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Pre-dispersal seed predation by *Bruchidius villosus* (Coleoptera, Bruchidae) in *Laburnum anagyroides* (Fabaceae, Genisteae)

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Abstract: The pre-dispersal seed predator, *Bruchidius villosus* (Coleoptera, Bruchidae) destroyed ca. 8% of seeds of its major host-plant, *Laburnum anagyroides* (Fabaceae, Genisteae), a tree-like legume, in Hungary. However, almost 40% of the pods were infested by the beetle. Females did not show a resource concentration response: with increasing number of seeds per pod, the number of uninfested seeds also increased. A high seed abortion rate of 75% left an average of two full-grown seeds per pod. Females laid three-four times more eggs on pods than the number of full-grown seeds present in a pod. Despite this, a high level (ca. 15%) of egg parasitism and pod abortion that reached levels up to 50% on pods which already bore bruchid eggs, decreased the infestation level. Larval parasitisation rate of *B. villosus* by chalcids and braconids exceeded 30%.

Nomenclature for plants follows: Tutin et al. (1968).

Introduction

Seed consuming organisms are known to influence important traits at plant population and community levels (Janzen 1971). Specifically, pre-dispersal predators that feed on developing seeds can affect plant performance and, through seed limitation, plant demography and population dynamics (Louda 1983). A variety of factors influence the impact seed predators have on plant populations: chemical constituents of seeds, their ephemeral availability, the clustered distribution of seeds within plant stands, plant life cycles and others (Crawley 1983, 1992).

Seed loss to seed predators, however, does not necessarily influence plant population dynamics. The availability of safe sites for germination is thought to be a decisive factor in plant recruitment (Andersen 1989, Crawley 1989). In spite of the availability of safe sites and with a low level of pre-dispersal seed predation, factors functioning post-dispersally can still cause seed limitation (Szentesi and Jermy 2003). It is generally believed that contrary to annuals, long-lived perennial plants form transient seed banks (Pickett and McDonnell 1989). However, the issue is controversial because grassland legume species that had the highest share in seed banks were perennial (Rice 1989). It can be assumed that, although crop size of perennial species cannot be predicted, their presence can be more predictable in space and time than that of annuals, therefore higher and more variable seed losses can be expected. On the basis of data (Crawley 1992, Szentesi 1999, Szentesi and Jermy, unpubl.) it seems that the upper boundaries of predation levels for perennials, and particularly for trees, are higher than those for annuals. Nevertheless, a thorough analysis is still lacking.

A substantial body of data on pre-dispersal seed predation of perennials are available (Waloff 1968, Janzen 1971, Moore 1978a, b, New 1983, Andersen 1989, Ehrlén 1994, Szentesi 1999 and others). The need for biological control agents to assist in the control of invasive perennial weeds has facilitated numerous studies on the bionomics of seed predators (e.g., Harman 1999, Redmon et al. 2000). Hence, special attention has been paid to some introduced fabaceous perennials, such as *Cytisus scoparius* (Memmott et al. 2000), *Ulex europaeus* (Miller 1970), or *Teline* (= *Genista*) *monspessulana* (Alexander and D'An-

tonio 2003) that rapidly change the stability and structure of the community which they enter. *Bruchidius villosus* (F.), a pre-dispersal seed predator in the tribe of Genisteae, has been intensively studied in New Zealand where it is used as a biological control agent for *C. scoparius* (Syrett et al. 2000, Syrett and O'Donnell 1987, Harman 1999, Haines et al. 2004). Studies on the beetle were also conducted in the UK (Parnell 1966, Waloff 1968, Syrett and O'Donnell 1987) where *C. scoparius* was a common host to *B. villosus* and results suggested that it was host specific to this plant.

Until this study, the effect of the pre-dispersal seed predator on plant performance of golden rain, *Laburnum anagyroides*, has not been known. Therefore, the aims of the present paper were: to provide data on the phenology and pre-dispersal seed predation of one of the major hosts of *B. villosus* in Hungary; to find out whether the pre-dispersal seed predator utilizes the usually considerable seed crop of this perennial legume by a density dependent manner, and to give information on the biology of *B. villosus* for biological control projects where it is used as a natural enemy against introduced legume weeds.

Materials and methods

The host-plant

Laburnum anagyroides (Fabaceae, Genisteae) is an endemic perennial bush or small tree inhabiting montane-prealpine dry forest edges in Central Europe on calcareous soil (Soó 1966). It is also grown as an ornamental and frequently grows wild. The plant is multistemmed, the bark is green, the leaves are trifoliolate, abaxial side with silvery hairs. The latter character distinguishes it from a related species, *L. alpinum* which has glabrous abaxial side of leaves and inhabits higher elevations in Southern Europe. The yellow flowers are large (2 cm) in inflorescences of 10-15 cm. The flowers are pollinated by insects. Pods are hairy when young, gradually become glabrous and pale yellow when ripe. Pods are dehiscent, seeds are black. Characteristic compounds of *L. anagyroides* are quinolizidine alkaloids (Wink et al. 1983, Wink 1984 and others) that are present in all parts of the plant and specifically accumulate in the reproductive organs, and are also taken up by organisms, including the pre-dispersal seed predator (Szentesi and Wink 1991).

The seed predator

Bruchidius villosus Fabricius 1792 [*B. fasciatus* (Oliv.) or *B. ater* (Marsham), Coleoptera, Bruchidae] is a member of endophagous seed predators of the green-pod-guild (Szentesi and Jermy 1995), and one of the most widely oligophagous of the bruchid seed predators. Adults were reared from nine perennial plant species in Hungary (Jermy and Szentesi 2003) all belonging to the tribe of Genisteae. However, host records (Wittenberg and Thomann 2000, Sheppard 1999, Szentesi and Wink 1991), and a compilation (Withers, T. and M. Haines, unpubl. results) indicated 16 plant species from Europe within the tribe.

The body is black, homogeneously covered by grey hairs. Information on its bionomics comes from investigations conducted on *Cytisus* (= *Sarothamnus*) *scoparius* (Parnell 1966, Waloff 1968), a common host of *B. villosus* in the UK. Before oviposition commences, females feed on pollen of the host or on that of neighbouring plants in spring/summer. Eggs are laid on young green pods in June, develop through four larval instars (although no data are presented by the authors cited), adults emerge from seeds in late August, and are able to survive two winters. However, there is no information on where overwintering occurs.

Parasitoids of B. villosus

At least one *Tetrastychus* sp. (Hymenoptera, Chalcidoidea) is reported both as a primary (on *B. villosus*) and as a facultative secondary (on the braconid, *Triaspis thoracicus* Curtis, Hymenoptera, Braconidae) parasite (Medvedeva 1978). *T. thoracicus* is a widely oligophagous parasitoid of bruchid larvae (de Luca 1970, 1977). This and another endoparasitoid braconid lay their eggs into the hosts' eggs and the first instar larvae enter the seeds carried by the host larvae (Parnell 1964, Charlet 2002). Among the parasitoid complex known from *B. villosus* (Parnell 1964), several chalcidoids and an egg-parasitoid (*Uscana*, Trichogrammatidae) species are described from *B. villosus* eggs (Steffan 1981).

Sampling, recording and observations

Sampling and observations on *L. anagyroides* were done in Budapest, Ady-liget (47^{o} 32' N, and 18^{o} 56' E, and ca. 310 m a.s.l.), Hungary, where six trees of more than 10 years old, and ca. 20 trees of less than 10 years old plants were available. Weekly observations of beetle behaviour, and plant phenological stages were made from 1998. Measurements of temperature on *L. anagyroides* plants and precipitation have been executed with data loggers (Onset Computer Corp.) at site since 2001. Mean (±SD) yearly precipitation at the locality of investigations was 468.1 ± 148 mm (2001-2004), range: 294-607 mm; mean (±SD) daily temperature in January was -2.7 ± 4.9 ^{o}C; and during the growing season (1 May– 31 August) at a height of 2 m was 19.5 ± 6.5 ^{o}C (N = 4 years).

Sampling for seed predator-infested pods was done in mid-August each year. Thirty-five to 70 infructescences per plant were picked when pods were ripe and individual infructescences were put into separate paper bags. The position of the pod on the infructescence axis was determined by counting all attachment points along the axis (i.e., including all aborted flowers and pods). Pods were opened and the number of intact (uninfested), aborted (ceased developing further than ovule stage), underdeveloped (shrivelled and smaller than a full-grown seed) and seed predator-infested seeds was determined under a binocular microscope and recorded for each pod. The number of first instar larval boring-holes and eggs parasitised by Trichogrammatidae species was counted. Emergence holes of chalcid and braconid parasitoids were also recorded. Pod size, and length of infructescence axis were measured and the position of pods on the axis were recorded.

To establish rate of falling of ripe infructescences and seeds from trees, 50 infructescences on three plants each were marked with colour bands in September, 2003. They were inspected for presence/absence of infructescences in the next year.

For two years, from the start of pod formation in June until pod opening in August, weekly samples of 5-11 pods which had been oviposited on were taken from one *L. anagyroides* bush and stored at -18^{o}C. The pods and seeds were dissected under the microscope and developing stages of *B. villosus* were recorded and measured by size.

Measurements

Seed size and seed shape of *L. anagyroides* were measured using a mechanical calliper with an accuracy of 0.05 mm. The three axonometric measures of 35 room-temperature dry seeds were taken holding the seeds in a standard position, i.e. hilum up. Seed shape (closeness to an ideal sphere) was expressed as the ratio of the smallest and largest seed measures (*sphericity ratio*). It was shown that seed shape affected occupancy of legume seeds by bruchid seed predators (Szentesi and Jermy 1995). Size of bruchid-infested and uninfested seeds from the same pods was also measured.

Seed mass was measured by an electronic balance (Sartorius A210P) with an accuracy of 0.1 mg. The mass of all uninfested seeds of samples, as well as the left-over endosperm of 49 bruchid-infested seeds was measured.

The body size of 184 *B. villosus* adults reared from *L. anagyroides* was also measured with the help of a binocular micrometer under 6× magnification. Elytra and thorax lengths were summed as a measure of body length. Head length was not included because it was in a bowed position and could not be accurately measured. Body width was measured by the width of elytrum at the shoulders, positioning the bruchids parallel to the microscope's visual plane.

Statistical procedures

For comparison of means, t-test, one-way ANOVA and post-hoc procedures (Scheffé) were used following Levene-test for homogeneity of variance. Correlations between variables are expressed by Pearson's r. All computations were performed using STATISTICA 6.1 software (Statsoft 1984-2003).

Results

The host-plant

Flowering started between 26 April and 23 May over 10 years, depending on the weather conditions. The main pollinators were bumblebees, but the seed predator could not be excluded as it entered the flowers and consumed pollen-grains. Pod-formation began between 13 and 31 of May. Pod hardening took place from 29 June, at the earliest, but usually from mid-July or early August. Pods opened from the second half of August allowing seed predators and parasitoids to exit pods. Flower and pod production suggest that masting occurs, since no crop developed locally in 1998 or regionally in 2000, and very few pods were produced in 2002 locally in comparison to regular production in intervening years (regular is defined as ca. 500 infructescences per full-grown bush/tree). In bumper crop years, such as 2003, on a ca. 3×3×3.5 m size, 15-year-old tree that had 12 stems of ca. 5-10 cm diameter at 50 cm height, there were ca. 1500 inflorescences counted on 22 May. But in the same year pod abortion was very large (probably due to drought): the number of aborted pods of 1-2 cm in length ranged between 10-50/100 cm^2, on the ground beneath two plants. Thirteen percentages of marked infructescences with open pods and seeds remained on three *L. anagyroides* plants for a further year.

Several important indicators of crop production are shown in Table 1 for 5 *L. anagyroides* plants. The axis length of infructescences ranged between 74 and 157 mm. The number of attachment points on infructescence axes was between 23 and 42, however, the number of pods recorded ranged between 10 and 18 only. Therefore, a substantial proportion (ca. 50%) of pods is aborted during pod development in any year. The lengths of pods were between 36 and 51 mm. An average of 8.1 ± 1.3 (SD) seeds were recorded per pod. Of these the number of

Table 1. Data on crop production of five *L. anagyroides* plant (means ± SD) in Hungary, in 1998.

Tree No.	No. of attachment sites on infructescence axis	Length of infructescence axis (mm)	No. of pods per infructescence	N	Length of pods (mm)	N
1	28.1 ± 5.9	87.6 ± 24.2	10.9 ± 3.8	56	40.7 ± 7.5	502
2	42.0 ± 4.2	157.1 ± 22.6	18.0 ± 5.1	35	39.3 ± 6.2	433
3	30.8 ± 10.0	98.3 ± 31.8	13.1 ± 5.1	24	38.6 ± 6.1	249
4	23.1 ± 4.4	74.4 ± 16.7	11.3 ± 3.8	16	36.5 ± 6.3	136
5	25.2 ± 6.1	83.2 ± 24.8	10.0 ± 5.8	28	51.7 ± 9.0	233
All	30.6 ± 9.0	102.3 ± 38.4	12.7 ± 5.5	159	41.3 ± 8.4	1553

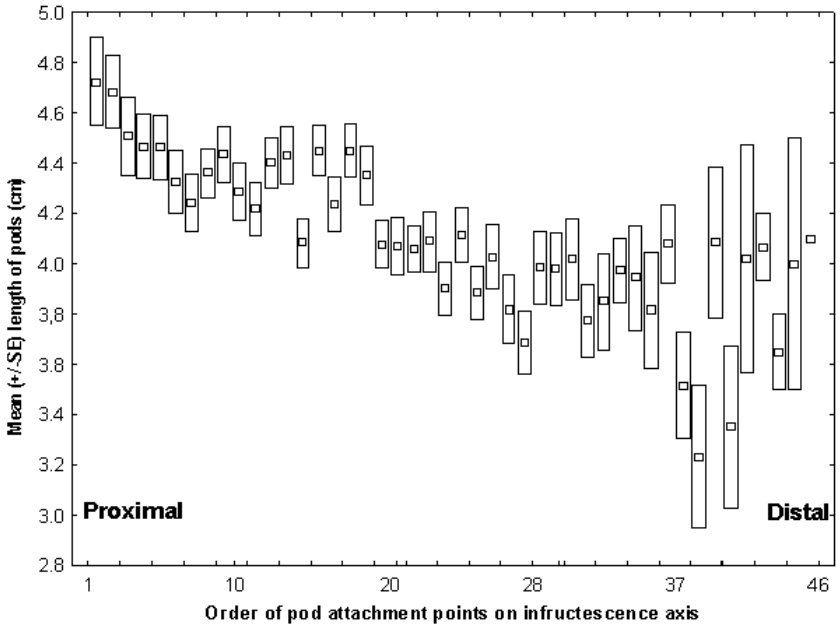

Figure 1. The distribution of pod-lengths along the infructescence axis of *L. anagyroides* as a function of all attachment points (including positions of aborted flowers and pods too).

aborted seeds was 5.4 ± 1.7, intact (uninfested) seeds 2.0 ± 1.4 and bruchid-infested seeds 0.5 ± 0.7 (N = 90 infructescences).

The distribution of pod lengths along the infructescence axes (Fig. 1) showed that, whereas proximal pods grew larger, those developing distally became variable in size, but were generally shorter (breakdown ANOVA: $F_{45,1701} = 2.9136$, $p<0.001$). The elongation of infructescence axis during growth plateaued (slowed down) and indicated a positive relationship with the number of pod attachment points (Fig. 2). The number of pods and mean pod length increased as infructescence axis became longer ($r= 0.4967$, $F_{1,110}= 36.03$, $p< 0.001$, and $r= 0.501$, $F_{1,110}= 36.85$, $p < 0.001$, N= 112 infructescences)

Uninfested and aborted seeds per pod were distributed relatively evenly along the infructescence axes. The mean number of aborted seeds varied less at the proximal end of the infructescences in comparison with the distal one, although the difference was not significant (Fig. 3, $F_{45,604} = 0.6840$, $p = 0.9431$). There was a significant increase in the number of intact seeds per infructescence as the length of infructescence axis elongated ($r=0.4589$, $p= 0.0012$, N= 47 infructescences). There was a highly significant positive correlation between the number of seeds per pod and number of intact seeds ($r = 0.7463$, $F_{1,648} = 814.52$, $p < 0.001$, N= 650).

Seed characteristics of L. anagyroides

L. anagyroides seeds had a 4.3 ± 0.2 (mean ± SD) mm length, 2.5 ± 0.1 mm width, and 3.4 ± 0.2 mm height. The sphericity ratio was 0.58 ± 0.04, and seed mass was 22.4 ± 5.0 mg (means ± SDs). Seed masses of *L. anagyroides* did not differ significantly between years (Table 2).

Seed predation on L. anagyroides

B. villosus adults fly well and they were present on *L. anagyroides* plants before opening of flowers. During flowering, they visited flowers of *L. anagyroides*, as well as those of other plants in the vicinity and consumed pollen-grains. Microscopic examination of *B. villosus* fecal pellets showed pollen-grains identical or similar to the ones collected from the flowers. The beetles continued to

Table 2. Seed masses of *L. anagyroides* trees in Hungary.

Years	Mean (±SD) seed mass (mg)	N
1998	20.9 ± 4.3	4440
1999	20.4 ± 5.0	7235
2000	23.6 ± 4.6	7963
2001	22.7 ± 5.1	7269
2002	24.9 ± 3.9	4168

visit flowers of other species after flowering ceased on *L. anagyroides* and from pod-formation they were observed feeding on fluids exuding from injured green pods.

Egg-laying started when developing green pods reached 1.5-2 cm length, which occurred from mid-May, and commenced until mid-July. Following this time, adults could not be detected on *L. anagyroides*. As pods elongated, the number of eggs laid increased (Fig. 4, $r = 0.5668$, $F_{1,648} = 306.716$, $p < 0.001$, $N = 650$). The mean (±SD) number of eggs per pod was 7.8 ± 4.0 (N = 38 infructescences, 12.0 ± 5.8 pods/infructescence). Thus, concerning the mean number of intact seeds per pod, overloading pods with eggs seems common. It appeared that the presence of eggs inhibited further egg-laying by *B. villosus*. If eggs were removed from pods, females re-oviposited on them at a rate of approximately 7 eggs per day for 33 days after which no replacement occurred. In total 266.4 ± 70.1 eggs were laid on 5 infructescences, whereas on the control plants only 64.6 ± 48.7 eggs were deposited

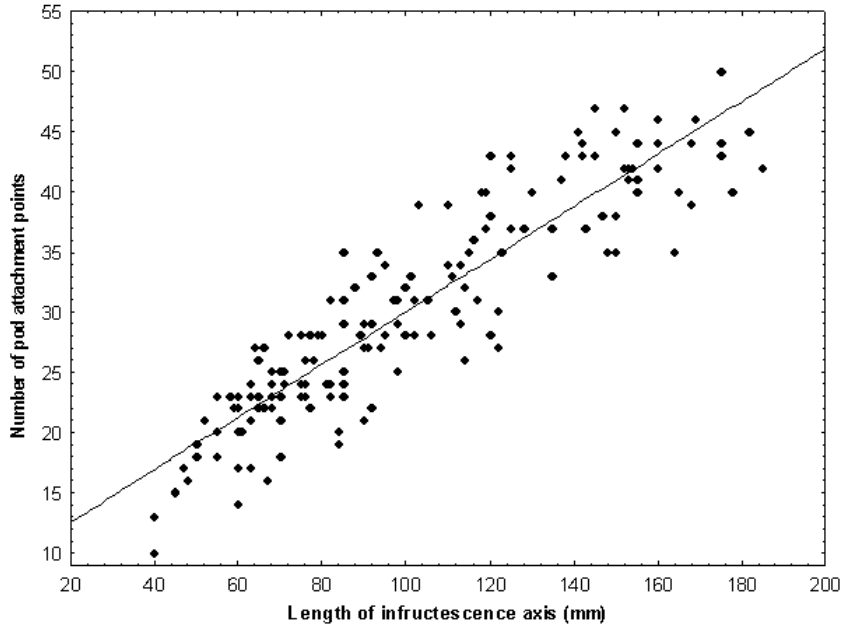

Figure 2. Relationship between infructescence length and the number of attachment points of pods in *L. anagyroides*.

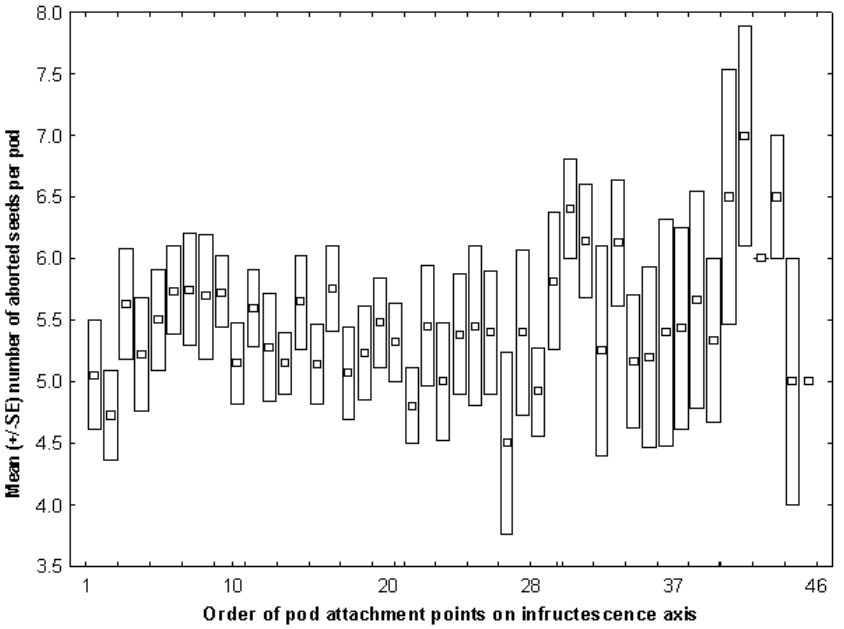

Figure 3. Distribution of aborted seeds in *L. anagyroides* pods along the infructescence axis as a function of all attachment points (including positions of aborted flowers and pods too).

until the same date, almost a 5-fold difference. On the other hand, as the number of eggs laid on pods increased, so did the number of intact seeds per pod ($r = 0.2296$, $F_{1,648} = 36.0489$, $p < 0.001$, $N = 650$). This suggests that there may be a "dilution effect", because as infructescence axis lengths became longer, first the number of eggs laid per pod decreased rapidly, then increased (Fig. 5, $r = -0.4527$, $F_{1,42} = 10.8244$, $p = 0.002$, $N = 44$. This finding was supported by the fact that the number of pods bearing eggs did not correlate with the elongation of infructescence axis ($r = 0.0816$, $p = 0.5983$, $N = 44$). There was no difference in the number of eggs laid along the length of infructescence axis (breakdown ANOVA: $F_{45,604} = 1.1813$, $p = 0.1977$) between pods or the number of bruchids (or parasitoids) which emerged per pod ($F_{45,627} = 0.7415$, $p = 0.8940$).

B. villosus larvae appear to have 4 instars, based on dissection of pods and seeds and head-capsule measurements (Table 3). Although, the head-capsule of second instar could not be measured due to lack of available specimens, the ratio between the head-capsule sizes of first and third instars was unusually large (3.08), which suggests the presence of yet another instar. The first instar lives in an almost fluidic environment inside the seed, from which the endosperm is formed and hardens slowly. The larvae consumed the majority of the endosperm per seed: as an average of 4.8 ± 3.0 (SD) mg (26.4% of the uninfested) endosperm remained after adult emergence. The presence

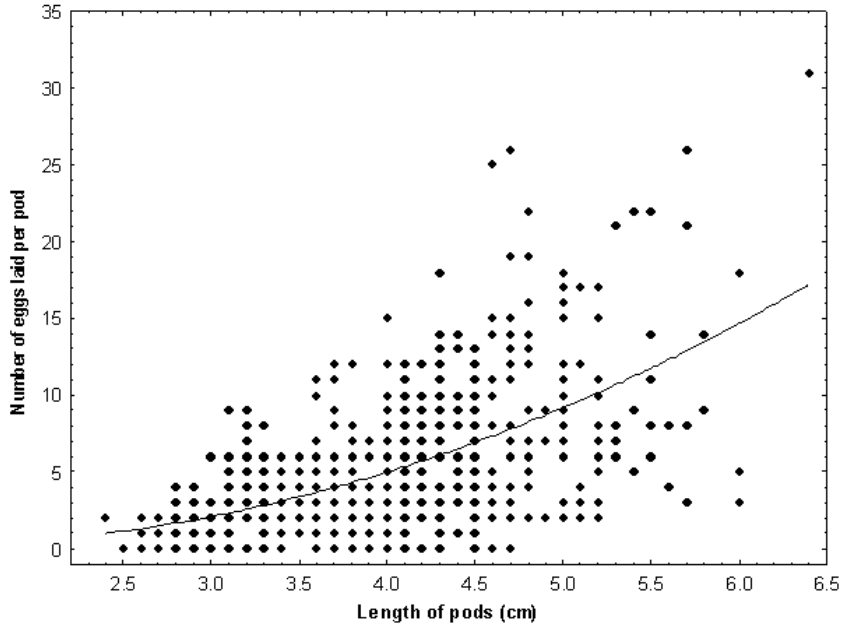

Figure 4. Correlation between pod length and the number of eggs laid per pod by *B. villosus* on *L. anagyroides* plants. (Second order polynomial fit: $r = 0.5668$, $p < 0.001$, $y = 1.21 - 1.65x + 0.65x^2$.)

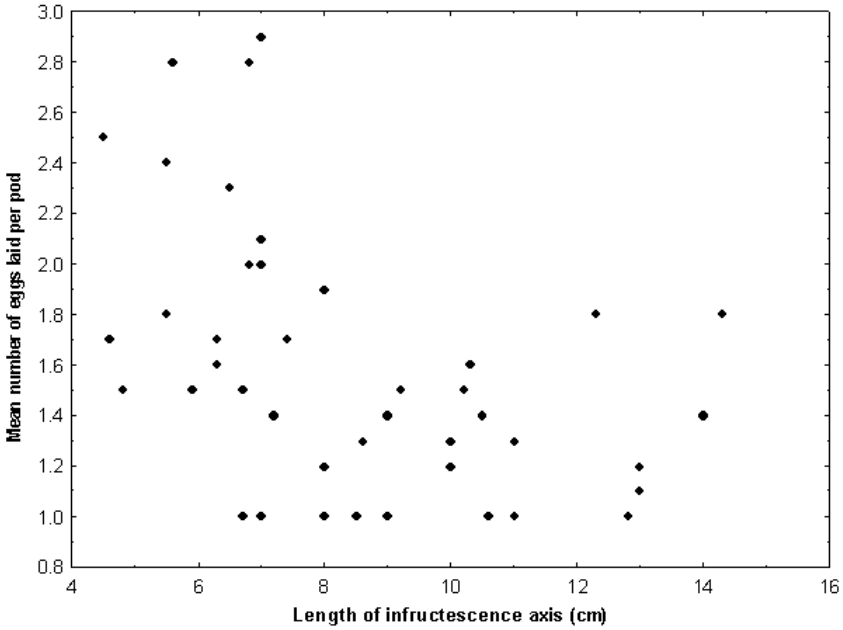

Figure 5. The mean number of eggs laid per pod by *B. villosus* as a function of infructescence axis length in *L. anagyroides*.

Table 3. Phenology of *L. anagyroides* pods and seeds, and its pre-dispersal seed predator *B. villosus* in Hungary in 2003 and 2004.

Date of sampling	Length (mm) and coloration of pods	Size (mm) and condition of seeds	Developing stage of *B. villosus*
30 May	58, green	4-5, green, endosperm is fluid	Embryo differentiation in eggs
6 June	70, green	4-6, green, endosperm is fluid	Most L_1s hatch. Some tunnel inside the pod wall and enter seeds. Body length: 0.6 mm
12 June	66, light green	5-7, light green, endosperm forms	Most L_1 enter seeds. Head capsule width: 0.12 mm
19 June	66, light green	5-6, light green, endosperm soft	L_3 larvae. Head capsule width: 0.37 mm*
26 June	71, greenish yellow	5-6, pinkish, endosperm soft	L_4 larvae. Head capsule width: 0.63 mm
4 July	71, yellow, shrivelling	5-6, dark purple, endosperm hardens	L_4 larvae and prepupae
11 July	65, yellow, dry	4-5, black, endosperm hardens	L_4 larvae and prepupae
18 July	63, yellow, dry	4-5, black, endosperm hardens	Pupae (not yet coloured)
25 July	64, yellow, dry	4.5, black, hard	Fully metamorphosed beetles. (Most are not yet coloured)

* The ratio (3.1) between the size of head-capsules of L_1 and L_3 instars indicate a missing size in-between the two, if Dyar's rule (1890) of head-capsule ratio (1.4) between developing instars is accepted.

of *B. villosus* within seeds significantly affected seed volume (calculated by the three axonometric measures). Seed volume was significantly larger in infested seeds compared to uninfested ones of the same pods: 37.7 ± 6.5 (SD) vs. 32.3 ± 6.6 mm^3 (*t*-test: $t_{calc} = 6.5728$, df = 252, $p < 0.001$). In addition, bruchid-infested seeds became significantly more flattened in shape (sphericity ratio: 0.52 ± 0.05 (SD) vs. 0.58 ± 0.06 ($t_{calc} = 9.0531$, df = 252, $p < 0.001$).

Of 1747 pods 673 (38.5%) contained developmental stages of *B. villosus*. However, only 7.6% of the seeds within these pods were infested by the bruchid. There was approximately one bruchid-infested seed in every second pod.

B. villosus adults cannot emerge from pods which have not dehisced. They hatch from seeds by pushing out a window of 1.51 × 1.88 mm size (N = 424) in the seed coat, and then remain inside the pod cavity until the valves of the pod split in half. Not all pods open from mid-August and some only open partially. As a consequence, many beetles overwinter inside the pods. Closed pods collected in winter (January) and opened manually at room temperature contained fully developed adults that soon became active. *B. villosus* adults reared from *L. anagyroides* had a 3.03 ± 0.16 (mean ± SD) mm body length and 1.97 ± 0.13 mm body width (N= 184).

Parasite load on B. villosus

B. villosus eggs parasitised by Trichogrammatidae could be observed on golden rain pods in the field from the end of May. The mean rate (±SD) of egg parasitisation was 15.09 ± 9.6%. Parasitisation of bruchids by chalcids was 17.83 ± 15.2% and by braconids 14.22 ± 9.4% (5 trees, 87 infructescences, 1183 pods, sampled in 1998).

Discussion

About 40% of the pods of *L. anagyroides* were infested by the pre-dispersal seed predator, *B. villosus*. However, only ca. 8% of seeds within these pods contained beetles (among 25 full-grown seeds ca. two seeds were infested). The seed predation level found in this study seems relatively low for a perennial plant species, however, it is within the range experienced in a large number of studies demonstrating that variability is the rule (Crawley 1992). For example, on another host of *B. villosus*, *C. scoparius*, seed destruction rates as high as 80% were shown (Redmon et al. 2000). How spatial and phenological changes of host-plants over time affect infestation levels is still to be investigated, but it is expected to be variable on the basis of fluctuations in crop size between years. On the other hand, a substantial spatio-temporal variation in pre-dispersal seed predator guild composition, as shown in a perennial vetch species, *Vicia*

tenuifolia (Szentesi et al. in press), can also contribute to the variability of seed loss.

Several factors contribute to the formation of this low level of seed predation reported in this study. One is the phenology of inflorescence development when flowers on the inflorescence axis begin opening and pod development proceeds from the proximal end and continues toward to the distal end of the axis. It is assumed that the number of flowers and later that of the pods is under the constraints of nutrient allocation (Stephenson 1981). In principle, the availability of egg-laying and larval development sites should determine seed predator population size. That is, the higher the number of oviposition sites, the larger seed predator population can be expected. With the elongation of the inflorescence axis the number of flower/pod attachment points increases (Fig. 2), seemingly approaching a plateau due to (1) physical limitations of axis surface, and (2) a potential maximum number of flowers/pods that can be nourished. However, as a consequence of the trade-off between seed number and seed size, ca. 50% of developing pods may be aborted, which mostly occurs three quarters of the way along the infructescence axis close to the distal end (Fig. 1). Although it was not measured, it can be assumed that a significant proportion of eggs deposited onto these pods by *B. villosus* are also lost. At this portion of the axis, the pod-length is more variable, and is generally smaller than elsewhere. Although *B. villosus* females prefer larger pods for egg-laying (Fig. 4), they still lay some eggs onto pods at this portion of axis (Fig. 5). The reason for the increased number of eggs deposited at the very distal end of infructescence could, therefore, be due to variation in pod development. When pods become unsuitable for egg-laying at the proximal end, pods at the distal part may reach the right size and/or quality being in synchrony with *B. villosus* oviposition. It is also plausible that pod development slows down with the distal pods due to nutrient allocation problems.

On the contrary, the number of aborted seeds within pods is independent of the pod's position along the infructescence axis (Fig. 3), which may suggest a different process in abortion. The abortion of seeds at ovule stage substantially decreases the number of seeds suitable for bruchid development (by 75%), to an average of two full-grown seeds per pod. In spite of this, only ca. 8% of such seeds contained a bruchid seed predator. Such a low seed infestation level is the more remarkable as the number of intact (uninfested) seeds significantly increased with longer infructescence axis and as pods' lengths increased. It seems that *B. villosus* does not show a "resource concentration" response. Similarly, larger pod clusters of *Asclepias syriaca* L. had more undamaged pods (Franson and Willson 1983), and *Hylemya* flies' seed predation response was not density dependent on *Polemonium* at the beginning of flowering season (Zimmerman 1980), or that of four *Bruchus* species on *Vicia tenuifolia* (Szentesi and Jermy, unpubl.). At the same time no resource assessment by females of *B. villosus* could be detected; on the average they laid ca. 4 times more eggs than the mean number of available full-grown seeds per pod. It is known that the body size of adult bruchid beetles correlate well with seed size (Szentesi and Jermy 1995). Thus, a source of variability is the remarkable body size variation within bruchid species due to seed size, which can also result in considerable differences in lifetime fecundity of females.

A further factor that contributes to the relatively low level of seed infestation is egg parasitisation that takes a toll of ca. 15% of eggs laid. It was also observed that some first instar larvae could not penetrate the tough inner lining of the pod wall while attempting to burrow from the egg on the pod surface to a seed within the pod, and became trapped in the pod wall. This may highlight an inadequate adaptability of larvae in relation to plant traits. In addition, intraspecific larval interactions within seeds can be expected to increase larval mortality. Indeed, Waloff (1968) reports 1.7-35% larval mortality of *B. villosus* on *Cytisus scoparius* due to intraspecific interaction depending on number of seeds per pod. The number of emerging *B. villosus* adults further decreases by ca. 32% due to larval parasitoids on *L. anagyroides*.

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