



ASPECTS OF THE REPRODUCTIVE BIOLOGY OF FIRE  
FOLLOWING SPECIES OF LEGUMINOSAE IN  
A *PINUS HALEPENSIS* MILL. FOREST

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## ASPECTS OF THE REPRODUCTIVE BIOLOGY OF FIRE FOLLOWING SPECIES OF LEGUMINOSAE IN A *PINUS HALEPENSIS* MILL. FOREST

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### SUMMARY

Regeneration of the majority of Papilionoideae after an intense fire incident in a mature Aleppo pine forest of Attica, Greece, occurs through germination of their persistent soil seed bank following the initiation of the rainy season. Twenty (20) saplings per m<sup>2</sup> comprising about 27 different species were established until the spring of the first post-fire year, while in the corresponding summer a considerable seed output of at least 3000 seeds/m<sup>2</sup> was produced. Of these latter seeds, only approximately 10% germinated in the second post-fire year, thus suggesting the onset of the formation of the soil seed bank. The relative numbers of individuals per unit area for the taxa encountered and the characteristics of the reproductive structures of certain legume species are discussed.

### INTRODUCTION

Fire is a disturbance (Rundel, 1981) causing damage, yet a temporary one, to established vegetation, provided that the ecosystems under investigation are fire-prone subjected to major - in terms of extent- disturbances only at long (normal) intervals, i.e. of 20-30 years. Thus, the impact of a severe fire incident on a *Pinus halepensis* Mill. forest of Attica, Greece, at first appears to equal desolation. An additional reason for such an impression is that the summer, which is the most favourable period for the outburst of fires in the Mediterranean basin, is characterized by a sort of inertia in terms of seedling emergence due to the predominate

However, even during the hot and dry summer months or in early autumn before the first rainfalls, resprouting shrubs such as *Asparagus* sp., *Quercus coccifera*, etc., have been found to produce resprouts. Such an observation partially contradicts to the idea that seeds can survive adverse conditions not tolerable by a vegetatively produced offspring (Fenner, 1985).

The subfamily Papilionoideae -referred to as legumes in the present paper- belongs to the family Leguminosae and includes obligate and facultative seeders, as well as resprouters. The seeders as a whole dominate amongst the fire-following legume population not only in terms of number of species but in terms of number of individuals as well, thus contributing to the increase of the community- and ultimately that of the ecosystem-diversity.

Annual legumes are obligate seeders, they need heat in order to germinate and they produce a large amount of seeds by the end of the first post-fire year. The phenomenon of some tiny saplings, which have either failed to grow sufficiently or germinated relatively late yet bear a load of pods, is rather common (pers. obs.). The stimulation of flowering and plant growth in general by fire has been outlined by many authors for a number of plant families (Old, 1969; Naveh, 1974; Arianoutsou-Faraggitaki & Margaris, 1981; Gill, 1981; Trabaud & Chanterac, 1985;).

It has long been realised that legumes form permanent seed banks in the soil. It is also widely understood that the role of seed banks is intimately connected with disturbance (Thompson, 1992), giving rise to questions concerning the percentage of seeds remaining in the soil and the possibility that they possess special attributes which distinguish them from those that germinate.

The formation and maintenance of soil seed banks can be seen as an alternative strategy to long distance dispersal as far as pioneer species of secondary succession are considered (Fenner, 1987).

Post-fire seed germination depends upon the duration of the fire and its effect on the physical properties of the soil (Ralston, 1971; Christensen & Kimber, 1975; Christensen & Muller, 1975; Arianoutsou-Faraggitaki & Margaris, 1981), on the position of the seeds in the soil (Trabaud, 1987; Moore & Wein, 1977) and certainly on the seed characteristics (Thanos & Georgiou, 1988).

It is well known that legumes form hard, impermeable seed coats which require high (constant or fluctuating) temperatures to break dormancy (Bewley & Black, 1982; Doussi & Thanos, in press) proceeding to germination after the autumn rainfalls (Papavassiliou & Arianoutsou, 1993). In the case of legumes germination from the seed bank takes place during the first post-fire months or not at all, as pointed out by Grubb (1988) for disturbances highly coupled with recruitment.

Prerequisite for the germination of the legume seed reservoir is that the fire incident occurs within the period that the seeds remain viable, provided also that the seeds possess mechanisms which detect the advantageous new state of the environment (Fenner, 1987). The timing of the formation of the soil seed bank is not yet known, but decline of the herbaceous legume population has been reported to begin on the fourth post-fire year in an Aleppo pine forest in Greece (Kazanis & Arianoutsou, in press). There is well-documented information on the disappearance of various herbaceous species 2-to-3 years after fire (Specht *et al.*, 1958; Muller *et al.*, 1968; Naveh, 1974; Kruger, 1977;)

The present paper deals with the population of legumes, mainly the annual plants, that are found in an Aleppo pine forest during the first year after fire. The population status has been investigated in terms of the reproductive biology of its constituents, including floristic information, population dynamics and characteristics of reproductive structures.

The nomenclature adopted for plant species is that used in Med-Checklist 4 (Greuter *et al.*, 1989).

## METHODS

The area under study is situated in the outskirts of Kapandriti (38° 15' N, 23° 52' E) in the prefect of Attica, Greece, at an elevation of 470 m and has a substrate derived from tertiary deposits. The predominate climate is typical Mediterranean, according to the bioclimatic study of Nahal (1981). It was burnt during a destructive fire which outburst on 5th September 1992 and last 10 days, consuming a total of  $4 \times 10^3$  ha of *Pinus halepensis* forest. There was no possibility to measure directly the intensity of the fire but the research area was carefully chosen so as to be on entirely consumed litter, without any pine needles or vegetation left.

One month after the fire 3 study sites were established in the centre of the overall burnt area, in order to avoid short and/or long distance invasion from the nearest unburnt vegetation. The sites were chosen as to differ in terms of orientation and inclination.

The dynamics of the herbaceous leguminous population was being observed on a monthly basis throughout the first post-fire year. Following the end of the growth period and by the time that fruit production and ripening had been completed for the majority of the species concerned, measurements were made in order to estimate the total seed output of the population as well as that of each species separately.

The number of individual plants of all species per unit area ( $m^2$ ) was calculated from a sample of 65 random circles, each 2 m in diameter. The measurements were performed on 11th July 1993, counting 20 samples for each of the first two sites and 25 samples for the third more

extensive site. For some of the plants, difficulty was faced concerning their systematics as the flowers were also needed in order to determine the species.

The number of fruits per plant was estimated from a sample of 10-20 random individuals for each species wherever possible. The measurements were made in the field, except for the species of *Trifolium* in which cases the infructescences of each plant were carried to the lab and measured there.

Seeds, fruits and/or pericarps of each of the collected species were air-dry weighed and consequently oven-dried at 80 °C for at least 48 hours, cooled in a desiccator and weighed again. Both air-dry and oven-dry measurements were made to the nearest 0.0001 g. The correspondent number used differed among the species according to the availability of the gathered material. It was observed that a sample of 50 seeds or pods was giving an average value which did not change when a more numerous sample was used.

## RESULTS

The meteorological conditions which prevailed during the year of the study (1992-1993, September) followed more or less the typical Mediterranean-climate curve, as shown in the ombrothermic diagram (Fig. 1) hereby comprising 40 years (1951-1989), without any noteworthy outbursts.

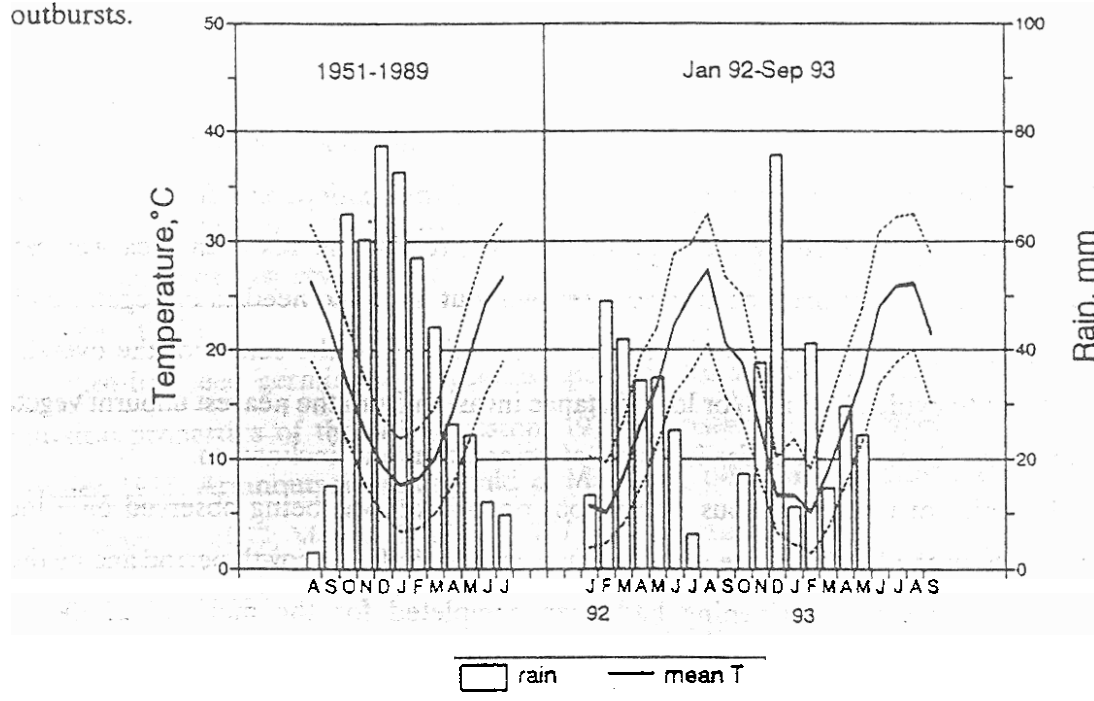


Fig. 1. Ombrothermic diagram of the Tatoi Meteorological Station (elevation 237m). On the right part, mean monthly values of temperature and precipitation for the period under study (January 1992-September 1993) are shown.

The species composition differed among the study sites with some species present only to one out of the three (Fig. 2). This was the case for *Tripodion tetraphyllum* found only at site a, *Securigera securidaca* and *Hymenocarpos circinnatus* present at site b and *Ononis* sp. at site c. On the other hand the most abundant in sites b and c species of *Vicia* sp. were absent from site a.

In the overall area the dominant taxa in order of magnitude were *Genista acanthoclada* and the two species of *Vicia* sp. (3 individuals per m<sup>2</sup>) and *Lathyrus aphaca* (1 individual per m<sup>2</sup>). Of the 26 -or 27 taking into account the two *Vicia* sp.- different taxa that were counted, 10 -or 11- were absent from site a, 7 from site b, and 4 from site c.

The number of individual plants per unit area (m<sup>2</sup>) for each taxon ranged from 0.02 to 3.8 at site a, to 6.0 at site b and to 5.1 at site c, with site a having the lowest number of species. The lowest number (0.005) of plants per m<sup>2</sup> for the overall area belongs to *H. circinnatus*.

Table 1 shows some characteristics concerning the reproductive strategies of legumes present in the area. The majority of the species (10 out of 22) have as dispersal unit the fruit while among the *Trifolium* species, four (4) use the infructescence and one (1) the fruit as dispersal units. In the case of *T. tetraphyllum*, the whole calyx containing the fruit is being dispersed and in additional three (3) species, *Coronilla scorpioides*, *Hippocrepis ciliata* and *H. unisiliquosa*, pod-segments are the dispersal units. Finally, there are four (4) species with dehiscent pods; thus, liberated, individual seeds constitute the dispersal units. Within the group of post-fire legumes, the number of seeds per dispersal unit varies from 1 to 29, while the number of seeds per fruit ranges from 1 to 20. A similar variation in oven-dry weights per dispersal unit (column E) and in the percentage of oven-dry weight allocated to seeds within a dispersal unit (column F) was observed.

Columns D and J can be arbitrary divided into three frequency categories, namely seed air-dry weight less than 1 mg: 5 species, 1-10 mg: 11 species and more than 10 mg: 6 species. Similarly, fruit biomass per plant less than 1 g: 7 species, 1-2 g: 8 species and 4-9 g: 4 species. Calculating the seed biomass as a percentage of fruit for the four species dispersed by seeds, it was found that 61.4% for *L. aphaca*, 74.3% for *L. cicera*, 51.5% for *Lotus ornithopodioides* and 65.2% for *V. sativa* was allocated to seeds within each pod.

Computing the same frequency categories for the seed rain in mg/m<sup>2</sup> (column I) we have found that 8 species contribute with less than 100 mg/m<sup>2</sup> to the soil, 7 species contribute with 100-1000 mg/m<sup>2</sup> and 4 species with more than 1000 mg/m<sup>2</sup>.

The number of seeds per plant range from around 50 for *S. securidaca* and *Onobrychis caput-galli* to more than 1000 for *L. ornithopodioides*, creating a total seed rain of about 3000 seeds/m<sup>2</sup>.

## DISCUSSION

The incident of fire in a mature pine forest initiates a secondary succession process, a prerequisite for which is the presence of a viable seed bank for the obligate seeders. In the case of legumes, it is generally known that they have long viability periods (Bewley & Black, 1982) which permit them to persist in the soil until their germination is induced by the heat shock of a fire.

In Kapandriti, a mean number of  $20 \pm 4$  saplings per  $m^2$  became established by spring 1993 (first post-fire year), as derived from the permanent plots set up in the field ( $35 m^2$ ). However, less legumes (i.e.  $13.3/m^2$ ) were counted in the 65 samples on 11.6.93, probably due to the higher area covered (around  $200 m^2$ ) and to the intervening drying out of some individuals. Such a number of plants gives us a hint of the seeds that have survived in a 25-30 years old Aleppo pine forest in Greece and which are also able to benefit from the fire.

Another question which remains to be answered concerns the chronological initialization for the formation of the soil seed bank. The amount of seeds produced and ultimately released, as opposed to those incorporated in the soil seed bank is not of close correspondence (Rabinowitz, 1980). Nevertheless, the annual seed input can be measured and related to the disappearance of some species, the persistence of others and the creation of their seed banks.

As shown in Table 1, a total number of 3059 seeds/ $m^2$  were released from the annual legumes and from those perennials that produce seeds during their first growth period (e.g. *Bituminaria bituminosa* which develops numerous seeds and *Ononis* sp. with just a few seeds). Perennials like *Dorycnium hirsutum* and *G. acanthoclada*, which were notably numerous within the population, start producing seeds in the summer of the second post-fire year (pers. obs.).

Such a seed rain is somewhat underestimated as it is derived from 22 out of the 27 species in Fig. 2, leaving out the two *Vicia* sp. which have not yet been identified, let alone two more species present, i.e. *Hedysarum spinosissimum* L. and *Medicago monspeliaca* (L.) Trautv. which were too sparse to appear in any of the 65 samples measured.

Until spring 1993 (2nd post-fire year),  $297.0 \pm 118.2$  individuals per  $m^2$  had appeared (pers. obs.); a number suggesting that a large amount of the seed rain had possibly been assimilated in the soil seed bank already by the end of the first post-fire year. In order to calculate the legume seed output in relation to the formation of the soil bank, we have to take into account the increase of the seed bank during the subsequent years, the percentage of seeds potentially lost through herbivory, as well as species dispersed by their infructescences, the latter rather remaining standing if they are not trampled over by passing or grazing animals (e.g. the four

*Trifolium* species of Table 1).

As the research area was subtly grazed in August of the first post-fire year, many seedlings, mainly *Trifolium* sp. and *Medicago* sp., were observed germinating from sheep dung during the following rainy season. It is obvious that the hard seed coats of legumes not only permit them to outlive the digestion of the animals but to advantageously exploit the nutrient-rich microenvironment of the dung by being triggered to germinate by the "softening" passage through the digestive track.

Legume seedlings emerge from seeds of the top 2-3 cm of the soil; during the second post-fire growth period, they even emerge from above the ground and establish successfully. The maximum temperature under which the dispersed seeds of the first year pass the summer in a previously burned pine forest in Greece, ranges from 53.0 °C on the soil surface, to 52.5 °C at 1 cm depth, 51.1 °C at 2 cm depth and 48.1 °C at 3 cm from the surface. The measurements were taken on 30.7.93 from 13.00 pm to 15.00 pm. It is suggested that the heat reaching the soil due to the rather open canopy plays a significant inductive role to the germination of the legume seeds from the second post-fire year onwards.

Observing the air-dry weight of the 22 species in Table 1, only that of *B. bituminosa*, a perennial weed, was as high as 26.5 mg with all the rest weighing less than 17 mg. Species which produce small-sized seeds so that they can incorporate more easily to the soil bank and opportunistic plants in open communities with allocation strategies that lead to production of smaller but more numerous seeds are mentioned in the literature. In addition, seed size has been reported to vary in relation to disturbance but also depending on the parent plant, without having been clarified which of the two factors prevails (Fenner, 1985). An interesting approach would be to follow the size differences in seeds during successional post-fire years, comparing also burned and unburned vegetation.

The percentage water content of the seeds of the species appearing in Table 1 was calculated and ranged from 2.9% for *S. securidaca* to 7.9 for *Scorpiurus muricatus*. It is possible that we are dealing with seeds at high dehydration.

In the present paper, a first attempt based on Ridley (1930) and Pijl (1972) was made in order to determine the possible dispersal mode of certain legumes. In general, the legume species present may be zoochorous (either endo- or epi-zoochorous), with ombrochory being an additional strong candidate. Regarding certain particular species, *T. stellatum* is clearly anemochorous, while the rest four species of the genus appear to be achorous. Achory seems to characterize *M. orbicularis* as well, the dispersal units of which are its indehiscent (synaptospermous) pods. For *B. bituminosa* anemochory is very likely in addition to epizoochory. The fruits of *M. lupulina* are "rollers" and the dispersal mode could be characterized as chamae-(anemo)-chory. The four species dispersed by seeds, i.e. *L. aphaca*,



*L. cicera*, *L. ornithopodioides* and *V. sativa*, are all active ballists; moreover, their spherical seed shape may enhance dispersal distance through movement on the soil. Finally, *M. minima*, *O. caput-galli* and *S. muricatus* might be dispersed by passing animals or may simply be achorous.

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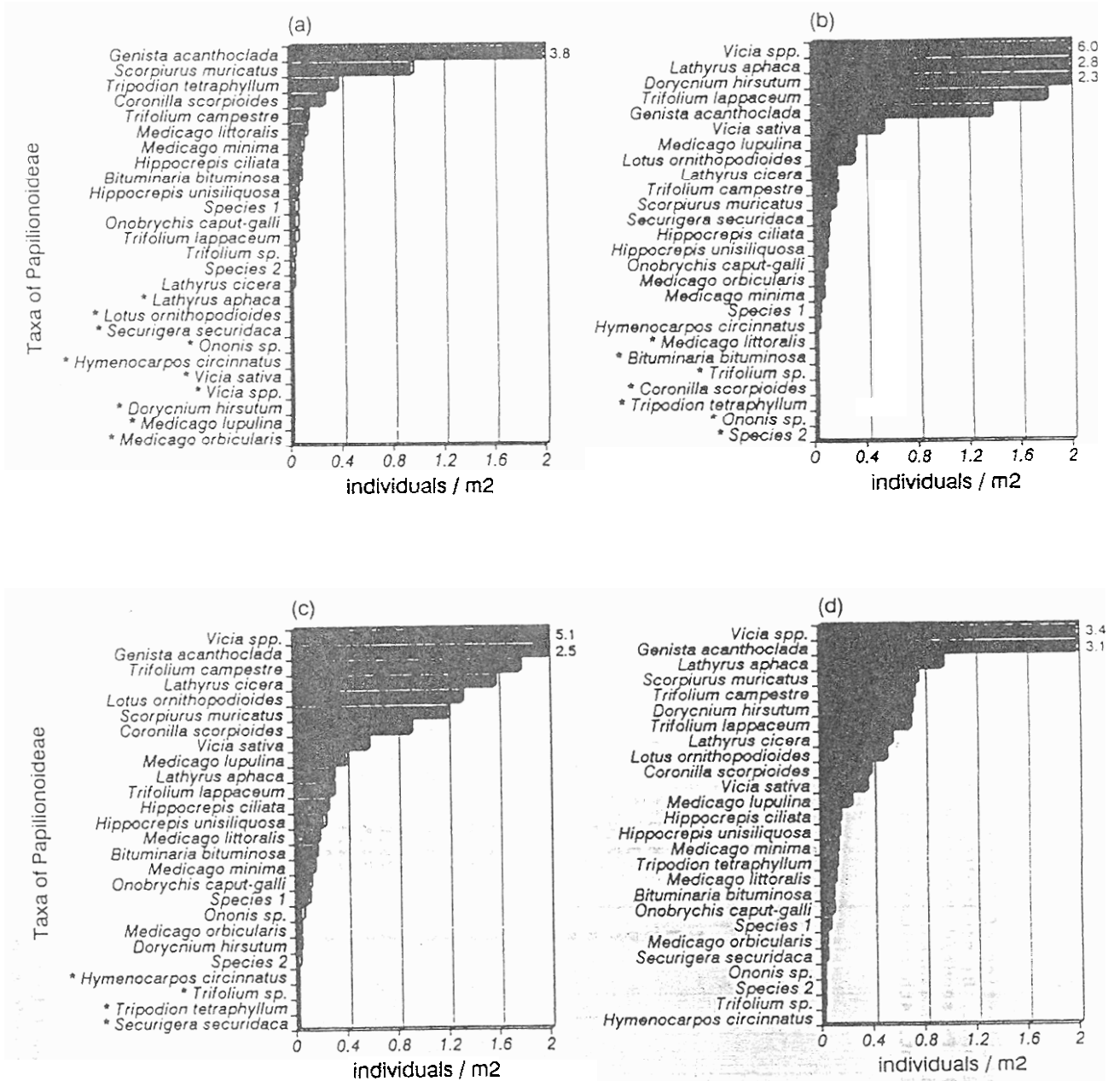


Fig. 2. The mean number of individuals per m<sup>2</sup> for the taxa of the subfamily Papilionoideae established during the first post-fire year at Kapandriti, Attica, Greece. The measurements were carried out on 11.6.1993 on the three experimental sites (a, b, c); d represents the average values of these sites. The asterisk (\*) corresponds to the taxa absent from the respective site. The numbers beside the bars correspond to the actual density values recorded.

Table 1. Reproductive structures characteristics of 22 species of Papilionoideae from Kapandriti, Attica, Greece.  
 Columns: A: type of dispersal unit, B: seeds/dispersal unit, C: seeds/fruit, D: seed weight (air-dry, mg)  
 E: dispersal unit weight (mg), F: seeds/dispersal unit (% wt/wt), G: seeds/plant, H: seed rain (seeds/m<sup>2</sup>)  
 I: seed rain (mg/m<sup>2</sup>), J: fruit biomass/plant (g).  
 -All weights (except seed weight, 4th column) refer to oven dried biomass.  
 -nd : not determined

Species	A	B	C	D	E	F	G	H	I	J
<i>Bituminaria bituminosa</i> (L.) Stirton	f	1	1	26.5	26.6	94.2	66	5	132.1	1.8
<i>Coronilla scorpioides</i> (L.) Koch	g	4.0 *	(2-)6-8(-9)	2.0	11.9	63.2	521	198	372.2	1.5
<i>Hippocrepis ciliata</i> Willd.	g	4.5 *	(1-)6-9(-10)	2.1 @	19.7	46.1	216	30	61.2	0.9
<i>Hippocrepis unisiliquosa</i> L.	g	3.5 *	(2-)4-8	3.6 @	26.5	44.9	163	21	72.0	1.2
<i>Hymenocarpus circinnatus</i> (L.) Savi	f	2.0	2	7.6	43.8	33.8	220	1	8.0	4.8
<i>Lathyrus aphaca</i> L.	s	1	(4-)5-6(-7)	8.0	7.4	100	468	445	3304.3	4.8
<i>Lathyrus cicera</i> L.	s	1	(4-)8-10(-11)	16.9	15.7	100	67	36	564.1	1.0
<i>Lotus ornithopodioides</i> L.	s	1	(7-)9-15(-20)	2.0 @	1.8	100	1128	564	1042.0	4.0
<i>Medicago littoralis</i> Loisel.	f	7.3	6-8(-9)	4.9	123.7	27.7	92	9	42.9	1.6
<i>Medicago lupulina</i> L.	f	1	1	0.8 @	1.1	71.5	447	103	78.3	0.5
<i>Medicago minima</i> (L.) L.	f	4.4	(2-)4-6	4.0 @	26.1	62.5	407	49	179.9	2.4
<i>Medicago orbicularis</i> (L.) Bartal.	f	15.0	15 @	4.4	109.4	58.4	331	10	42.2	2.4
<i>Onobrychis caput-galli</i> Lam.	f	1	1	16.7	39.9	39.0	47	4	58.1	2.0
<i>Scorpiurus muricatus</i> L.	f	8.9	(6-)8-10(-11)	10.7	87.6	68.0	653	489	4804.4	9.4
<i>Securigera securidaca</i> (L.) Degen & Dorfler	f	7.9	(2-)8-10	7.4	96.5	56.8	47	1	10.2	0.6
<i>Trifolium angustifolium</i> L.	i	29.0	1	0.9 @	90.7	27.2	193	nd	nd	0.6
<i>Trifolium campestre</i> Schreber	i	34.5	1	0.2 @	19.1	37.2	1023	736	151.7	0.6
<i>Trifolium lappaceum</i> L.	i	22.4	1	0.7 @	65.0	23.3	282	195	131.6	0.8
<i>Trifolium lappaceum</i> L.	i	18.1	1 #	0.4 @	25.2	25.4	nd	nd	nd	nd
<i>Trifolium stellatum</i> L.	f	1	1	2.3	7.3	29.9	95	nd	nd	0.7
<i>Tripodion tetraphyllum</i> (L.) Fourr.	c	2.0	(1-)2(-3)	13.5	49.8	50.7	327	36	449.9	5.2
<i>Vicia sativa</i> L.	s	1	(6-)7(-9-)10	11.2	10.3	100	360	126	1300.7	6.1

f : fruit  
 s : seed  
 g : segment  
 i : infructescence  
 c : calyx+pod

@ : Mean value of a sample weighed in total.

! : A percentage of 63.5 of the pods beared seeds.

# : A percentage of 81.9 of the pods beared seeds.

\* : Estimate; the pods may break into single- or multi-seeded segments