

FECUNDITY ABOVE THE SPECIES LEVEL: OVULE NUMBER AND BROOD SIZE IN THE GENISTEAE (FABACEAE: PAPILIONOIDEAE)

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Per-fruit components of fecundity (ovules per ovary, seeds per fruit, seed : ovule ratio, and patterns of seed maturation within pods) were studied in 33 species of the Genisteeae, a legume tribe of mostly Mediterranean shrubs, e.g., *Cytisus*, *Ulex*, that also includes more widespread herbs such as *Lupinus*. Species identity explained most variance in both potential (ovules) and realized (seeds per fruit and seed : ovule ratio) fecundity, and although significant population-specific effects existed, these were relatively small, indicating that estimates of fecundity were not particularly prone to environment-induced changes. Average seed : ovule ratios varied between 20% (for a few species in which fixed rates of embryo abortion result into single seeded pods) and 100% (annuals), but most taxa were in the 40%–60% range. The probability that an ovule near the base of the ovary matured into a seed was significantly lower than the pod average in the majority of species. As indicated by the large size of stigmatic pollen loads, this was unlikely to result from insufficient pollination but rather from preferential embryo abortion. High abortion rates next to pod base occurred in both presumed selfers and obligate outcrossers. Evidence points to relatively stereotyped reproductive ways and high reproductive coherence in the tribe, with major departures from the norm being high seed : ovule ratios exhibited by annual *Lupinus* (associated with selfing), and low ratios shown by species with single seeded pods (associated with fixed rates of embryo abortion).

Keywords: Mediterranean, shrublands, seed-set, abortion, reproduction.

Introduction

Researchers have sometimes found evidence that a number of reproductive attributes of plants can be subject to considerable phylogenetic constraint (Herrera 1989; Eriksson and Bremer 1991, 1992; but Lord et al. 1995). Investigations on character correlation or syndromes in plants have also provided support for this view (Herrera 1992; Fischer and Chapman 1993; Jordano 1995). Relatively invariant reproductive patterns in a plant group have the potential to limit the development of coevolutionary relationships with mutualists, which makes the issue of phylogenetic constraint relevant to the debate on whether pollination and seed dispersal systems should in general be regarded as specialized or generalized (Herrera 1995; Waser et al. 1996; Waser 1998).

Most studies on group-specific reproductive patterns have focused on traits directly involved in mutualistic relationships such as flowering and fruiting phenology (Kochmer and Handel 1986; Smith-Ramirez et al. 1998) and life-form and breeding system (Renner and Ricklefs 1995; Buide et al. 1998). Fruit attributes that have an obvious bearing on seed dispersal have also been viewed in this light (e.g., Jordano 1995). Seemingly, however, morphogenetic constraints should affect *all* plant attributes, not just those regulating relationships with other organisms or the environment. The problem of focusing only on such traits when studying phylogenetic constraints is that you cannot know whether the correlation-covariance pattern that

affects this kind of attribute is weaker or stronger than overall trait covariation. In other words, there is no knowledge of the context of phylogenetic constraint affecting other plant traits.

To know how and whether common phylogeny is posing a severe constraint on the evolution of reproductive attributes, it could be useful to see how neat is the group pattern exhibited by ecologically determined characteristics relative to the group behavior regarding other traits. Suppose, for example, that we find a very distinct pattern at the family level for a given characteristic (e.g., number of ovules in the ovary) that becomes blurred or nonexistent for its environmentally determined aftermath (seed number). If this happens, the importance of phylogenetic constraints should be considered low with regard to ecological forces. Conversely, a similar pattern for both sets of traits would indicate that phylogenetic cohesion is so strong that it can indeed override environmental effects.

Biosystematists have argued that some plant organs can be more evolutionarily constrained than others. In the Leguminosae, for example, there are more morphological and functional modifications in fruits than in flowers or seeds (Polhill et al. 1981), a situation reflected in the diversification of this family. In this article, I report on how unrestrained are several components of fecundity (ovule number, seed number, seed : ovule ratios, and seed abortion patterns) that may be subject to ecological effects to varying degrees. The study group is the tribe Genisteeae (Fabaceae: Papilionoideae), a lineage with about 500 species of which ca. one-half belong to 18 genera of mainly Mediterranean shrubs (the so-called *Genista-Cytisus* complex), while the remaining are annual and perennial herbs in the genus *Lupinus* (America and Europe). Di-

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agnostic features of this tribe include a bilabiate calyx and monadelphous stamens with dimorphic anthers (Bisby 1981).

The following questions are addressed: Is there a group pattern for potential (ovules) and realized (seeds) fecundity? How variable are pod-filling patterns among taxa of this group? Do breeding systems and filling patterns correlate in some way? Answers to the latter question may contribute to the current knowledge on male gametophyte selection mechanisms and maternal screening of progeny quality in the Leguminosae (Bawa and Buckley 1989).

Study Area

Research was carried out across the western half of Andalucía (southern Spain), a region of ca. 45,000 km² that includes the two mountain ranges bordering the lower Guadalquivir River Valley and an extensive coastal area near the Atlantic Ocean. The region has a typical Mediterranean climate with dry summers and mild, rainy winters and supports a variety of sclerophyllous scrub types on sand dunes, riversides, as well as limestone and sandstone mountains. Maximum and minimum distances among any two study localities were 210 km and 19 km. Their names and the corresponding letter codes used are listed in a note to table 1.

Study Organisms

Most Genisteeae in the study area are shrubs, often spiny, which typically develop after destruction or disturbance of evergreen-oak forests. They are sometimes dominant in scrub, e.g., species of *Ulex*, but may also represent just one component of diverse, mixed formations including taxa of several

families. Genisteeae have good sprouting abilities following fire and disturbances in general, which contrasts with other co-occurring, frequent scrub components, e.g., the Cistaceae. Over the geographical scale of this study, richness of Genisteeae at a given site increased with increasing soil fertility and rainfall (Arroyo and Marañón 1990).

Most studied taxa bloom in spring, March–May (Herrera 1986; Arroyo 1990), and disperse seeds during the summer. Less frequently, autumn and winter flowering also occurs, e.g., in *Ulex* species. The mostly yellow flowers are chiefly pollinated by bees and, with few exceptions (e.g., *Retama* species), produce no nectar (Herrera 1985). Experimental hand pollinations have shown that conventional self-incompatibility is absent but, at least in shrubby taxa, some form of postzygotic barrier to inbreeding seems to exist (Rodríguez Riaño 1997; P. E. Gibbs, unpublished data). This, along with the vast numbers of flowers produced by individual plants, hundreds to thousands, results in extensive fruit abortion at early stages. Insect exclusion from flowers customarily reduces fruit production to values near zero (e.g., 0.2% in *Stauracanthus genistoides*, 0% in *Ulex minor*, and 0% in *Cytisus grandiflorus* [Herrera 1987]; 0% in *Retama sphaerocarpa* and 0% in *Cytisus striatus* [Rodríguez Riaño 1997]). Annual species of *Lupinus*, however, may set abundant fruit even inside an insect-proof greenhouse (S. Talavera, personal communication). Pod size in the studied group ranges from 5 mm long in *Genista triacanthos* to 80 mm in *Spartium junceum*. At least in some genera (*Cytisus*, *Ulex*, *Stauracanthus*), carunculate seeds are released violently from pods and may then be gathered by foraging ants (Pijl 1972; Bossard 1991; J. Herrera, personal observation).

Table 1

Between-Population Variations for the Number of Ovules in the Ovary, Seeds per Fruit, and Seed Set in Genisteeae

Species	Localities ^a	Ovules/ovary ^b			Seeds/fruit ^b			% Seed set ^b		
<i>Adenocarpus telonensis</i>	A B (150)	7.0 (0.1)	6.7 (0.1)	ns	3.5 (0.2)	4.3 (0.2)	ns	49 (3)	66 (3)	*
<i>Calicotome villosa</i>	D E (52)	9.0 (0.1)	8.9 (0.1)	ns	3.8 (0.3)	3.8 (0.3)	ns	42 (3)	43 (3)	ns
<i>Cytisus baeticus</i>	D F (52)	12.0 (0.2)	12.4 (0.2)	ns	6.2 (0.3)	5.2 (0.4)	ns	43 (3)	52 (3)	ns
<i>Cytisus grandiflorus</i>	G A (56)	13.4 (0.2)	11.8 (0.1)	*	6.2 (0.5)	3.4 (0.3)	**	47 (3)	29 (2)	*
<i>Genista cinerea</i>	K L (120)	6.0 (0.1)	5.7 (0.1)	ns	2.3 (0.1)	1.8 (0.1)	ns	40 (2)	32 (3)	ns
<i>Genista polyanthos</i>	N O (85)	7.3 (0.2)	5.9 (0.1)	*	2.5 (0.3)	1.6 (0.1)	ns	33 (3)	29 (2)	ns
<i>Genista triacanthos</i>	A B (150)	4.0 (0.1)	4.9 (0.1)	**	1.0 (0)	1.0 (0)	ns	20 (1)	16 (1)	ns
<i>Genista umbellata</i>	P Q (79)	4.9 (0.1)	4.5 (0.1)	ns	2.5 (0.1)	2.0 (0.1)	*	52 (3)	43 (3)	ns
<i>Retama monosperma</i>	T G (33)	5.8 (0.1)	5.9 (0.1)	ns	1.1 (0)	1.0 (0)	ns	20 (1)	17 (0)	ns
<i>Spartium junceum</i>	K U (95)	15.5 (0.2)	18.3 (0.2)	**	12.8 (0.3)	12.9 (0.5)	ns	83 (2)	71 (3)	ns
<i>Stauracanthus genistoides</i>	T R (38)	5.4 (0.1)	4.1 (0.1)	**	2.7 (0.2)	2.0 (0.1)	*	51 (3)	49 (3)	ns
<i>Teline liniifolia</i>	B E (51)	4.5 (0.1)	3.7 (0.1)	**	2.5 (0.1)	1.6 (0.1)	**	57 (3)	44 (2)	ns
<i>Teline mompessulana</i>	B E (51)	7.8 (0.1)	7.8 (0.1)	ns	4.1 (0.2)	2.9 (0.2)	ns	53 (3)	38 (3)	ns
<i>Ulex argenteus</i>	V W (20)	5.0 (0.1)	6.2 (0.1)	*	2.5 (0.1)	2.1 (0.1)	ns	51 (3)	34 (2)	ns
<i>Ulex australis</i>	X R (19)	5.4 (0.1)	6.3 (0.1)	*	2.3 (0.1)	2.7(0.1)	ns	43 (3)	43 (2)	ns
<i>Ulex minor</i>	Y Z (22)	6.0 (0.1)	6.4 (0.1)	ns	2.1 (0.1)	2.5 (0.2)	ns	35 (2)	39 (3)	ns

Note. Values are plant means (s.e.m.) based on five individuals per population. Significance for population means differences are also indicated (Student's *t*-test).

^a The letter codes corresponding to location are A, Valverde del Camino; B, Puerto Galis; C, Carcabuey; D, Ubrique; E, Los Barrios; F, El Coronil; G, El Rompido; H, Estepona; I, Cabra; J, Aracena; K, Los Villares; L, Atajate; M, Ojén; N, Tharsis; O, El Garrobo; P, Rute; Q, Coín; R, Hinojos; S, Olivares; T, Mazagón; U, El Burgo; V, Cartaya; W, Punta Umbría; X, Aznalcázar; Y, Almonte; Z, Asperillo; MT, Montoro. Numbers in parentheses are distances in km.

^b ns = not significant. Numbers in parentheses are s.e.m.

* $P < 0.05$.

** $P < 0.01$.

Table 2
MANOVA on Components of Fecundity for the 16
Genisteeae Species in Table 1

Variable:	Univariate statistics				
	r^2	Source	SS	df	F
Ovules/ovary	0.958	Species	4.6	15	189.1
		Population	0.2	16	5.9
		Error	0.2	128	
Seeds/fruit	0.914	Species	11.9	15	86.2
		Population	0.6	16	4.2
		Error	1.2	128	
Seed set	0.774	Species	11,322.5	15	25.72
		Population	1572.5	16	3.35
		Error	3755.9	128	
Multivariate statistics					
		Wilk's λ	F	df	
Source:					
Species		0.004	43.6	45/375	
Population		0.331	3.5	48/375	

Note. Factor population is nested under "species" in this analysis. For all F statistics shown, the significance level is <0.001 .

Methods

Fecundity

Variations in per-fruit components of fecundity were studied in 33 species representing some 70% of the Genisteeae in the area (nomenclature and species numbers follow Tutin et al. 1980; see Talavera 1999 for a more recent taxonomic account). Of these, 17 were studied in two populations and the remaining 16 only in one. Collected fruits were always near maturity and increases in size or abortion were not expected thereafter, a stage that was established unambiguously by visiting each site at least twice.

No attempt was made to obtain estimates of fruit : flower ratios (i.e., fruit set) since this would have required repeated visits to census plants. Given the distances between localities, the relatively synchronous flowering, and the number of species involved, this would have been impracticable. Moreover, fruit : flower ratios seemed to be rather low as a whole (for open pollinated flowers in natural populations: 12% in *Cytisus grandiflorus*, 5% in *Ulex parviflorus*, and 16% in *Ulex minor* on a single year [Herrera 1987]; 5% and 6% in *Retama sphaerocarpa* and 13% and 20% in *Cytisus striatus*, in two consecutive years [Rodríguez Riaño 1997]) and prone to substantial yearly variations (Rodríguez Riaño 1997). As a result, per-flower estimates of fecundity for a few individuals per population in a single year would probably not have contributed much to establish general fertility patterns. Instead, per-fruit components, which were expected to be less subject to individual and local variations, were used throughout.

Except for the rare *Cytisus malacitanus*, of which only four plants could be located, fruits were examined from at least five randomly chosen individuals per population. Fruits were collected at random from several branches per plant and kept in separate bags until ovules and seeds were scored. Ovules

are linearly arranged inside the ovary, so that the positions (rank order relative to the style) where seeds had formed were easily noted. Ovular positions were then individually tested for significant departures from average seed set by comparing the frequency observed at that position against 95% confidence intervals of the species' mean.

In general, I censused 10 fruits per plant and a total of 50 fruits per population, although in several taxa with single seeded fruits (*R. sphaerocarpa*, *Genista haenseleri*, and *Genista triacanthos*) I examined a larger number in order to increase the sample size of low-frequency ovular positions and to compensate for empty fruits, i.e., pods that were externally normal but contained no viable seed. These were in general rare, as were those attacked by insect predators. Both types of pods have been excluded from the analysis.

Stigmatic Pollen Loads

Pollination intensity was studied in five species, including two with few-seeded fruits (*Retama monosperma* and *Ulex eriocladius*), two with an intermediate (modal for the Genisteeae) number of seeds per fruit (*Stauracanthus genistoides* and *Genista polyanthos*), and one with many-seeded fruits (*Genista falcata*). In all of these species, and after dissecting fruits to count seeds and ovules, I separated the still attached style, softened it with NaOH for a few minutes, and placed it on a slide with a drop of aniline blue. Pollen grains adhered to the stigma were then counted under UV light with a fluorescence microscope. Numbers reported represent minimum estimates, since an unknown fraction of the grains originally deposited on the stigma might have detached by the time the fruits were collected.

Data Analysis

In the analysis of among-population variability variates are plant means. Before MANOVA (PROC GLM in SAS 1990), these were either log (ovules and seeds per fruit) or arcsin (seed : ovule ratios) transformed. Further analyses of variations among taxa used fruit means as variates and, if data from >1 population per species were available, these were combined into a single sample.

Results

The studied species set abundant fruit except for *Genista hirsuta*. At population O of this species, I could gather only 66 developed pods from five plants and, of these, 44 contained aborted seeds only. At population MT (160 km away) I could collect 107 fruits from five shrubs, but 90 contained only aborted seeds. Discarding empty pods, in population O there were one seed and five undeveloped ovules per fruit on average, and the seed : ovule ratio was 17% ($n = 22$). Averages for population MT were one seed and six undeveloped ovules per fruit, and a seed : ovule ratio of 15% ($n = 17$). I judged both viable seed pod samples insufficient, and this species was omitted from the analyses below.

Table 3
Numbers of Ovules per Ovary, Seeds per Fruit, and Percent Seed Set in 32 Species of Genisteae

Species	Ovules/ovary	Seeds/fruit	Seed set	<i>n</i>
<i>Adenocarpus telonensis</i>	6.9 (0.1–11)	3.9 (0.2–39)	58 (2–40)	100
<i>Argyrolobium zanonii</i>	4.7 (0.1–18)	4.1 (0.1–26)	86 (2–20) ^b	50
<i>Calicotome villosa</i>	9.0 (0.1–10)	3.8 (0.2–53)	42 (2–53)	100
<i>Chamaespartium tridentatus</i>	5.3 (0.1–15)	2.3 (0.2–49)	44 (3–52)	50
<i>Cytisus baeticus</i>	12.2 (0.1–10)	5.7 (0.3–43)	47 (2–44)	100
<i>Cytisus fontanesii</i>	7.0 (0.1–14)	1.9 (0.1–45)	27 (2–43)	50
<i>Cytisus grandiflorus</i>	12.6 (0.1–11)	4.8 (0.3–62)	38 (2–58)	100
<i>Cytisus malacitanus</i>	7.2 (0.1–11)	2.2 (0.2–70)	31 (3–73)	45
<i>Cytisus reverchonii</i>	11.5 (0.1–8)	3.2 (0.3–57)	28 (2–58)	50
<i>Cytisus striatus</i>	9.2 (0.1–9)	4.0 (0.2–43)	45 (3–42)	50
<i>Cytisus villosus</i>	10.0 (0.2–11)	5.4 (0.3–34)	53 (2–32)	50
<i>Genista cinerea</i>	5.9 (0.1–12)	2.1 (0.1–48)	36 (2–50)	100
<i>Genista falcata</i>	22.8 (0.3–11)	9.5 (0.5–33)	42 (2–33)	50
<i>Genista haenseleri</i>	8.3 (0.1–12)	1.0 (0–0) ^a	12 (0–11)	100
<i>Genista polyanthos</i>	6.6 (0.1–20)	2.1 (0.2–71)	31 (2–63)	100
<i>Genista triacanthos</i>	4.4 (0.1–18)	1.0 (0–0) ^a	23 (1–20)	168
<i>Genista umbellata</i>	4.7 (0.1–13)	2.3 (0.1–43)	48 (2–41)	100
<i>Lupinus albus</i>	5.5 (0.1–10)	4.6 (0.1–23)	85 (3–23) ^b	59
<i>Lupinus angustifolius</i>	6.1 (0.1–9)	5.0 (0.2–24)	82 (3–22) ^b	50
<i>Lupinus hispanicus</i>	4.4 (0.1–11)	4.0 (0.1–18)	91 (2–15) ^b	60
<i>Lupinus luteus</i>	4.3 (0.1–12)	3.9 (0.1–15)	91 (2–13) ^b	50
<i>Retama monosperma</i>	5.9 (0.1–15)	1.0 (0.02–23) ^a	18 (1–38)	120
<i>Retama sphaerocarpa</i>	4.7 (0.1–14)	1.1 (0–26) ^a	23 (1–31)	100
<i>Spartium junceum</i>	16.9 (0.2–12)	12.9 (0.3–24)	77 (2–24) ^b	100
<i>Stauracanthus boivinii</i>	2.5 (0.1–24)	1.6 (0.1–45)	63 (4–42)	50
<i>Stauracanthus genistoides</i>	4.7 (0.1–20)	2.4 (0.1–47)	50 (2–42)	100
<i>Teline liniifolia</i>	4.0 (0.1–17)	2.0 (0.1–49)	49 (2–46)	120
<i>Teline mompessulana</i>	7.8 (0.1–10)	3.5 (0.2–48)	45 (2–49)	100
<i>Ulex argenteus</i>	5.6 (0.1–18)	2.3 (0.1–43)	42 (2–48)	98
<i>Ulex australis</i>	5.9 (0.1–15)	2.5 (0.1–39)	43 (2–41)	100
<i>Ulex eriocladus</i>	7.1 (0.1–8)	1.7 (0.1–58)	25 (2–58)	50
<i>Ulex minor</i>	6.2 (0.1–14)	2.3 (0.1–45)	37 (2–42)	100
Means for all taxa	7.5 (0.7–55)	3.4 (0.4–72)	47 (4–47)	

Note. Values are fruit means (s.e.m. – coefficient of variation). *n* = total number of fruits examined.

^a Values correspond to species with largely single seeded legumes.

^b Seed to ovule ratios that are unusually high (and indicative of selfing).

Variations among Populations

The numbers of ovules per ovary differed significantly among populations in eight species, but only four species showed significant variations in the number of seeds per fruit (table 1). Average seed : ovule ratios differed between conspecific populations in two species. However, population-specific variability seemed unrelated to spatial distance: e.g., conspecific plants 150 km apart might have either similar (e.g., *Adenocarpus telonensis*) or significantly different (e.g., *Genista triacanthos*) mean ovule numbers, and the same applied to populations separated 20 km or less (e.g., *Ulex* species).

A more detailed analysis (MANOVA; table 2) of between population variations, incorporating jointly all three studied fecundity components as predicted by species and population factors, indicates that species accounts for most of the overall variance, but the effect of population is still significant. The variance expressed at the population level is modest (respectively, 5%, 7%, and 13%, for ovules, seeds, and seed set; PROC VARCOMP in SAS).

Variations among Species

Mean ovule numbers (table 3) were three to 23, but most species had seven or fewer, and the frequency distribution is markedly skewed (fig. 1). In contrast, seed numbers are much more concentrated around the modal value of three and, with only two exceptions, all species had seven or fewer. Seed number was a fixed trait in two *Genista* species and the two species of *Retama*, all with single seeded fruits (although the number of ovules was far greater than one in such taxa; table 3). Yet another instance of monospermic fruits developing from several-ovuled ovaries was the abnormally infertile *G. hirsuta* (see above).

Seed sets ranged from 10% to 100%, but there was a distinct modal value ca. 50%, which is coincident with the median of the frequency distribution (fig. 1, bottom). The lowest values were found in species with single seeded fruits and the largest ones in annual *Lupinus* (table 3). Species with single seeded fruits tended to have both relatively low (ca. 20%) and constant (CV ca. 25%) seed sets. (Because the number of ovules

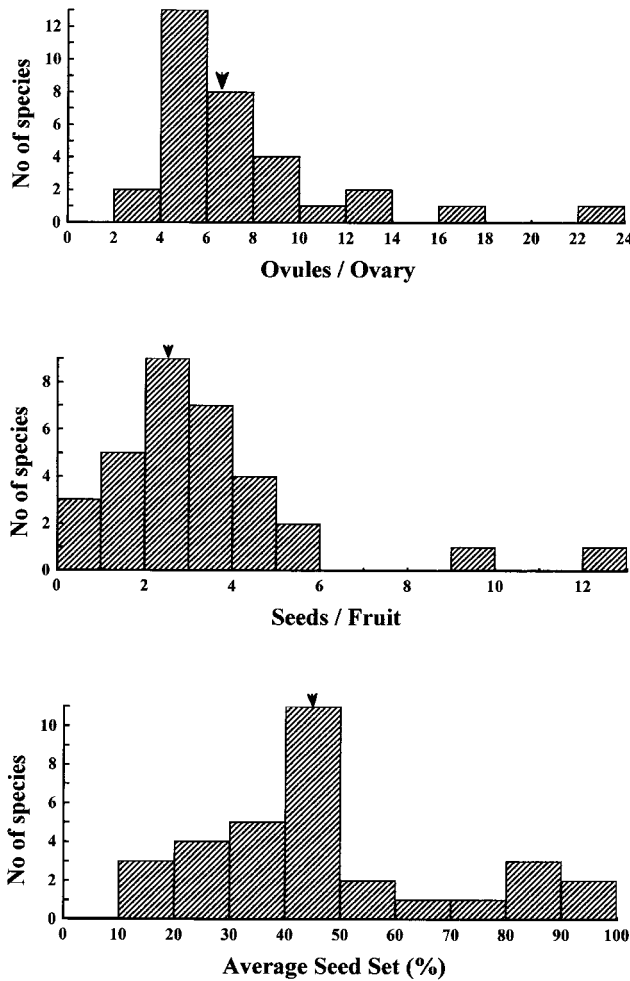


Fig. 1 Frequency distributions for components of fecundity considered in this article.

in the ovary is not fixed, some variation exists in spite of seed number being constant.) Species in which seed number is variable, however, show a distinct pattern of decreasing variability with increasing success in ovule-to-seed transformation; i.e., the larger the proportion of ovules that develop into seeds, the smaller the variation from one pod to another (Spearman rank correlation $R = -0.514$, $P < 0.01$, $n = 28$). This is likely to be, at least in part, the outcome of breeding systems that profit from self-fertilization to varying degrees: four annuals and two presumed perennial-selfers stand out with very high and constant seed sets, while the remaining taxa make up a continuum of success versus variability values (fig. 2).

Variations within the Ovary

In most species, certain ovule positions were more likely to produce mature seeds than others, and some intraovary asymmetry (i.e., at least one ovular position had a probability below or above the mean) was found in 24 species (72%). When the probability that an ovule set a seed was tested for independence against the distance (rank order) to the style, significant heterogeneity was detected in 21 (65%) of species (table 4). Most

often, the basal half of the ovary showed a lower probability of setting seeds, while the distal (stylar) half either showed a higher-than-average probability (11 species) or no significant deviation from the mean.

Usually, the probability that the basal ovule would set a seed was well below the lower 95% confidence limit of average probability (fig. 3; note that these are just examples of the more usual pattern, chosen to illustrate the fact that the trend exists regardless of ovule number, seeds per fruit, seed set, growth form, or breeding system). In addition, low probability of maturing into seed often was not restricted to the basal ovule but extended to subsequent ovules, too, with up to four rank values in *Spartium junceum* and two rank values in *G. triacanthos* (note that the former has many-seeded legumes, while in the latter these are invariably one-seeded). It is also noteworthy (fig. 3) that the filling profile of *Lupinus albus* (a presumably selfing annual) is similar to that of *Cytisus baeticus* (an outcrossing shrub).

There were few exceptions to the dominant pattern (fig. 4). In some of these, the trend to decreased seed set near the base of the pod still existed (*A. telonensis*, *Retama monosperma*), but it failed to reach statistical significance. More truly exceptional were the profiles of *Lupinus hispanicus* and *Lupinus angustifolius*, in which ovules closest to style had the lowest probability of resulting into a seed.

Pollination Intensity

Estimates of stigmatic pollen loads for five taxa (table 5) show that, in spite of stigmas being relatively small, they commonly have many pollen grains attached (often >100 in *Genista falcata*) and, invariably, in excess of the number of ovules. The ratio of pollen grains to seeds reached a maximum in the single seeded pods of *R. monosperma*. The number of pollen grains on the stigma correlated significantly with the number of seeds eventually produced by the fruit only in *Genista polyanthos* ($R = 0.295$, $P < 0.01$, $n = 87$).

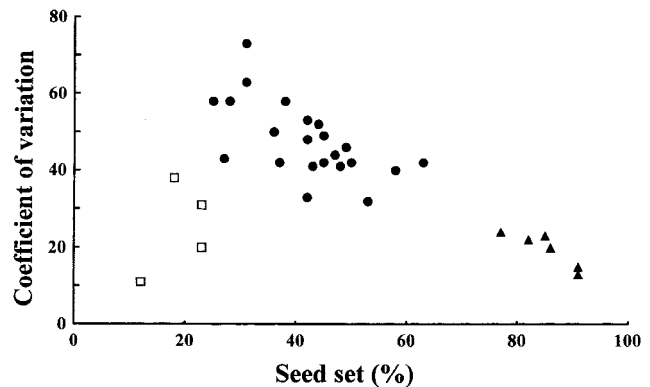


Fig. 2 The relationship between average seed sets and their corresponding coefficients of variations in 32 Genistee species. Open squares and triangles designate taxa with monospermic fruits and presumed selfers, respectively.

Table 4
Within-Ovary Patterns of Seed Production in Genisteeae

	Position × probability independence			Probability of transforming an ovule into seed relative to average ^a	
	χ^2	df	P	Stylar half	Basal half
<i>Adenocarpus telonensis</i>	6.4	6	ns	ns	ns
<i>Argyrolobium zanonii</i>	4.1	4	ns	ns	ns
<i>Calicotome villosa</i>	9.6	9	ns	ns	Lower
<i>Chamaespartium tridentatus</i>	5.7	5	ns	ns	Lower
<i>Cytisus baeticus</i>	43.1	12	***	Higher	Lower
<i>Cytisus fontanesii</i>	8.6	6	ns	ns	ns
<i>Cytisus grandiflorus</i>	16.0	12	ns	ns	Lower
<i>Cytisus malacitanus</i>	2.7	6	ns	ns	ns
<i>Cytisus reverchonii</i>	38.4	11	***	Higher	Lower
<i>Cytisus striatus</i>	3.4	8	ns	ns	ns
<i>Cytisus villosus</i>	22.0	9	**	ns	Lower
<i>Genista cinerea</i>	43.8	5	***	Higher	Lower
<i>Genista falcata</i>	37.3	23	*	Lower	Lower
<i>Genista haenseleri</i>	39.0	8	***	Higher	Lower
<i>Genista polyanthos</i>	18.5	6	**	ns	Lower
<i>Genista triacanthos</i>	34.6	4	***	Higher	Lower
<i>Genista umbellata</i>	13.0	4	**	ns	Lower
<i>Lupinus albus</i>	37.1	5	***	Higher	Lower
<i>Lupinus angustifolius</i>	48.2	5	***	High/Low	High/Low
<i>Lupinus hispanicus</i>	13.1	4	*	Lower	ns
<i>Lupinus luteus</i>	9.9	3	*	ns	Higher
<i>Retama monosperma</i>	7.0	5	ns	ns	ns
<i>Retama sphaerocarpa</i>	11.3	4	*	ns	Lower
<i>Spartium junceum</i>	109.4	18	***	Higher	Lower
<i>Stauracanthus boivinii</i>	2.0	2	ns	ns	ns
<i>Stauracanthus genistoides</i>	23.9	4	***	Higher	Lower
<i>Teline limifolia</i>	15.0	3	**	Higher	Lower
<i>Teline mompessulana</i>	38.8	7	***	Higher	Lower
<i>Ulex argenteus</i>	12.8	5	*	ns	Lower
<i>Ulex australis</i>	14.6	5	**	ns	Lower
<i>Ulex eriocladus</i>	10.3	6	ns	ns	ns
<i>Ulex minor</i>	30.6	6	***	Higher	Lower

Note. For each taxon, the positions of ovules in the ovary were tested for independence against the probability of resulting into a seed. Significance of the test indicates nonevenness in fecundity. The direction of the asymmetry (either lower or higher than average) is also indicated. ns = not significant.

^a “Higher” and “lower” mean that at least one ovular position presented a rate of seed production respectively above or below 95% confidence intervals of the mean. In a few instances (*Calicotome villosa*, *Chamaespartium tridentatus*, *Cytisus grandiflorus*), there were positions in which the probability of setting seed was significantly lower than average, but the trend was not strong enough for the position × probability independence test to detect any significant effect.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Discussion

Although related, ovule number, seeds per fruit, and seed set offer different quantitative views of the female component of plant reproduction (reviews in Lloyd 1980; Stephenson 1981; Stephenson and Bertin 1983; Primack 1987; Lee 1988; Burd 1994). Ovule number reflects a gamete packaging decision that may have consequences on the way sibling embryos are nourished and interact with each other. The seed complement of fruits, however, is determined not only by commitments derived from dispersal, development, and fertilization but also from environment-dependent factors such as polli-

nator and resource availability that are beyond direct plant control.

Population Differences in Ovule and Seed Number

If realized fecundity is more environmentally determined than potential fecundity (Burd 1994, 1995), one would expect estimates of seeds per fruit and seed set to be more variable among conspecific populations than ovule number. In the studied Genisteeae this is supported by data, with variance expressed at the population level increasing from ovule number (5%), to seed number (7%), and to seed set (13%). Furthermore, partial coefficients of determination in the MANOVA also de-

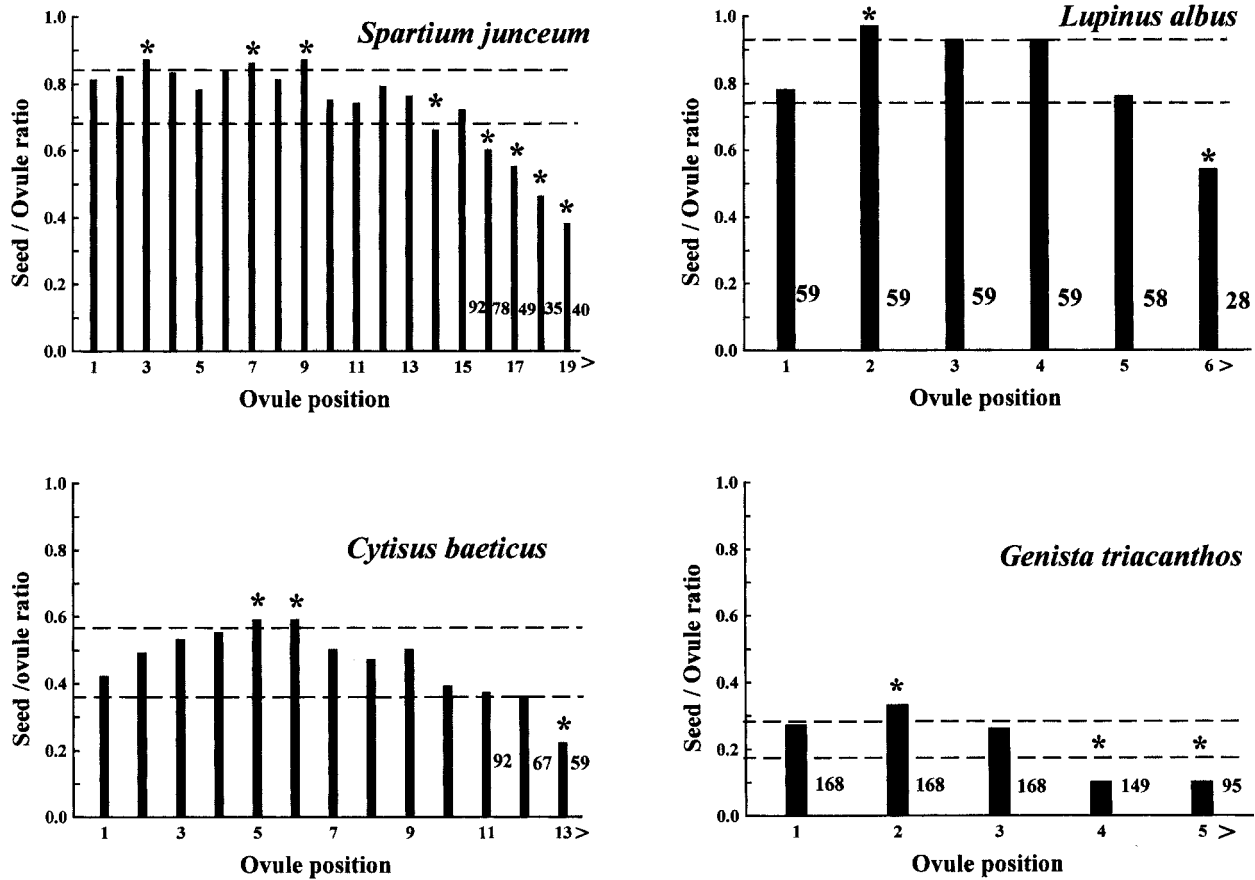


Fig. 3 The most frequent pattern of seed production inside pods of Genisteeae. Bars represent probabilities that ovules at varying distances from the style will set a seed, with lower position numbers corresponding to ovules closer to the style. Numerals by the bars are sample sizes ($n = 100$ ovules if no number is given). Horizontal dashed lines delimit 95% confidence intervals of mean seed set, and asterisks mark positions in which the probability of yielding a seed is beyond confidence limits for the corresponding sample size. For clarity, only the confidence interval for the maximum value of n is shown.

creased from ovules to seed set, indicating that the model's ability to explain observed variation solely on the basis of species and population identity decreased from ovules to seeds and seed set.

It might seem paradoxical that, given the increase in variance from ovules to seeds, only two species showed significant population differences regarding seed set, while eight did regarding ovule number. This is likely to result from a side effect of the relatively more stochastic nature of seed number and seed set compared with ovule number, namely decrease in statistical power (i.e., detecting a significant difference among two means requires a larger sample size). Thus, seed : ovule ratios often differed considerably among conspecific populations, but individual plants at each locality also varied considerably, and population means tended to remain statistically indistinguishable. Obviously, larger plant sample sizes may be needed to detect populational differences in this plant group.

Variations among Species

Components of fecundity studied here were highly species specific, as demonstrated by taxon identity accounting for

nearly 90% of the observed variance in the MANOVA. However, there existed distinct modal values for ovule number, seeds per fruit, and seed set that shape a group-specific pattern. Ovule number might be expected to show moderate variations among species and genera because of a common phylogeny, but it was to some extent surprising that the average proportion of ovules that set a seed was so often in the range 40%–60%.

I hypothesize that this results from largely stereotyped reproductive patterns within the lineage. Some or many species of this group probably have some kind of late-acting self-incompatibility (Rodríguez Riaño 1997), and one might expect them to have a mixed mating system. This would agree with both the extensive abortion of whole young fruits and also with extensive abortion of embryos inside developing pods. While accurate estimates of pod abortion are unavailable, data in this study indicate that within-pod abortion of embryos is often ca. 50% in the Genisteeae. In association with low pollination success, much lower seed sets have been reported on occasion (e.g., *Cytisus scoparius*, Parker 1997; *Cytisus multiflorus*, Rodríguez Riaño 1997), but this is not likely to be

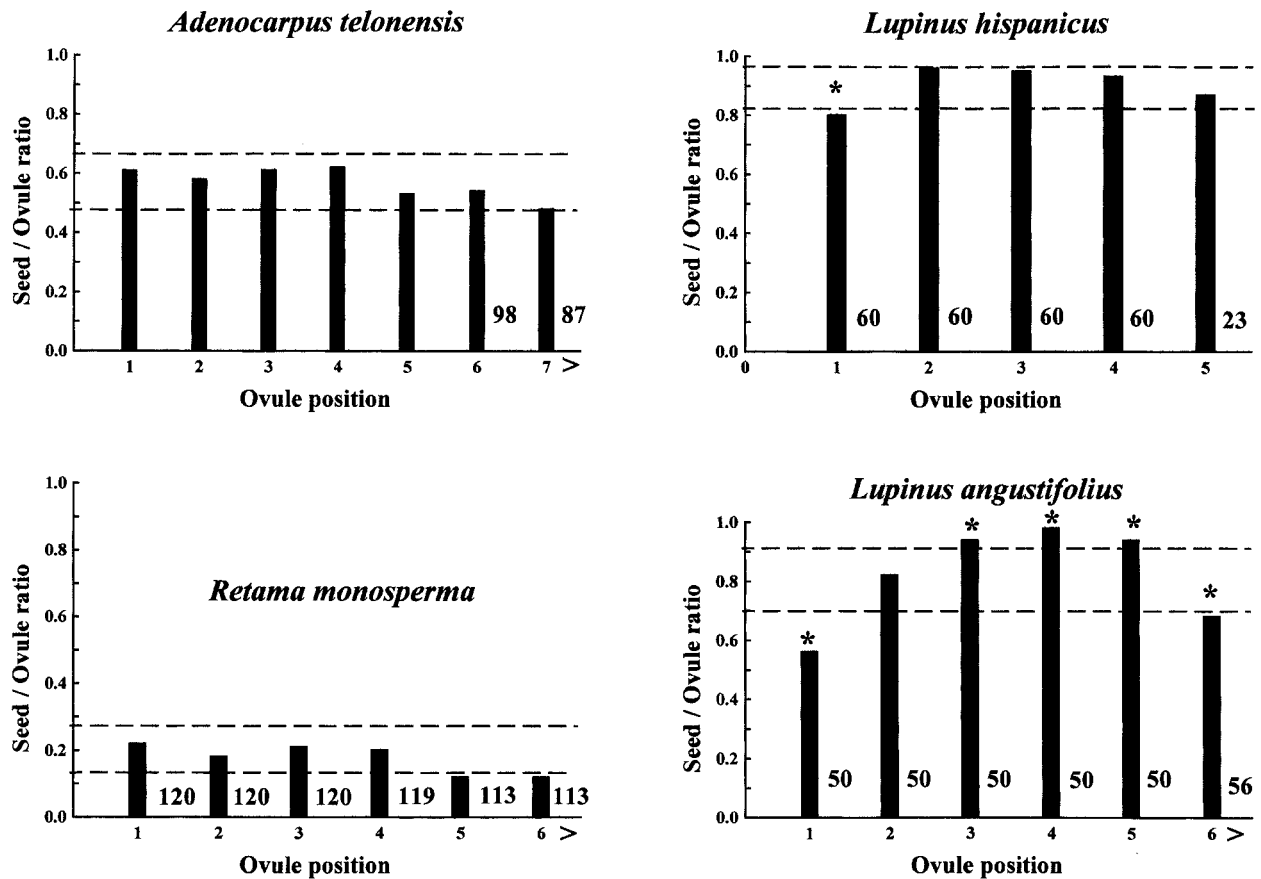


Fig. 4 Unusual filling profiles of Genisteeae pods. See fig. 3 for captions

the case in the natural populations of this study in which bee pollinators are very common. With adequate pollinator service, even naturalized populations seem to observe the 40%–60% rule (50% for *Chamaecytisus palmensis* in New Zealand; Webb and Shand 1985).

Exceptional in this regard are the low seed : ovule ratios of taxa with single seeded pods (e.g., *Genista* subgenus *Voglera* and species of *Retama*), and the unusually high values of *Argyrolobium*, *Spartium*, and *Lupinus*. Selective pressures related to seed dispersal and/or seedling establishment may result in the abortion of all embryos except one in fruits (Casper and Wiens 1981) and thus be responsible for the first anomaly. At the other extreme, *Argyrolobium*, *Spartium*, and *Lupinus* have been considered to be anomalous Genisteeae by taxonomists on morphological grounds (Bisby 1981), and it is possible, therefore, that they might differ from the other genera also in their breeding system. Specifically, the results for annual *Lupinus* are in sharp contrast with those of most other Genisteeae. Values near 90% found in this study support the notion that these taxa are largely self-compatible and have either autogamous or insect-induced self-pollination (e.g., *Lupinus palaestinus* and *Lupinus pilosus*, Pazy 1984; *Lupinus nanus*, Karoly 1992; *Lupinus bicolor*, Karoly 1994; *Lupinus texensis*, Helenurm and Schall 1996).

Position Effects within Pods

Basal ovules set seed less frequently than distal (stylar) ovules in the majority of studied Genisteeae. Since stigmatic pollen loads examined in a subset of species indicated that many more pollen grains germinated than were necessary to fertilize all ovules, this dominant, distal-skewed filling pattern is unlikely to result from insufficient pollination. Rather, it probably reflects higher embryo abortion rates at positions distant from the style, a frequent situation in the Leguminosae (Nakamura 1988; Bawa and Buckley 1989) and, in general, in plants with linearly arranged ovules (Bawa and Webb 1984).

While Lee and Bazzaz (1986) related preferential abortion of proximal (basal) embryos to resource limitations within the fruit, this has been interpreted adaptatively by Bawa and Buckley (1989) as a way to increase progeny quality through differential abortion of less vigorous embryos following a phase of intense pollen tube competition within the style. Bawa and Buckley argued that basal ovules are likely to be fathered by slow-growing microgametophytes, which in turn would result in less vigorous (and thus more prone to being aborted) progeny being produced at the base. There is supporting evidence for this phenomenon in *Phaseolus coccineus* (Rocha and Stephenson 1991a, 1991b). According to the selective hypothesis, however, basal abortion should not occur in predominantly

Table 5
Average Numbers of Pollen Grains Recorded on the Stigmas (Attached to Fruits) of Five Genistee Shrubs

Species	% Grains on the stigma			Grains/ovule	Grains/seed
	\bar{X}	s.e.m.	<i>n</i>		
<i>Genista falcata</i>	40	6	45	1.8	4.2
<i>Genista polyanthos</i>	30	4	87	4.5	14.3
<i>Retama monosperma</i>	18	4	24	3.0	18.0
<i>Stauracanthus genistoides</i>	17	1	79	3.6	7.1
<i>Ulex eriocladus</i>	27	3	48	3.8	15.9

Note. See table 3 for fruit characteristics in these taxa.

autogamous species (fig. 3 in Bawa and Buckley 1989), while in the Genistee it occurs in both outcrossers and selfers. Thus, and at least in this group, basal abortion might not be adaptive but be determined by vascular anatomy and represent simply a morphogenetic constraint (Watson and Casper 1984). Genetically or developmentally determined abortion patterns have been reported by a number of previous studies in other plant groups (Casper and Wiens 1981; Guth and Weller 1986; Gorchoff 1988; Andersson 1990; Herrera 1990).

Seed-filling patterns have been determined in this study by contrasting observed frequencies against confidence intervals, a method that, to my knowledge, had not been used previously. Most researchers have either regressed observed frequencies on ovule positions or used contingency tables to detect the region of the ovary where abortions occur, but this does not allow unambiguous identification of abnormally low- or high-probability positions inside pods (to say nothing of mere visual examination). If ovular positions are not tested individually, supposed patterns may lack materiality and hypotheses that

attempt to explain the reasons behind it can be meaningless. Bawa and Buckley (1989) recognize that the way a pod is filled with seeds will depend on the order of fertilization inside the ovary, so that, if it does not begin at ovules near the tip but at middle or basal ones, preferential seed abortion might respectively occur at both ends or at the tip. In this study, a few *Lupinus* species span a variety of filling patterns, indicating that research addressed to determine the order of fertilization in species of this genus may be helpful to understand how and if microgametophytic competition occurs in the Genistee.

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