THE EVOLUTION OF PLANT ARCHITECTURE

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ALLOCATION OF REPRODUCTIVE RESOURCES WITHIN INFLORESCENCES OF *ANTHYLLIS VULNERARIA* SUBSP. *VULGARIS* (FABACEAE)

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Abstract

The grouping of flowers in inflorescences is a common characteristic of plants and has important implications for resource distribution. It was investigated whether the position of inflorescences on plants of *Anthyllis vulneraria* subsp. *vulgaris* affects fruit set, seed weight, and/or fruit weight. *Anthyllis vulneraria* subsp. *vulgaris* is a perennial herb. Each plant comprises several independently arising flowering shoots. Each shoot bears several inflorescences which flower acropetally. The results indicate that fruit set, seed weight and fruit weight all vary significantly ($p < 0.0.5$) among inflorescences within shoots, and are in all cases higher for early-flowering than for later-flowering inflorescences of a shoot. This ranking order is not an artifact due to among-inflorescence differences in phenology, since neither fruit set, seed weight nor fruit weight differed significantly between inflorescences of the early and late subperiods of the population flowering period. These results suggest that shoots of *Anthyllis vulneraria* subsp. *vulgaris* function as semi-autonomous units in regard to resource utilization.

Introduction

Architectural effects could be responsible for fruit and seed development patterns (Diggle, 1995). In this sense, the role played by a flower in the plant's overall reproductive strategy may differ according to the position of that flower within the inflorescence, and flowers within the same inflorescence may have different reproductive "values" (Stephenson, 1981; Lee, 1988). In many species, early-opening flowers or inflorescences have a higher probability of setting fruit than late-opening flowers or inflorescences. This may for example be due to allocation of more resources during the early stages of the flowering period (see Ashman and Baker, 1992 and references therein). In addition to such temporal advantages, spatial advantages may also be relevant. In some species, proximal flowers have a higher probability of setting fruit and tend to produce heavier seeds, than more distal flowers. This may be related to preferential access to nutrients. 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, Ehrlen, 1993; Guitián, 1993; Vaughton, 1993).

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The causes and consequences of variation are central to studies in evolutionary ecology (Willson et al. 1990). In this sense, the possible effect of plant architecture on reproductive characters must constitute one central aspect of plant studies. The aim of the work reported here, is to contribute to existing knowledge about the causes that promote such variations in fruit set, fruit weight and/or seed weight. To this end, the floral biology of *Anthyllis vulneraria* subsp. *vulgaris* (Koch) Willk. (Fabaceae) was investigated with the aim of answering the following two questions. First, do fruit set, fruit weight and/or seed weight differ among plants, among shoots of the same plant and/or among inflorescences of the same shoot? Second, do inflorescences which open at different times differ in the amount of resources (for fruit and seed production) received? To investigate these questions, fruit set, fruit weight and seed weight in inflorescences at different within-plant and within-shoot positions and also in inflorescences opening at different times in the population flowering period were monitored.

The plant and the study area

Anthyllis vulneraria subsp. *vulgaris* (Koch) Willk. (Fabaceae) is a perennial herb of 15–30 cm in height. Its aerial parts consist of a variable number of shoots. The flowers are 0.7–1.2 cm long and arranged in capitate inflorescences. The base of the inflorescence is enclosed by an involucrum comprised of two multipartite foliar bracts. Each shoot may bear between 2–4 inflorescences. The capitula of a given shoot open one-by-one and acropetally. In the study area, flowering commences in mid-March and continues until July. The fruit is a monospermic legume which matures approximately two weeks after fertilization.

The principal pollinator is the long-tongued bee *Anthophora acervorum* (Anthophoridae, Hymenoptera) and insect visits are necessary for fruit production. Mean flower duration is 8 days, and mean fruit-set in the study area and study year was 65.9% ± 12.5%. Supplementary pollination with nonself pollen does not improve either fruit set, fruit weight or seed weight.

The study was carried out in Vilardesilva in the El Bierzo region of northwest Spain in an area characterized by a mosaic of habitats. The studied population was in calcareous grassland community at an altitude of about 600 m. Climate in this area is typically Mediterranean.

Methods

A. Among- and within-plant variation

In spring 1993, eight plants were marked with plastic tags and subsequently fruit set, fruit weight and seed weight for each inflorescence on each plant were determined. To keep a record of flowering order (of inflorescences on each shoot, and of shoots on each plant), indelible inks were used. On each plant, shoots were marked with blue ink if their first flower/s opened in week 1 (of the plant flowering period), with red ink if their first flower/s opened in week 2, or with yellow ink if their first flower/s opened in week 3. Shoots in each category are hereafter referred to as "early", "intermediate" or "late" shoots, respectively; all shoots fell into one or other of these categories. Within each shoot, the first inflorescence to open was marked with blue ink, the second with red ink, the third with yellow ink and the fourth (if there was a fourth) with green ink. None of the shoots studied has more than four inflorescences.

B. Seasonal variation

To account for the possible effect of flowering period on fruit set, fruit weight and seed weight, comparisons were made only between inflorescences whose anthesis had taken place at about the same time (1 week); to this end, two four-week subperiods (early and late) were defined. During the first half of April 1993, all 87 inflorescences of four plants (hereinafter referred to as "early plants") which were about to commence anthesis were marked. A month later, all 77 inflorescences of another four plants (hereafter referred to as "late plants") which were likewise about to commence anthesis were marked.

C. Data analysis

To investigate whether fruit-set, seed weight and/or fruit weight varied significantly among inflorescences within each shoot (hereafter referred to as *inflorescence flowering rank*), shoots within each plant (hereinafter referred to as *shoot flowering rank*) or plants, MGLH nested analysis of variance was used. To analyze the *plant* effect, the "shoots within each plant" MS was utilized as error term, while to analyze *shoots flowering rank* effect, the "inflorescences within each shoot" MS was utilized as error term. Percentage fruit-set data were first subjected to an arc-sine transformation. All statistical analyses were performed with the statistical package SYSTAT (Systat Inc., 1992).

Results

A. Among- and within-plant variation

In nested analysis of variance, neither the factor *plant* nor the factor *shoot flowering rank* had significant effects on fruit-set, fruit weight or seed weight (Table 1). However, the factor *inflorescence flowering rank* had significant effects on fruit set ($F = 16.2$, $p < 0.001$), fruit weight ($F = 750.5$, $p < 0.001$) and seed weight ($F = 501$, $p < 0.001$) (Fig. 1).

TABLE 1. Results of nested analysis of variance to investigate the effect of the factors *plant*, *shoot flowering rank* (*plant*) and *inflorescence flowering rank* (*shoot flowering rank*) on fruit set level, fruit weight and seed weight.

Factor	Fruit-set			Fruit weight			Seed weight		
	F	d.f.	p	F	d.f.	p	F	d.f.	p
Plant	0.03	7	n.s.	0.51	7	n.s.	0.91	7	n.s.
Shoot (plant)	0.12	17	n.s.	0.05	17	n.s.	0.05	17	n.s.
Inflorescence (shoot)	16.23	8	0.000	750.5	8	0.000	501	8	0.000

B. Seasonal variation

Early and late plants did not differ significantly in either inflorescence fruit set ($F = 0.4$, $p > 0.05$), fruit weight ($F = 0.2$, $p > 0.05$) or seed weight ($F = 0.1$, $p > 0.05$) (Fig. 2).

Discussion

The results for *Anthyllis vulneraria* subsp. *vulgaris* show that inflorescence fruit-set level, mean fruit weight and mean seed weight were all affected by the inflorescence's position in the flowering order for that shoot. On the same shoot,
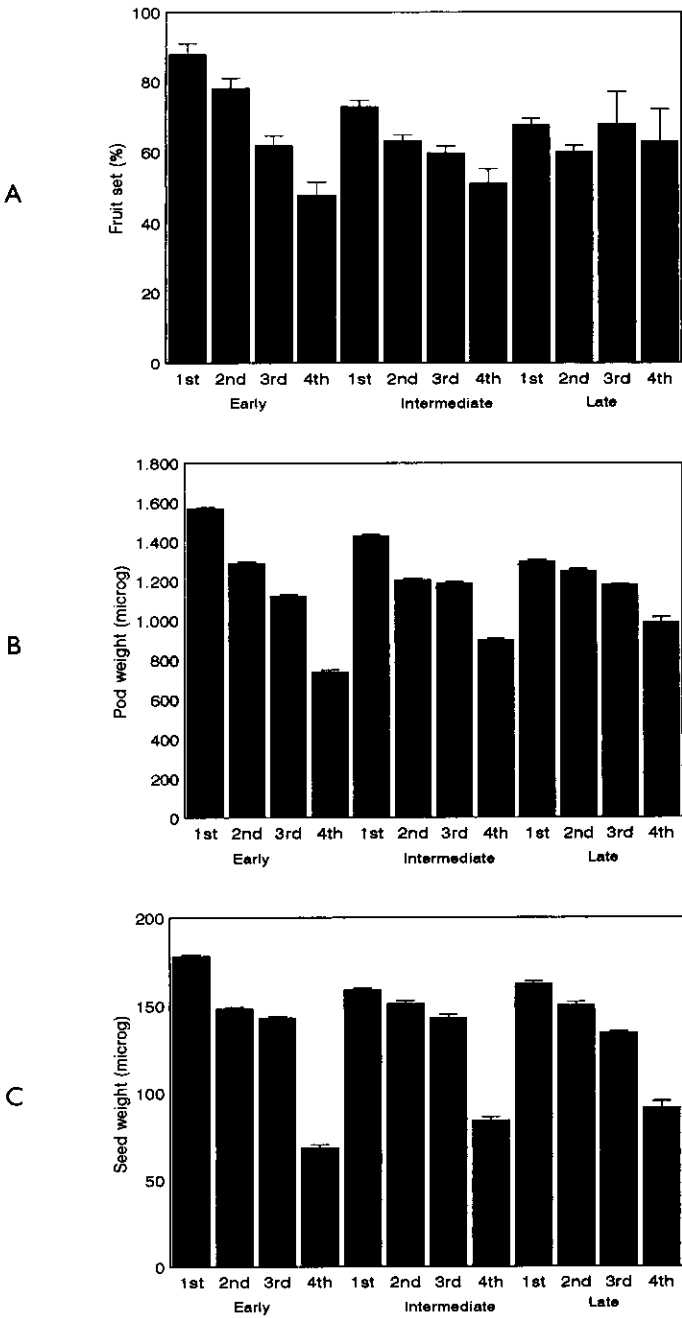
FIG. 1. Mean fruit-set level (**A**), fruit weight (**B**) and seed weight (**C**) for inflorescence (flowering rank 1–4) of early, intermediate and late shoots of the eight plants monitored in spring 1993. Vertical bars represent standard errors
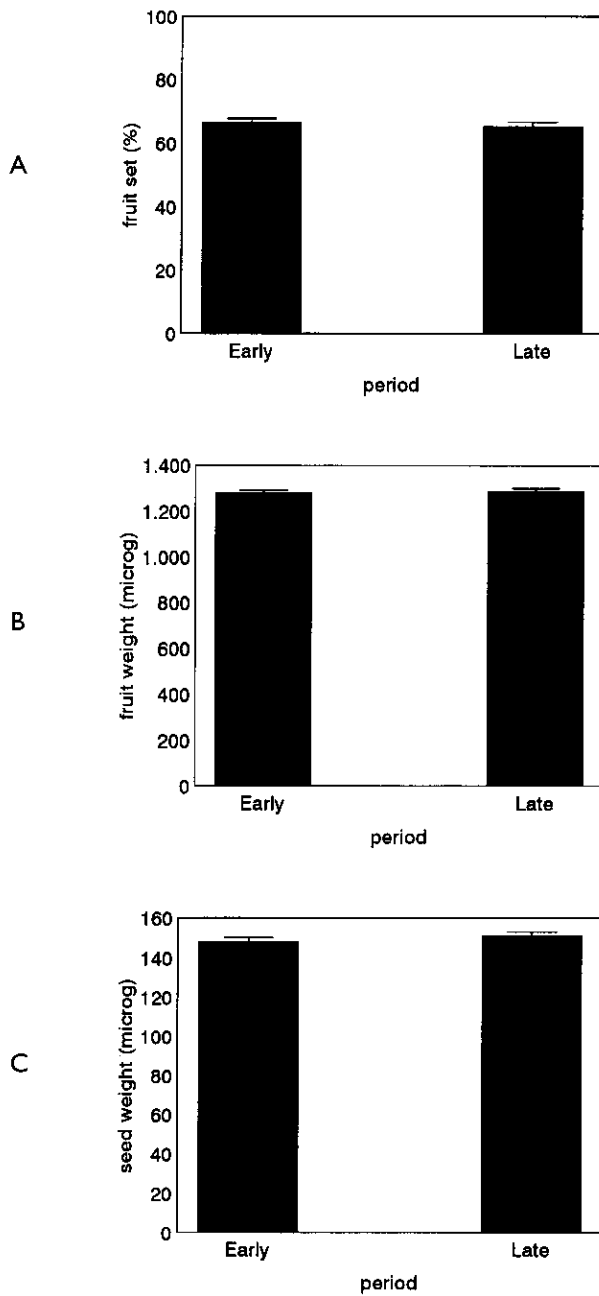
FIG. 2. Mean fruit-set (**A**), fruit weight (**B**) and seed weight (**C**) for inflorescences of the early-flowering and late-flowering plants monitored in April and May 1993 respectively. Vertical bars represent standard errors.

inflorescence mean fruit weight varied by a factor of up to two, and inflorescence mean seed weight by a factor of up to almost three (Fig. 1).

Phenology- and/or position-dependent within-plant variation in seed size and/or weight has been documented in many species. In some studies, such variation has been attributed to environmental factors affecting the whole plant. Stamp (1990), for example, observed that seed weight in *Erodium brachycarpum* flowers declined over the flowering period, and suggested that this was due to senescence as a result of declining soil water availability. Navarro (1998), in a study of *Salvia verbenaca,* observed within-plant variation in seed weight over the flowering period, and suggested that this might have been due to differences over time on pollen/pollinator availability. The results for *Anthyllis vulneraria* subsp. *vulgaris,* however, suggest that the observed within-shoot among-inflorescence differences (in fruit-set level, fruit weight and seed weight) are not due to environmental variation over the shoot flowering period. First, these variables do not differ significantly either between early- and late-flowering plants (see Fig. 2) or among shoots of the same plant (see Table 1). Second, complementary results on *Anthyllis vulneraria* subsp. *vulgaris* argue against variation in pollen receipt being the cause of the observed differences; hand-pollination of inflorescences in the study population during the 1993 flowering period did not improve fruit set, seed weight or fruit weight with respect to control inflorescences whose flowers had opened at the same time (Navarro, L., unpublished data).

These results suggest that the differences observed in reproductive variables have an architectural cause; that is, that inflorescence fruit-set level, mean fruit weight and mean seed weight are consistently higher for the proximal (early-opening) inflorescences of a shoot than for more distal (later-opening) inflorescences of the same shoot, regardless of possible variations in environmental conditions over the shoot flowering period. Similar patterns (i.e., consistently higher fruit-set levels and higher mean weight of female reproductive structures in proximal inflorescences than in more distal inflorescences) have been observed in numerous other taxa (e.g., Maun and Cavers, 1971; Hendrix, 1979; Waller, 1982; Wyatt, 1982; Nakamura, 1988; Rocha and Stephenson, 1990). Such findings have often been attributed to spatial advantages of more proximal embryos (being closer to subtending leaves) (Watson and Casper, 1984; Sage and Webster, 1987). Often, though, spatial advantages are difficult to disentangle from temporal advantages, since proximal flowers or inflorescences are frequently the earliest to open (as in *Anthyllis vulneraria* subsp. *vulgaris*). Lower fruit-set levels and seed weights in later-opening flowers have been reported for species such as *Clintonia borealis* (Galen et al., 1985) and *Petrocoptis grandiflora* (Guitián and Navarro, 1996). Such patterns may be attributable to "competition" (i.e., early-developing/proximal reproductive units sequester more resources than late-developing/distal units, on a "first-come-first-served" basis; see Stephenson, 1981; Bawa and Webb, 1984; Solomon, 1988; Lee, 1988) or to "inhibition" (i.e., early-developing reproductive units in some way inhibit the development of subsequent units). Such models are based on the assumption that the reproductive unit in question (for example, inflorescence or shoot) acts as a semiautonomous unit, in that the amount of resources allocated to each unit is fixed before fertilization (see Watson and Casper, 1984; Solomon, 1988; Ashman and Baker, 1992). The results for *Anthyllis vulneraria* subsp. *vulgaris* suggest that shoots of this species function as semi-autonomous units (*sensu* Watson and Casper, 1984) in regard to resource utilization. This study illustrates the necessity of addressing aspects of plant architecture and its consequences when investigating resource allocation.

Acknowledgements

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