The Effect of Seed Predation on Pod Abortion by the Prairie Legume, *Baptisia leucophaea*

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ABSTRACT

The effect of seed predation on pod abortion was examined within a population of *Baptisia leucophaea*. The perennial is infested by the predispersal seed predator, *Apion rostrum*. The difference between pods initiated and pods ripened, or pod loss, served as an estimate of pod abortion. Plants treated with sticky Tanglefoot in an attempt to reduce weevil infestations showed significantly higher mean counts of seeds/plant, pods ripened per plant, and lower pod loss. Tanglefoot reduced seed predation and pod abortion in *B. leucophaea*. Pod inflation indicates pollination, but some only partially inflate and tend to wither prior to ripening. These pods were found to possess significantly fewer seeds than inflated pods, suggesting the legume selectively aborts pods having few seeds. Weevils, however, were not found in these pods. Thus, the effect of seed predation on selective abortion of the partially inflated pods could not be determined.

INTRODUCTION

Fruit abortion is common among plants and is usually explained as either an inability to ripen all fruits or as a means to remove damaged fruits which are unlikely to contribute to plant fitness (Janzen 1977, Niesenbaum 1996, Stephenson 1981, Stephenson et al. 1988). Maximization of seed production may depend on both explanations during an average year within a heterogeneous environment when the potential seed yield is not realized. In the following study, pod abortion was examined within a population of *Baptisia leucophaea* Nutt. (Fabaceae) within a reconstructed tallgrass prairie plot in northeastern Illinois. Of special interest was the effect of predispersal seed predation by *Apion rostrum* Say (Coleoptera: Curculionidae) on pod abortion.

B. leucophaea, or the cream wild Indigo, is widely distributed throughout mesic prairies of the Midwest (Knoph 1979, Ladd 1995). The perennial blooms from early May to June, producing creamy-yellow flowers along mostly single racemes (Swink and Wilhelm 1994). Plants clump in groups of 20 or more and project their sprawling racemes outward from the aggregate. Renewed shoot growth by the Indigo begins with spring thaw and continues until flowering. Major pollinators are *Bombus bimaculatus* Cresson and *B. fraternus* Fabricius (Petersen 1996). Pods, formed soon afterward, ripen by mid August when above-ground tissues begin to die. Seeds are released as pods dehisce or fragment. Plants reach a length of about 1 m and clumps become hidden within the emergent tall grass growth by August.

The smaller stature, earlier growth and pod production by *B. leucophaea* relative to its tallgrass congener, *B. leucantha* Say, has been explained as a strategy to reduce seed predation (Haddock and Chaplin 1982). *B. leucantha* has been found to selectively abort pods having few seeds, a quantity affected in part by seed predation (Petersen and Sleboda 1994). However, *B. leucophaea* is less conspicuous and also shows more reproductive development prior to the time when seed predators are most abundant. Hence, it was interesting to examine how sensitive *B. leucophaea* is to seed predation. In the local area, *A. rostrum* is the only seed predator of both *Baptisia* species. Overwintering adults oviposit into pods as they first develop. The weevil larvae then consume seeds as their only source of nutrition. Larvae pupate by July. Adults emerge within 10 days and disperse as pods open.

MATERIALS AND METHODS

The study site was a 0.06 ha reconstructed tallgrass plot located on the northeastern corner of the College of DuPage campus. The college lies within residential DuPage County. Usually burned annually in the fall or spring, the 25-year old plot is dominated by big bluestem (*Andropogon gerardi* Vitman) and Indian grass (*Sorghastrum nutans* (L)). About 150 *B. leucophaea* populate the plot of which 105 were randomly selected for study during spring bloom.

Eighty plants were used in the "Tanglefoot experiment" which examined how pod loss is affected by reduced weevil infestations. Pod loss served as an estimate of pod abortion. Reduction of weevil infestations was attempted in 40 of the plants by applying a thin smear of sticky Tanglefoot (Tanglefoot Co., Grand Rapids, MI) around basal and median sections of racemes. Tanglefoot, which consists of castor oil (70%), natural gum resins (25%), and vegetable wax (5%), restricts movement of climbing insects and has been effective in reducing infestations of *A. rostrum* on *B. leucantha* (Petersen 1989, 1990). The remaining 40 plants were left untreated and served as controls. We expected that less seed predation would result in higher mature seed count/pod, more plants with ripening pods, and decreased pod loss. The difference in the mean mature seed count/plant between treatments indicated the effectiveness of Tanglefoot in reducing weevil predation. Seed count/pod was measured by sampling five ripened pods per raceme. The pods sampled were the most proximal, distal, and three between. If a raceme had fewer than five pods, then all were sampled. Seed count/plant was computed as the product of the mean count of seeds/pod in the pods sampled multiplied by number of pods ripened. The number of plants ripening pods and fraction pod loss were computed from the difference in pods initiated to those ripened per plant. Seed count/plant and fraction pod loss/plant were compared between the Tanglefoot and control treatments using one-tailed Mann-Whitney tests. The number of plant ripening pods were compared between treatments by applying the ln-likelihood ratio test (Zar 1984) where the expected frequency for each group was computed using the grand mean fraction of plants ripening pods. Also measured was the mean *A. rostrum* count/plant following the same procedure used to determine seed counts/plant. This measurement, however, was not used to evaluate the effectiveness of Tanglefoot. In the event that the weevil might promote pod abortion, the number of weevils in aborted pods would remain unknown, and thus, bias counts taken when pods ripened.

The remaining 25 plants were used to study the characteristics of aborted pods. Pollination is indicated by pod inflation (Haddock and Chaplin 1982). However, many pods only partially inflate, with half the length or less inflated. These pods are smaller in length and maximum diameter between lines of dehiscence than pods that fully inflate, and invariably wither on racemes or detach beneath plants prior to the time of ripening. The interest of this experiment was to examine if the "partially inflated pods" fail to fully develop because of having few seeds as caused by weevil seed predation. The 25 plants were subdivided into 5 groups of 5. The groups were sampled sequentially during summer. The most proximal and distal pods of each pod type (i.e., partially inflated or inflated) on a raceme were sampled. Pods were measured for length and maximum diameter between lines of dehiscence. Counts of seeds and weevils were taken. Weevils also were noted for life stage. The first subgroup was sampled on 24 June as pods began to form and overwintering adult *A. rostrum* were observed on plants. Sampling of the remaining subgroups occurred at about 10-day intervals to permit the following of weevil development. The final sample was done on 5 August as the pods began to ripen and the new generation of weevils had matured. A distribution-free randomization method (Potvin and Roff 1993) was used to compare mean counts of undamaged seeds/pod and of weevils/pod. The probability (P) of obtaining the observed absolute difference between means among 5000 simulated permutations was used to compute significance. Standard error (SE) of each P was calculated as $\sqrt{P(1-P)/N]}$, where N was 5000 or the number of permutations.

RESULTS AND DISCUSSION

A summary of the Tanglefoot experiment is provided in Table 1. Eighteen (51%) of the control plants ripened pods in comparison to 34 (89%) of the Tanglefoot treated plants, a difference which was significant ($p<0.05$; G=5.823; df=1). Pods initiated were not significantly different between treatments. However, the Tanglefoot treatment showed significantly higher mean seed count/plant and pods ripened, as well as a significantly lower mean fraction pod loss than the control. Significant findings are evidence that seed predation by *A. rostrum* promotes pod abortion.

Pod expansion was complete by the middle of July (Table 2). Pods partially inflated were smaller in length and had smaller maximum diameters between lines of dehiscence than those inflated. Mean seed counts/pod from both pod types did not decrease after the 16 July low values. This observation coincided with the pupation and maturation of weevils (Table 3). Mean seed count/pod was significantly lower among pods partially inflated. These pods which are prematurely aborted by *B. leucophaea* have relatively few or no seeds. Developing seeds among plants, in general, are known to produce auxins, gibberellins, and cytokinins that control mobilization of nutrients into, and thus the maintenance of, fruits (Bidwell 1974, Street and Opik 1984). The lack of seeds, and thus pod-maintaining hormones, can explain selective pod abortion. However, the effect of seed predation on this selective pod abortion remains uncertain as no weevils were found within the partially inflated pods. Possibly, these pods lacked the nutrition necessary to support developing weevils or were unacceptable oviposition sites for discriminating *A. rostrum*.

A comparison of plant propagation under field conditions would be required to examine the conclusions of Haddock and Chaplin (1982) concerning the contrasting life history strategies between *B. leucophaea* and *B. leucantha*. However, in light of the cessation of ripening partially inflated pods that lack seeds, competition for a limited number of pollinators may provide an alternative explanation to the timing of reproductive development. Early prolific flowering may enable *B. leucophaea* to attract the few spring pollinators, but at a consequence of subsequent excess pod production. Rapid growth and ripening of pods to support those which mature seeds may enable reproductive success for the small legume in the rapidly emergent tallgrass community. This alternative hypothesis predicts greater pod loss in plants having few seeds attributed to predation. Nonetheless, evidence is required concerning abortion of pods in which seeds have been eaten. Future investigations should more carefully follow all pod types to the ripening stage to scrutinize the relationship between seed and *A. rostrum* count/pod.

ACKNOWLEDGEMENTS

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Table 1. Summary of *Baptisia leucophaea* reproductive yield and *Apion rostrum* counts (x ± s (n)). Significance pertains to statistical comparison between control and Tanglefoot treatments of reproductive yield counts. Symbols: C = control treatment; T = Tanglefoot treatment; *significant (p<0.05); and NS = not significant.

	Treatment		Significance
	C	T	
Seed count/plant	18.4 ± 38.9 (34)	19.1 ± 31.8 (36)	*
Pods initiated/plant	21.9 ± 10.6 (35)	26.4 ± 2.5 (38)	NS
Pods ripened/plant	4.5 ± 5.5 (35)	6.1 ± 0.9 (38)	*
Fraction pod loss/plant	0.81 ± 0.25 (35)	0.76 ± 0.03 (38)	*
Apion rostrum count/plant	6.3 ± 6.6 (16)	4.0 ± 4.3 (32)	

Table 2. Comparison of pod length and maximum diameter of pods fully inflated and those partially inflated on *Baptisia leucophaea* (x ± s) according to sampling date. All sample sizes equaled 10. Symbols: FI = pods fully inflated; and PI = pods partially inflated.

Date	Pod type	Length	Diameter
24 June	FI	32.3 ± 3.97	5.35 ± 1.56
	PI	17.9 ± 3.28	1.85 ± 0.47
9 July	FI	28.9 ± 4.51	11.7 ± 3.59
	PI	14.6 ± 4.93	3.50 ± 2.17
16 July	FI	38.0 ± 6.86	16.2 ± 3.22
	PI	14.4 ± 6.83	4.20 ± 2.66
25 July	FI	33.7 ± 5.08	16.4 ± 3.56
	PI	12.1 ± 2.90	3.11 ± 1.84
5 August	FI	35.2 ± 3.36	16.3 ± 1.44
	PI	14.4 ± 2.55	5.00 ± 2.09

Table 3. *Apion rostrum* development and statistical comparison of *A. rostrum* counts/pod and seed counts of *Baptisia leucophaea*/pod ($\bar{x} \pm s$) according to sampling date. All sample sizes equaled 10. Symbols: FI = pods fully inflated; PI = pods partially inflated; P = probability; and SE = the standard error of the probability.

Date	Pod type	Contribution of *A. rostrum* life stage (%)	Weevils/ pod	P; SE	Seeds/pod	P; SE
24 June	FI	Egg (86%), larva (14%)	0.7 ± 0.8		7.8 ± 3.6	0.49; 0.003
	PI				8.9 ± 5.5	
9 July	FI		0 ± 0		14.3 ± 1.5	0.002; 0.001
	PI		0 ± 0		6.2 ± 5.4	
16 July	FI	Larva (88%), pupa (12%)	0.8 ± 0.6	0; 0	3.0 ± 2.2	0.013; 0.002
	PI		0 ± 0		0 ± 0	
25 July	FI	Pupa (100%)	0.1 ± 0.3	0.002; 0.028	5.6 ± 3.3	0; 0
	PI		0 ± 0		0.9 ± 1.9	
5 August	FI	Pupa (8%), adult (92%)	1.3 ± 1.1	0.001; 0	3.6 ± 3.5	0.008; 0.001
	PI		0 ± 0		0.6 ± 1.4	