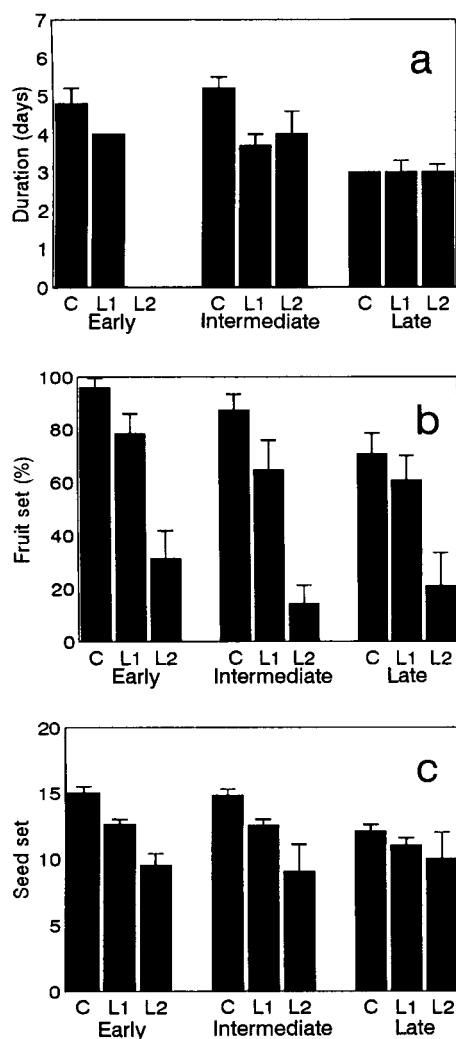
Results

The flowers of an inflorescence do not open simultaneously; the first to open is the central flower, followed by first-order lateral flowers and finally second-order lateral flowers. The duration of central flowers was greater than that of lateral flowers. The nectar volume of central and lateral flowers also differed. Fruit set varied according to position in the inflorescence (Table 1). The mean number of ovules per flower was 21.2 ± 2.0 for central flowers, 19.4 ± 2.3 for first-order lateral flowers and 16.5 ± 1.8 for second-order lateral flowers ($F_{2,27}$ = 13, p < 0.0001).

Table 1. Mean values ($x \pm$ SD) for duration (days), total nectar production (mg of sugar), and fruit set (%) of *P. grandiflora* flowers at different positions in the inflorescence (untreated inflorescences).

Flower position	Duration (n)	Sugar (n)	Fruit set (n)
Central	5 ± 2 (34)	0.30 ± 0.16 (40)	98.5 ± 12.0 (69)
First-order lateral	4 ± 1 (37)	0.15 ± 0.09 (59)	71.4 ± 38.5 (123)
Second-order lateral	3 ± 1 (36)	0.11 ± 0.05 (27)	42.9 ± 40.8 (127)
F (ANOVA)	42.7***	26.8***	39.7***

Note: Fruit set percentages were calculated for each flower type in each inflorescence; the value shown is the mean for all inflorescences. Percentages were subjected to an arcsine transformation before analysis of variance. ***, $p < 0.001$.

Fig. 1. (*a*) Mean duration of central (C), first-order lateral (L1), and second-order lateral (L2) *P. grandiflora* flowers opening at different times (early, intermediate, or late; see text). (*b*) Mean fruit set by central, first-order lateral, and second-order lateral *P. grandiflora* flowers opening at different times. (*c*) Mean seed set by central, first-order lateral, and second-order lateral *P. grandiflora* flowers opening at different times. Bars show standard errors of the mean. All data are for untreated inflorescences.

Table 2. Results of analysis of variance in fruit set and duration of *P. grandiflora* flowers, with the factors position (central, first-order lateral, or second-order lateral) and treatment (decentring or no treatment).

Source	SS	df	F ratio	p
Fruit set (%)				
Treatment	5.21	1	13.720	0.0003
Position	2.90	1	7.652	0.0065
Treat × position	0.18	1	0.467	0.4955
Error	49.74	131		
Duration (days)				
Treatment	6.55	1	2.481	0.118
Position	7.72	1	2.928	0.089
Treat × position	0.92	1	0.348	0.556
Error	345.80	131		

significant effects on flower duration. However, both factors had significant effects on fruit set (Table 2). The interaction position × treatment had no significant effect on fruit set, indicating that first- and second-order lateral flowers do not differ in their response to inflorescence decentring.

Total fruit set did not differ significantly between decentred and untreated inflorescences ($F_{1,28} = 1.8$, n.s.) (see Table 3).

Flower duration declined as the flowering period progressed. Averaged over all inflorescence positions, early flowers lasted 5 ± 2 days, intermediate flowers 4 ± 1 days, and late flowers 3 ± 1 days (Fig. 1).

Analysis of covariance with the position factor and the covariate opening subperiod (early, intermediate, or late) indicated that opening subperiod is a significant source of variance only in flower duration, and that position is a significant source of variance in flower duration, fruit set, and seed set, even when the effect of opening subperiod is accounted for (Table 4). Fruit set was higher for central flowers than for first-order lateral flowers, and higher for first- than for second-order lateral flowers; as can be seen from Fig. 1, this ranking order was maintained when early, intermediate, and late inflorescences were considered separately.

Comparison of flowers in inflorescences subjected to decentring and flowers in the corresponding control inflorescences indicated that neither position nor treatment had

Discussion

The opening sequence of *P. grandiflora* inflorescences starts with the central flower and continues with the first- and then the second-order lateral flowers. Our observations indicate that central flowers have higher fruit set than lateral flowers.

Table 3. Mean values ($x \pm$ SD) for duration and percentage fruit set of first- and second-order lateral flowers and of the whole inflorescence, for untreated and decentred inflorescences of *P. grandiflora*.

	Untreated inflorescences	Decentred inflorescences
Duration (days)		
First-order lateral	4 ± 1	4 ± 2 ($n = 30$)
Second-order lateral	3 ± 1	4 ± 2 ($n = 52$)
Whole inflorescence	4 ± 2 ($n = 15$)	4 ± 2 ($n = 15$)
Fruit set (%)		
First-order lateral	71.4 ± 38.5	93.8 ± 16.5 ($n = 30$)
Second-order lateral	42.9 ± 40.8	78.8 ± 30.0 ($n = 52$)
Whole inflorescence	74.2 ± 39.0 ($n = 15$)	85.1 ± 27.0 ($n = 15$)

Note: Fruit set percentages were calculated as described for Table 1. Note that whole-inflorescence values refer to all flower types for untreated inflorescences, but only to lateral flowers for decentred inflorescences. Data for central flowers in untreated inflorescences are listed in Table 1.

Table 4. Results of analysis of covariance in duration, fruit set, and seed set of *P. grandiflora* flowers, with the position factor (central, first-order lateral, or second-order lateral) and the covariate opening subperiod (early, intermediate, or late).

	Source	SS	df	F	p
Duration (days)	Position	17.15	2	5.6	0.0046
	Subperiod	25.45	2	16.7	0.0001
	Error	187.21	123		
Fruit set (%)	Position	51 695.79	2	33.4	0.0000
	Subperiod	6 095.08	2	3.8	0.0942
	Error	74 245.21	96		
Seed set (%)	Position	777.35	2	24.9	0.0000
	Subperiod	322.78	2	3.6	0.0877
	Error	6 609.27	423		

This phenomenon, previously reported for plants with similar inflorescences (see Muñoz and Devesa 1987; Herrera 1991), has been interpreted as an indication that the mobilization of resources for fruit production occurs largely after pollination (Stephenson 1981). According to this hypothesis, the first flowers to be pollinated subsequently receive the most resources for fruit production and therefore make a greater contribution to female reproductive success.

Our results also show that central flowers have more ovules than lateral flowers, indicating that a priori investment differs among flowers of the same inflorescence. In a recent review, Diggle (1995) pointed out that systematic variations in organ size or number among flowers at different positions in an inflorescence may be 'architectural effects'; whether the observed variation implies differences in resource allocation, and if so whether these differences are fixed or can be adjusted by the plant, are separate questions.

In addition, removal of the central flowers of an inflorescence led to increased fruit set by the lateral flowers of that inflorescence. This suggests that, in response to loss of the central flower (as a result of snail herbivory, for example), the inflorescence compensates by reallocating resources to lateral flowers. Similar results have been obtained with other species (e.g., Herrera 1991). A proportion of the lateral flowers in *P. grandiflora* inflorescences can thus be consid-

ered to be "reserve flowers" that set fruit only when the central flower is prevented from doing so (i.e., they act as "reproductive insurance;" see Lee and Bazzaz 1982; Holtsford 1985; Ehrlén 1993; Guitián 1993; Vaughton 1993). Overall fruit set of plants with decentred inflorescences did not differ significantly from that of control plants, indicating that fruit set is limited by some factor other than the number of available ovaries, and suggesting that interovary competition for limited maternal resources occurs within inflorescences (Stephenson 1979, 1981; Holtsford 1985; Ehrlén 1993; Vaughton 1993). Similar conclusions were reached by Wyatt (1980) in a study of within-inflorescence variation in fruit set in *Asclepias tuberosa* and by Herrera (1991) in a study of *Lavandula stoechas*. These authors suggested that early competition between ovaries has profound effects on fruit set. These results are in accordance with the Lloyd et al. (1980) hypothesis that, in plants with highly organized inflorescences in which flower arrangement causes early differences in the available resources, the potential number of fruits is restricted during ovary development.

Schoen and Dubuc (1990) have postulated that the evolution of inflorescence size and number in non-selfing plants (such as *P. grandiflora*) is governed by several factors. One such factor is resource distribution pattern: if resources are distributed sectorally within the plant, this will favour the evolution of numerous small inflorescences. The results of the present study are consistent with this possibility.

Our results indicate that neither inflorescence fruit set nor inflorescence seed set are affected by between-inflorescence differences in flowering phenology. In a previous study of a population of *P. grandiflora* in the El Bierzo region, we found fruit set to be independent of between-plant differences in flowering phenology (Guitián and Sánchez 1992). Thus, neither between-plant nor between-inflorescence differences in flowering phenology have relevant effects on female reproductive success in this species. That between-inflorescence differences have no affect on fruit or seed production suggests that female reproductive success is unaffected by within-season variation in resource availability (Solomon 1988; Ashman and Baker 1992).

In conclusion, our results indicate that resource allocation within inflorescences of *P. grandiflora* may be modified in

response to extrinsic disturbance (e.g., flower loss due to herbivory), suggesting that inflorescences function as semiautonomous units (sensu Watson and Casper 1984). Within each inflorescence, the pattern of fruit is a consequence of competition for the limited resources available for fruit production. Fruit set within inflorescences of *P. grandiflora* thus follows the pattern expected for a reproductive IPU in which flowers not only differ in the amount of resources received before anthesis, but in which resource allocation may be modified after anthesis in response to extrinsic disturbance (as indicated by the observed effects of removal of the central flower on fruit maturation).

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