

PREDISPERSAL SEED PREDATION OF THE INTRODUCED FALSE INDIGO, *AMORPHA* *FRUTICOSA* L. IN HUNGARY

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Amorpha fruticosa is a widespread leguminous shrub from the United States now found in Hungary and in most of Central and Southeast Europe. Its predispersal seed predator (pre-DSP), in the new habitat, the bruchid *Acanthoscelides pallidipennis* is also native to the USA. Loss of seed crop to the seed predator only rarely exceeds 40%, which may indicate a predator-satiation strategy in *A. fruticosa*. The plant species is exploited by three bruchid species and by a leaf/flower-consuming and stem-galling lepidopterous community of at least nine members in the USA, and the level of parasitisation of *A. pallidipennis* is regularly high. On the contrary, neither the plant, nor its seed predator are used as resources by, respectively, other phytophagous insect herbivores and parasitoids from the local fauna in Hungary (i.e. both of them are unutilised resources). *Amorpha* contains rotenone, a natural insecticide, and this may explain the lack of consumption by non-adapted phytophagous insects in Hungary.

Key words: seed predation, Bruchidae, indigobush, rotenone, introduced species

INTRODUCTION

Seed predation is thought to be an important regulating factor in plant population dynamics and it is one of the thoroughly studied examples of this process (LOUDA 1982, CRAWLEY 1983, 1989a, 1989b, WATKINSON 1986). Seed predators are organisms that consume plant propagules and generally kill potential plant individuals (JANZEN 1971, AULD & MYERSCOUGH 1986 and others); therefore, they have a direct, easily measurable impact on plant fitness. Theoretically, specialized herbivores without food limitation are not likely to achieve population levels high enough to limit plant population growth (CRAWLEY 1989a), especially in the case of such plant strategies as predator satiation (JANZEN 1971), or if seedling recruitment is not limited by the availability of microsites for germination. Also, the impact of seed consumption cannot be directly compensated for by the plant (e.g. by compensatory regrowth; ISLAM & CRAWLEY 1983). Selection exerted by the postdispersal seed predator (post-DSP) most likely affects seed dispersal strategies (CASPER 1988), whereas predispersal seed predation (pre-DSP) may result changes in crop size (HARPER 1977) and crop apparency.

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The influence of seed-consuming organisms on a plant population depends on size, diet specialization, numerical population response, etc., of the seed predator, and also on plant reproductive characters. For this context the leguminous shrub *Amorpha fruticosa* and its pre-DSP, *Acanthoscelides pallidipennis* are considered here. False indigo (= indigobush) is an introduced and naturalized plant species in continental Europe. Seed predation of *Amorpha* in its natural habitat (in the USA) was documented by ROGERS & GARRISON (1975), among others.

The objectives of the present work were to collect and evaluate data that would form the basis for future investigations on the impact the pre-DSP of *Amorpha* may have on its host plant's population dynamics. They included studies on the biology of both the plant and its seed predator raising questions such as:

- whether exclusion of pre-DSP results in an increased seed production;
- how infestation patterns vary in space and time;
- how local plant colonisation proceeds;
- how local herbivorous and entomophagous faunas respond to the plant and its pre-DSP's presence.

MATERIALS AND METHODS

The plant

Amorpha fruticosa L. (Leguminosae, Astragaleae) in North America inhabits mostly stream banks. For a general description of its morphology, ecology and taxonomic relationships see REHDER (1951), HEGI (1975), KRUSSMANN (1976), and RICKETT (1979). The species was brought to England and grown as an ornamental as early as 1724, and to continental Europe about 1750 (HEGI 1975). In Hungary, following the First World War, it quickly spread along the shores of the Danube and Tisza rivers during the 1920–30s. By 1938 it was reported to outcompete oak seedlings along the river Sava, and by 1950 it was abundant everywhere in the country (PRISZTER, S. pers. comm.). Its southernmost European occurrence was reported from Turkey (DAVIS 1970). It is present in Russia (CZEREPAKOV 1973) and mainland China (FAN 1981).

Habitats primarily preferred by the false indigo in Eastern-Central Europe are water shorelines, flood areas, wet meadows (accompanying species: *Glyceria*, *Echinochloa* spp., *Polygonum lapathifolium*, *Bidens tripartitus*), gallery forests (accom. spp.: *Salix alba*, *S. fragilis*, *S. triandra*) and rarely marsh-meadows with *Alopecurus pratensis* (Soó 1966). The species seems to be associated with areas having a normal or high water table, or where temporary inundations occur; however, it can also be found in dry places.

Sampling and observations

Sampling and observations were begun in 1980 in diverse parts of Hungary (Table 6) and lasted for about a decade. Random samples of flowers, and pods at different phenological stages were regularly collected. Usually 7–11 infructescences were collected, their lengths measured, the number of pods counted and 10 to 20% of the pods of a raceme randomly taken as a sample to determine infestation of the infructescences. These pods were individually placed into small vials and the adult beetles allowed to emerge in the laboratory. This method was adapted as the bruchid species, if allowed, was able to produce at least one more generation in samples taken to the labora-

tory, thus making infestation levels unrealistic. Large samples (10000–20000 pods) were also collected to obtain parasitoids of *A. pallidipennis*.

The same plant populations were regularly visited, sampled, censused and observed to obtain data for plant and seed predator phenology, including behaviour in flowers or on other plant parts, oviposition, abundance of adults on the vegetation, etc. The number of eggs laid, hatching rate and oviposition sites were noted.

In one year (1986) samples of pods were taken weekly: (a) from mid-July until the end of August, letting the adults emerge in order to learn the earliest possible infestation date (relative to the rate of endosperm development), and (b) from September through November, freezing the pods after collection to kill all instars, and then dissecting them to determine the developmental phases before overwintering. The data on age-class distribution of the pre-DSP was compared by Duncan's multiple range test for unequal sample size.

The pod "rain" of fruiting plants was followed for two seasons at two localities by placing 1/16 m² (25 × 25 cm size) plastic net-trays randomly on the soil surface under plant populations estimated to be 5–10 years old. The sum of the tray surface areas were 5 and 1 m², respectively. The trays were checked at least twice each season by counting the number of intact pods and those having emergence holes. The first inspection (May) gave the number of pods fallen during late autumn and winter, while the second (October) sample was a mixture of pods that had overwintered on the plant + aborted and ripe pods of the new season.

In order to gain information about reproduction strategies of the plant species, pollinators were observed, flowers were isolated by nets, and root system of 19 individuals of various ages were examined (by partial or full excavation) to obtain evidence of vegetative propagation and/or root-root system connections of individuals.

The soil seed banks under parent plants were also sampled. Eight samples (a mixture of soil and plant litter), 48 ± 22 g each, were taken at 1–2 cm depth, brought to the laboratory, and the pre-DSP adults allowed to emerge.

The seed predator and other phytophages

The seed-consuming guild on *A. fruticosa* consists of three *Acanthoscelides* spp. in the USA (JOHNSON 1979) (Table 1) and one in China (FAN 1981). In Hungary, the only phytophagous seed predator is *Acanthoscelides pallidipennis* (Motschulsky) (Coleoptera, Bruchidae), a pre-DSP. It is an introduced species, native to North America, where it also infests *Errazurizia rotundata*, *Amorpha californica*, *A. canescens* and *Parryella filifolia* (all members of the tribe Amorpeae; CENTER & JOHNSON 1974, JOHNSON 1979, 1981). It is not known when *A. pallidipennis* arrived to Europe. On the basis of museum records the first collections were from 1972 (Hungary, Bulgaria) and 1975 (Yugoslavia). The first specimens (two distinct samples) were identified by JOHNSON (1979, pers. comm.), but the species was described as new to Europe by WENDT (1981) based on data available from Hungary. By body and genitalia morphology the adults were remarkably uniform, a finding quite surprising because US populations are enormously variable (JOHNSON 1979, pers. comm.).

A survey of faunistic data on *A. fruticosa* in its native land indicates that at least three gelechiid moth species (one forms stem galls), six species from the families Pieridae, Hesperidae, Saturniidae and Notodontidae exploit the plant in various ways (TIETZ 1972, HODGES 1974, 1978) (Table 1). Most species are specialists on leguminous plants. In Europe, two scale species (*Eulecanium corni* and *Neopulvinaria imeretina*, the latter is an introduced species) (MITIĆ-MUŽINA 1960, SCALTRITI 1977) were reported to be occasionally present on *A. fruticosa*. The difference between the numbers of phytophagous insect species inhabiting *Amorpha* in its native and new habitats is significant ($\chi^2 = 7.9611$, $df = 1$, $p = 0.005$).

An experiment was performed to exclude the pre-DSP from *A. fruticosa* in 1993. Twenty-five racemes were randomly selected on different individuals of a mature, productive *Amorpha* stand (number of racemes per stem: 32.2 ± 17.0, mean ± SD, $n = 21$; number of raceme-bearing stems/m²: 7.2 ± 3.8, $n = 13$) in Szentendre-island, and at the start of pod initiation (June 10) for each of the following treatments: (a) sprayed with insecticide in two-week intervals and also bagged with a nylon net, (b) sprayed with water and also bagged with net, and (c) unsprayed and

Table 1. Phytophagous insect species on *A. fruticosa* in the US and in Central Europe.

Species	Source
USA	
Lepidoptera	
<i>Agonopterix dimorphella</i> CLARKE	HODGES 1974
<i>A. argillacea</i> WALSINGHAM	HODGES 1974
<i>Automeris io lilith</i> STRECKER	
<i>Catocala amestris</i> STRECKER	
<i>C. consors</i> (ABBOT et SMITH) ¹	
<i>Dasylophia anguina</i> (ABBOT et SMITH)	HODGES 1978
<i>Epargyreus clarus</i> (CRAMER)	
<i>Achalarus lycidas</i> (ABBOT et SMITH)	
<i>Zerene caesonia</i> (STOLL)	
Coleoptera	
<i>Acanthoscelides pallidipennis</i> MOTSCH.	
<i>A. submuticus</i> (SHARP)	JOHNSON 1979
<i>A. floridae</i> (HORN)	
CENTRAL EUROPE	
Coleoptera	
<i>Acanthoscelides pallidipennis</i> MOTSCH. ²	WENDT 1981
Homoptera	
<i>Eulecanium corni</i> LEON. ³	MITIĆ-MUŽINA 1960
<i>Neopulvinaria imeretina</i> HADZ. ⁴	SCALTRITI 1977

¹Uncertain, though *A. fruticosa* is mentioned as a food plant.

²Introduced.

³Occasional.

⁴Occasional and introduced.

unbagged. For insecticide treatment an organic phosphate ("Ultracide") was applied in a concentration of 0.2% (v/v). On Sept. 24 the racemes from all treatments were collected and evaluated for bruchid infestation.

The parasitoids

No parasitoid species native to North America seem to have been introduced far that attack *A. pallidipennis* in Hungary. ROGERS and GARRISON (1975) noted 3.5–9.4% parasitism by a single eulophid (*Horismenus productus* Ashmead) in the USA. This species, however, is a member only of a larger parasitoid guild present on *A. fruticosa* (CUSHMAN 1911).

Phytochemistry

Extracts prepared from the plant are toxic to arthropods (BRETT 1946a, b, BRETT & HODNETT 1947, HANSBERRY & CLAUSEN 1945). CROMBIE and PEACE (1963) and CROMBIE *et al.* (1971,

1973) proved that biosynthesis of rotenone takes place in the plant. Rotenoids were also isolated from fruits of *A. fruticosa* by SOMLEVA and OGNANOV (1985) and KASIMOV *et al.* (1972). Besides toxicity, the insect antifeedant property of chemicals isolated from pods of *A. fruticosa* was also demonstrated on non-adapted phytophagous species (GOMBOS & GASKÓ 1977, GOMBOS 1985). Pustules on the pods' surface contain resinous material and the entire plant smells of terpenoids. *Amorpha* possesses the nonprotein amino acid amide (τ -methylene glutamine) (BELL 1971), but lacks canavanine (BARNEBY 1981).

RESULTS

The plant

In addition to the central stem, several new vegetative shoots grow from the same root and extend the ground surface coverage of the plant. Similar-sized individuals slowly close the area between themselves, eventually reaching each other and providing an almost continuous canopy. New seedlings cannot be found under such multi-stemmed individuals (although germinated seeds having 2–3 cm long radicles may be found in the seed bank under the parent plants because shading is not strong). Seedlings spread around the outskirts of such large individuals, which sometimes approach 30 m in diameter.

New individuals are recruited from seeds. No root-root connections were found among individuals excavated at Szentendre-island in 1987. Although roots at first ran superficially, later they grew deeper and no vegetative reproductive structures were seen on them.

New shoots grow in May, flowering is mainly in June. The fragrant flowers open first at the lower part of an inflorescence (raceme). Outcrossing seems to be the fundamental breeding system, although self pollination is possible (HEGI 1975). (I have isolated several inflorescences with dense nylon nets. Pods never grew on such inflorescences. This does not exclude self-compatibility, only that pollinators may be needed for pod production.) Pollinators are mostly honeybees, and the pre-DSP bruchid itself. There are three or four inflorescences, 9–18 cm long per stem. The number of flowers per inflorescence is 291.5 ± 57.2 at blooming, while some days later that of the small pods is 246 ± 107.6 (mean \pm SD; $N = 46$, Szentendre-island, 1983), a ca. 20% decrease. Pods are one seeded, indehiscent, covered by pustules. They are 3–4 mm long in mid-July and reach full maturity and length by the end of August, and early September. The pods are 5–10 mm long, and slowly but continuously drop when ripe. The first pods that drop are overwhelmingly aborted and rarely harbour developing bruchid larvae that reach adult-stage (among 623 pods only 6% yielded adults). A substantial proportion remains on the parent plant, overwinters and can even be found the next summer. The number of infructescences from the previous year's crop counted the next year in May was still 15.3 ± 9.8 (mean \pm SD; $N = 38$, Szenten-

Table 2. Number of infructescences overwintering on plants, and of pods dropped into trays under a single *A. fruticosa* bush. Locality: Nagykovácsi-Júlianna major (means \pm SD).

Date	No. of pods dropped		No. of racemes remained on plant ²	No. of pods re- mained on plant ²
	per tray	per square meter ¹		
10/14/1987	–	–	222	–
until 3/30/1988	76 \pm 27	1223 \pm 440	82	51 \pm 33
until 5/19/1988	80 \pm 32	1272 \pm 512	58	26 \pm 15
until 6/1/1988 ³	92 \pm 37	1476 \pm 604	0	0
until 8/17/1988 ⁴	79 \pm 43	1272 \pm 693	–	–

¹ Assuming homogeneity of distribution.² Pods of the main racemes.³ No last year pods remained on plant.⁴ Early falling pods of the new growing season.

dre-island, 1988) per largest plant stems (2–4 cm diam. at 50 cm height). (See similar data in Table 2 for a smaller bush at another locality.) Before the onset of winter, 155.4 \pm 47.6, 175.6 \pm 60.5, and 143.0 \pm 50.9 (mean \pm SD) pods could be found at three localities, respectively (N = 7, 1988), representing again a further ca. 20% decrease in comparison with the number of flowers. The number of larger (1–4 cm diam.) plant stems per m² was 12 \pm 3 (N = 14 plants) while the number of infructescences per stem was 9.0 \pm 10.1 (N = 46; both data from Szentendre-island, 1988). The number of fallen pods per m² (a rough estimate) through three collection periods is given in Table 3. Values calculated for another locality differed substantially due to size and age of plants (Table 2).

Dropped pods (either infested with the bruchid or intact) are buried in the soil and covered by leaf/twig litter. Samples taken from the upper soil layer under the parent plant [48 \pm 22 g soil] contained 314.6 \pm 187.3 (mean \pm SD) pods. The time required to accumulate this number is not known. Such samples, however, probably do not adequately represent the seed bank in the soil (BENOIT *et al.* 1989).

Table 3. Pods dropped by an *A. fruticosa* population into trays placed under the plants (Szentendre-island, 1987–89, starting with 84 trays).

Interval of crop collecting	Percent of trays recovered	No. of pods counted per tray	No. of pods calculated for m ² ¹	Percentage of infested pods in trays
Oct. 1987 – May 1988	59.5	315 \pm 219	5049 \pm 3505	1.8 \pm 1.6
May 1988 – Oct. 1988	40.5	371 \pm 295	5928 \pm 4711	4.0 \pm 4.1
Oct. 1988 – May 1989	28.6	202 \pm 100	3236 \pm 1604	3.7 \pm 4.4

¹ Assuming homogeneous distribution.

In 1987 a ca. 1 km long \times 10 m wide indigobush population was discovered which had a crop from the previous year (with many pods on the plants), but no new fruits, therefore, it was considered a "nonmasting" population. Numerous adults of the pre-DSP were collected on this population which was ca. 1 km away from the nearest *Amorpha* population bearing a large fresh crop ("masting" population).

The seed predator

Adults emerge from infested pods on or under the host plant for at least three months beginning in June. They are very mobile, fly well and prefer sunlit surfaces. While flowers are available, they actively move into them (and frequently emerge covered with pollen). They also occur on leaves of *Amorpha*, and in the absence of host plant inflorescences, on flowers of nearby plants (e.g. *Matricaria*). Occasionally adults could be observed in sunflower (*Helianthus annuus*) heads (HORVÁTH 1987). They also temporarily occupy the surrounding vegetation. Sweep netting on the host-plant (following flowering) resulted in 9 ± 7 adults, and on non-host plants in the vicinity 0.9 ± 0.9 adults (mean \pm SD; 10 sweep-net strokes; Szentendre-island, 1987).

Table 4. Egg-load of *A. fruticosa* infructescence axes at pod ripening and before pod-drop (means \pm SD).

Locality/date of sampling	N	Raceme axis length (cm)	No. of eggs/raceme axis ¹	No. of ripe pods/raceme	Bruchid infestation (%)
Balatonzamárdi					
Aug. 1980 ²	19	8.7 \pm 3	9.7 \pm 9.6	71 \pm 44	61 \pm 11
Aug. 1985	11	14.6 \pm 1.4	101.5 \pm 60.2	209 \pm 77	29 \pm 7
Oct. 1986	11	12.4 \pm 1.8	210.0 \pm 114.4	160 \pm 35	6 \pm 6
Sept. 1987	11	16.3 \pm 1.9	72.5 \pm 75.4	245 \pm 91	11 \pm 11
Oct. 1988	7	12.2 \pm 1.2	59.4 \pm 53.1	155 \pm 48	32 \pm 25
Szentendre-island					
Oct. 1987	11	15.4 \pm 1.5	21.9 \pm 18.1	232 \pm 56	12 \pm 8
Oct. 1988	7	11.9 \pm 3.1	2.7 \pm 3.7	176 \pm 61	7 \pm 8
Sárosd					
Dec. 1988	7	11.6 \pm 1.9	55.3 \pm 42.6	143 \pm 51	18 \pm 19

¹Eggs laid under the calyx are not included.

²Overwintered racemes. Counted and measured next summer (1981).

Most egg-shells must have been washed down during winter.

Egg-laying starts about mid-July, when pods are hardly bigger than the surrounding tube-like calyx (3–4 mm). (An ovule of $0.5\text{--}1 \times 2$ mm is attached to the distal end of the pod.) Two sites in the flowers are used by females for oviposition: one is the axis of the raceme (Table 4), and the other is the gap between the pod wall and calyx-tube. Egg-laying females thoroughly examine the pod surface by running around it, touching it from time to time with the antennae, palpi and with the tip of the ovipositor. Following oviposition the female drags the ovipositor on the pod's surface. While the raceme axis is sometimes densely packed with eggs, only 1–5 eggs/pod are laid under the calyx. The eggs laid on the raceme axis are unevenly spaced into groups and most of them are fertile (bear larval exit holes). It is probable that infestation level is based on the former, and only to a minor extent by larvae hatching from eggs laid on the raceme axis. There is no significant correlation between pod density (= the no. of pods/raceme axis length in mm) and the number of eggs laid on raceme axis (Fig. 1, linear regression, $n = 98$, $r = 0.0761$, NS). Similarly, percentage of damaged pods along the raceme axis is not correlated with increasing number of pods (Fig. 2, $n = 98$, $r = -0.0728$, NS). In fact the relationship is density-independent. Therefore, there is little contribution to infestation from eggs laid on the raceme axis. Their numbers sometimes surpass the number of pods on the raceme by the end of pod ripening (mid-October, 1986; mean ratio and SD is 1.35 ± 0.73 , extremes: 0.7 and 2.6, $n = 11$), while opposite relationships were found in another year (in July: 0.28 ± 0.16 , $n = 7$; in August: 0.46 ± 0.25 , $n = 21$; in October 0.43 ± 0.41 , $n = 7$, all data from the same locality, 1988).

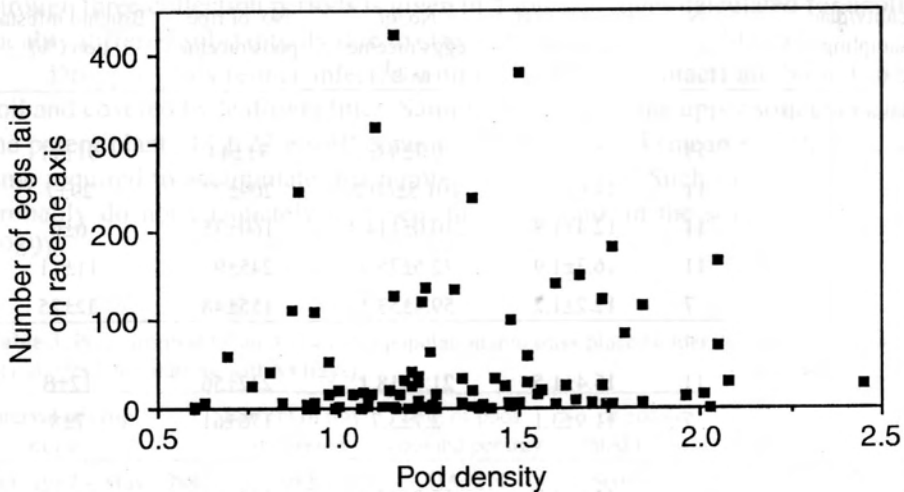


Fig. 1. Scatterplot of the number of eggs laid by the seed predator, *A. pallidipennis* on raceme axes as a function of pod density (total number of pods/total axis length in mm) on *A. fruticosa*. The scatterplot comprises data from the localities Szentendre-island, Balatonzamárdi, Sárossd and Üröm, from years 1986–89 ($n = 98$)

Emerging first instar larvae have legs and bore into the pods under the calyx, then enter the seed at its proximal end. (First instar larvae sometimes bore deep holes on the raceme axis.) During development the yellow-coloured larva consumes the larger part of the seed, however, some endosperm sometimes remains at the distal end. The number of stadia is not known to me. Adults from eggs of early oviposition in the same year may emerge in September-October, however, the overwhelming majority overwinter as quiescent larvae (Table 5, and WENDT 1981). The larvae pupate within the seeds, the adults produce exit holes at the proximal end of pods (right above the calyx). The one-seeded pod's endosperm is large enough for one larva only.

Crop loss of indigobush to *A. pallidipennis* varied according to year and locality (Table 6), but it never reached 100%. The exclusion experiment saved ca. 6% pods from being infested with the pre-DSP. A combination of insecticide spray and bagging resulted in a bruchid infestation level of $0.06 \pm 0.17\%$, the spray with water plus bagging produced $0.15 \pm 0.35\%$, and unsprayed and unbagged control had a pod infestation level of $6.29 \pm 6.57\%$ ($n = 25$). There was an infestation level of $17.5 \pm 3.2\%$ of pods by *A. pallidipennis* extracted from the soil samples.

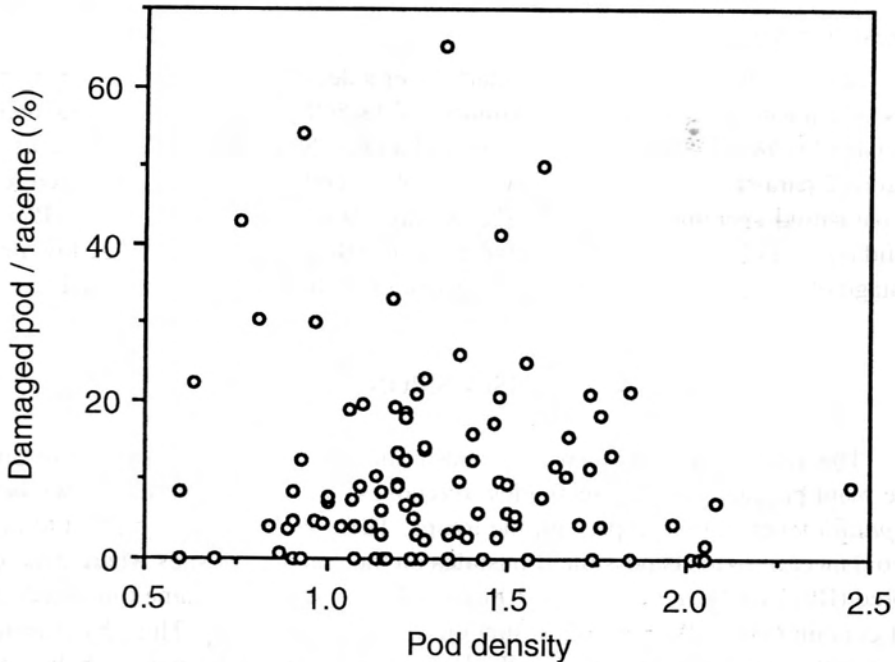


Fig. 2. Scatterplot of infestations caused by the seed predator, *A. pallidipennis* as a function of pod density (total number of pods/total raceme axis length in mm) on *A. fruticosa*. The scatterplot comprises data from the localities Szentendre-island, Balatonzamárdi, Sárosd and Úröm, from years 1986–89 ($n = 98$)

Table 5. Age-class distribution of *A. pallidipennis* larvae before overwintering (n = 7±15 pods each; means±SD).

Date (1986)		"Young" ¹	"Old" ²	Infestation (%)
		larvae (%)		
September	15	30±11a	10±20b	39±26a
October	1	22±8ac	13±22ab	34±19a
	8	11±7bc	16±18ab	28±24a
	20	7±7b	22±12ab	27±19a
	29	6±6b	27±16a	23±11a
November	4	7±7b	27±28ab	20±25a
	12	1±3b	27±11a	21±13a
	24	4±5b	29±7a	25±9a

¹ L₁-L₂?² L₃-L₄?

Means followed by the same letters in a column are not significantly different at the 0.1% ("young") and 5% ("old") probability levels (DNMR-test for ESS, see Materials and Methods).

The parasitoids

Many pods were collected regularly over a decade. On occasion, low numbers of parasitoids emerged. For instance, of 18,560 pods collected at Szentendre-island (1988) there were 7.05% bruchid and 0.15% parasitoid infestations (a total of 2 parasitoid specimens). The result of several years' collections were ca. 30 parasitoid specimens from the *Pteromalus*, *Dinarmus*, *Mesopolobus* (Pteromalidae), *Eupelmus* (Eupelmidae) and *Triaspis* (Braconidae) genera. A low percentage of egg parasitisation by *Trichogramma* sp. has also been detected.

DISCUSSION

The relationship between indigobush and its pre-DSP is an intimate one. The plant produces toxic insecticides (rotenones). Presently it is not known how *A. pallidipennis* larvae cope with the toxins. There are at least two possibilities: Avoidance of toxins is possible if pustules on the pod are the sites where they are stored (BRETT 1946a, CENTER & JOHNSON 1974), and at the same time seeds do not contain or possess only a low amount of such substances. Thus, by entering the pod through a site devoid of such glands, the toxins can be avoided behaviourally. [A quite opposite situation was described by CENTER and JOHNSON (1974) for *A. submuticus*, another pre-DSP of *A. fruticosa*, where the first instar larvae preferred entering the pod via the pustules.] More likely is the possibility that the

seeds do possess such chemicals because both dormant seeds and seedlings of *A. fruticosa* contain pre-rotenoid chemicals that are mobilised during germination and early growth (CROMBIE *et al.* 1973). In this case, the bruchid, while inside the seed, must "handle" the toxins metabolically, perhaps in the way described by SZENTESI and WINK (1991) for another pre-DSP species inhabiting the alkaloid-bearing *Laburnum anagyroides*.

Table 6. *A. pallidipennis* infestation of *A. fruticosa* pod samples in Hungary (N = 7–56 racemes; means±SD).

Site of collection	Year	Adult emergence (% of pods)
Balatonzamárdi	1985	30.0±32.4
	1986	5.8±6.2
	1987	11.4±10.6
	1988	31.9±25.0
	1989	9.6±7.7
Szentendre-island		
"masting" population	1983	1.4±1.8
"masting" population	1987	11.6±7.5
"non-masting" population	1987	0
"masting" population	1988	7.1±7.5
"masting" population	1989	2.9±3.0
"non-masting" population	1989	12.7±6.5
"masting" population	1993	6.3±6.6
Tiszaug – river Tisza shore	1984	4.6±4.2
Szarvas – river Körös shore	1985	19.8±11.6
Botanical garden	1984	17.7±10.0
Botanical garden	1985	0
Vácrátót- Botanical garden	1983	16.0±15.3
	1984	1.1±1.3
Budapest	1983	16.0±15.3
Ohat	1984	7.6±8.7
Balatonszabadi	1983	14.5±9.2
Sárosd	1987	0
Nagykovácsi-Júlianna major	1988	18.2±19.4
	1984	11.1±15.9
	1986	19.3±16.6
Üröm-Pilisborosjenő	1989	6.9±7.1

Impact and exploitation patterns of A. fruticosa by its pre-DSP.

Herbivore exclusion experiments (e.g. WALOFF & RICHARDS 1977) clearly show that plant performance is better in the absence of herbivores. Available information (see CRAWLEY 1989b) indicates that invertebrate herbivores sometimes are able to affect the population dynamics of introduced plant species. JERMY (1984) assumed that the effect of herbivores on introduced plant populations was due to the absence of natural enemies allowing the herbivore population to reach outbreak levels. On the basis of occasionally high (87%) pod infestation by *A. pallidipennis*, ROGERS and GARRISON (1975) hypothesized that the seed predator was able to regulate indigobush populations to some extent in the USA. Although released from the impact of native natural enemies (see Table 1) the bruchid still rarely produces a crop loss over 40% in Central Europe. My exclusion experiment on *A. fruticosa* saved about 6% of pods from its pre-DSP that may gain significance at locations only where plant recruitment is possible due to free sites. Infestations by the bruchid are uneven by locality (Table 6), by plant and among racemes, and are much lower than what the number of available pods would allow, and this indicates that the plant may satiate its seed predator.

The data obtained in this study are not sufficient to draw quantitative conclusions on plant population dynamics as affected by the pre-DSP. Nevertheless, they do give some information on plant performance. It seems that *A. pallidipennis* is neither food-limited on *A. fruticosa*, nor limits the distribution and spread of its host plant. Instead, the inability of seedling recruitment by the shortage of available microsites around parent plants may be more important. The number of seeds exponentially decreases by distance from the parent plant (HARPER 1977, HOWE 1986) and even there, establishment depends on many factors. In spite of the large number of pods produced/m²/year by *Amorpha*, only those that were dispersed at some distance from the parent plant had a chance for survival. The high terpene content of pods and other plant parts might hamper germination under the parent plant, although to date no such investigations have been carried out.

The egg-laying habit of the pre-DSP seems contradictory. Despite the potential for a higher infestation level of pods, it does not occur even when the number of eggs laid on a raceme axis considerably surpasses the number of pods available on that raceme (Table 4, 3rd line). Some factors must cause a high L₁ mortality. The larvae hatching from eggs laid under the calyx tube are at an advantage in entering the pod in comparison with those from eggs placed on the raceme axis that must crawl along the axis to find a pod. Dragging of the ovipositor, possibly connected with pod-marking behaviour, also seems to have a dubious significance as usually more than one egg is laid under the calyx. Uneven distribution of eggs along racemes may be explained by the order of pod maturation (lower to upper). Similar oviposition patterns (i.e. overload of pods by eggs) are

quite abundant among bruchid species (LABEYRIE 1990, SZENTESI & JERMY 1995, SZENTESI *et al.* 1996).

In view of these data, the questions arise whether the ovipositing *A. pallidipennis* females were able to assess resource size, and what factors influenced egg-laying. Two raceme characters may determine the assessment: raceme axis length and number of pods on the raceme. Neither is egg-load affected by pod density (Fig. 1), nor does infestation level correlate with it (Fig. 2). It is possible, however, that egg-load assessment is influenced at the early stage of pod production, when the crop is about 40% higher in comparison to that at pod ripening (the difference is the result of pod-abortion). The imperfection of female oviposition behaviour may also be a contributing factor.

Possible escape mechanisms by A. fruticosa

One escape mechanism may be connected with masting. It could serve as a predator satiation mechanism when crop is abundant (masting year) followed by year(s) without crop (JANZEN 1971, HARPER 1977). It is supposed that many leguminous species are able to change the size of crop synchronously within a population, and *A. fruticosa* is one of the shrub species having cyclic cropping (SILVERTOWN 1981). Occurrence of such a seed predator avoidance strategy may be expected. Although it is not experimentally proven, my observation supports this view. Previous year and next year infestation levels (varying greatly, Table 6) should, theoretically, give some information on the population size changes of the seed predator, however, to prove or manipulate this experimentally is almost impossible (CRAWLEY 1989a). Another escape mechanism could be provided by the phytochemical properties of the species. Although, it has not been investigated experimentally, it is very likely that non-adapted herbivores as well as members of the third trophic level are affected by toxins present in *A. fruticosa*. Several food chain studies demonstrated that, among experimental conditions, an elevated or close to natural concentration of plant allelochemical in the host's diet would seriously affect survival of the primary parasitoid (THURSTON & FOX 1972, BENN *et al.* 1979, PRICE *et al.* 1980, CAMPBELL & DUFFEY 1981, BARBOSA *et al.* 1986, THORPE & BARBOSA 1986).

A. fruticosa and its seed predator as unutilised resources

It is a widely held view that some introduced plant species rapidly and successfully spread at the place of introduction because (1) they were free from their native herbivores (JERMY 1984), and (2) they usually occupied disturbed areas first. Established introduced-immigrant species free from consumers in the new habitats may exist as unutilised resources or occupy "empty niche space" (PRICE 1984, LAWTON 1982, 1984, STRONG *et al.* 1984, ARTHUR 1987, WALKER & VALENTINE 1984, COMPTON *et al.* 1989, but see CRAWLEY 1987, for counterar-

guments). Seemingly, since its introduction, *A. fruticosa* is an "unexploited" or only occasionally used resource by herbivores of the local phytophagous insect fauna in Central Europe. The only representative in Central Europe of the seed predator community in the USA is *A. pallidipennis*; therefore, the partitioning of the seed resource is incomplete in the invaded areas. To the contrary, there are at least nine, mostly oligophagous lepidopteran species on *A. fruticosa* in its native habitat (Table 1). The utilization of the pre-DSP as a resource by parasitoids is also more intensive in the USA, although it is restricted to one parasitoid species (ROGERS & GARRISON 1975). In Central Europe parasitisation is insignificant (ca. 0–0.2%) and occasional, and is probably exerted by species of wider host preference. In this sense *A. fruticosa* and its seed predator are indeed unutilised resources in their new habitat.

As for the factors affecting the presence or absence of herbivores, chance events (JERMY 1990) may be more important than previously thought. In addition, some (e.g. chemical) properties of the plant also have to be taken into account. For instance, BIRCH *et al.* (1985) demonstrated that rotenoids of *Lonchocarpus* are indeed toxic to the non-adapted seed predator, *Callosobruchus maculatus*. However, it is also a possibility that potential colonists may be lacking in the invaded habitats (LAWTON & STRONG 1981).

Introduced species are able to change genetically (BERENBAUM 1991). The plant was brought into Europe perhaps 200 years earlier than its seed predator. During this time phytochemical changes might have taken place influencing present relationship with the seed predator and actually resulting in lower infestation levels than those reported by ROGERS and GARRISON (1975) for the USA. Another point might be a lower genetic variability of the bruchid population originating from a single introduction (JOHNSON 1979, pers. comm.), although this assumption was made only on the basis of morphological examination and no other (e.g. molecular) studies were carried out.

* * *

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