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TRADE-OFFS AMONG COMPONENTS OF BAPTISIA LEUCANTHA (FABACEAE) REPRODUCTIVE YIELD IN RESPONSE TO SEED PREDATION

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ABSTRACT

A general hypothesis in plant ecology is that trade-offs in nutrient allocations among components of reproductive yield act to minimize losses in overall yield of an environmentally stressed plant. This hypothesis was tested using *Baptisia leucantha* as the study subject and the seed predator, *Apion rostrum*, as the environmental stress. Sticky Tanglefoot was applied to one group of plants to reduce *A. rostrum* predation in both 1985 and 1988. During both years Tanglefoot groups yielded higher grand mean counts of seeds/pod, pods/plant, and larger mean shoot sizes, as indicated by basal diameters, than control groups comprised of plants that were not treated with Tanglefoot. However, the control groups did show a heavier grand mean mass/seed. Grand mean mass/seed was also the least variable of the components of plant yield within all groups of both years. In 1988, pods that were aborted from a third group of plants had significantly fewer seeds than those not aborted, suggesting *B. leucantha* selectively aborts pods. *A. rostrum* affects the number of seeds/pod and therefore should also influence pod abortion. This accounts for the fewer pods matured by the control plants that were not treated with Tanglefoot. The higher grand mean mass/seed and invariability of the component, plus the selectivity in pod abortion, are evidence that trade-offs had occurred among the components which tended to buffer against decreases in total yield.

INTRODUCTION

A general hypothesis in plant ecology proposes that trade-offs in nutrient investments among components of reproductive yield act to minimize losses in overall yield of an environmentally stressed plant (Janzen, 1977; Lee and Bazzaz, 1982; Primack and Antonovics, 1981; Stephenson, 1981; Stephenson and Winsor, 1986; Wilbur, 1977). The present study tests this hypothesis using a widely distributed legume in the Midwest, *Baptisia leucantha* T&G (Fabaceae)(Larisey, 1940) as the study subject, and as the environmental stress, the beetle *Apion rostrum* (Curculionidae) which is a seed predator of *B. leucantha* to the extent that it may consume over 5% of an annual seed crop (Haddock and Chaplin, 1982).

In Northeastern Illinois, where the study site is located, a seasonal cycle of growth by *B. leucantha* begins with new above-ground growth as the ground thaws in March. Flowering occurs from May to June with *Bombus* spp. being the major pollinator (Haddock and Chaplin, 1982; personal observation). New flowers appear as indeterminate racemes elongate. Racemes usually number one to two per plant, but may number as many as fourteen. By late June, the plants have reached their maximum height of 1 to 2m, flowering has about ceased, and pods have already formed. Many pods are aborted as the growing season progresses. Racemes may eventually bear over 200 mature pods. The cycle ends as seeds are dispersed by gravity when the pods dehisce from fall through the following spring.

A. rostrum begins its lifecycle within sealed pods of *B. leucantha* (Haddock and Chaplin, 1982). The beetle larvae emerge a few days after oviposition during June and consume developing seeds which are their only source of nutrition. Once reaching the adult stage, the beetles may stay within pods, or disperse as the pods dehisce, to overwinter (Haddock and Chaplin, 1982; personal observation). Come June, the adult *A. rostrum* re-emerge and oviposit into the pods of *B. leucantha*.

STUDY SITE

The study site was a restored 550m^2 tallgrass prairie plot located on the campus of the College of DuPage, DuPage County, IL. Restoration of the prairie began in the early 1970s. Today it is dominated by big bluestem (*Andropogon gerardi* Vitman) and Indiangrass (*Sorghastrum nutans* (L.)). Approximately 150 *B. leucantha* are scattered throughout the prairie. Mowed lawn, and a road carrying residential and college traffic lie north of the prairie. A marsh and an old field border the western and southern sides, while a forest is establishing on the eastern side. Mature *Acer saccharum* Marsh, *Maclura pomifera* Schneid, and *Juglans nigra* L., plus a weedy growth of young *Ulmus americana* L. and *Prunus virginiana* L., dominate the forest. The tallgrass prairie was burned in the fall of 1985 and the spring of 1986 during the course of this study.

MATERIALS AND METHODS

The components of *B. leucantha* reproductive yield studied were mass/seed, the number of seeds/pod, and the number of pods/plant. Plant size, as indicated by above ground biomass, was also considered since size can influence reproductive yield (Harper, 1977). The effects of seed predation on these four components were examined by reducing infestations with Tanglefoot (Tanglefoot Co. Grand Rapids, MI) in the DuPage Prairie. Tanglefoot is a sticky substance which reduced infestations of climbing insects on plants. A thin smear of Tanglefoot was applied around the bases of plants and all racemes, as well as around intermediate portions of all racemes, of 11 and 18 randomly selected plants during June of 1985 and of 1988, respectively. Twenty and 25 randomly selected plants in 1985 and 1988, respectively, served as the untreated controls. A comparison of the number of pods/plant between the Tanglefoot and control treatments was done during late July of 1988. No significant difference ($p > 0.05$, Mann-Whitney test) in the number of pods/plant was found.

During October of both years, the number of pods/plant was counted on all of the then post-senescent plants. Then, five pods were sampled from each raceme: the most proximal pod, the most distal pod, and three spaced evenly between. If a raceme had less than five pods, all pods were removed.

Plant size was determined in the field by recording the basal diameters (BD) of plants at the first node. Preliminary analysis showed that BD has as significant positive relationship ($p < 0.05$; $t = 6.62$; $r^2 = 0.46$; $n = 53$; linear regression) to air-dried weight of senescent shoots in *B. leucantha*.

Pods taken from the field were left to air-dry at room temperature for one week. Then, the number of seeds/pod and the number of *A. rostrum*/pod were recorded. The latter measurement provided a measure of the effectiveness of Tanglefoot in reducing *A. rostrum* infestations of pods. Ten seeds from each pod were randomly selected and weighed to the nearest tenth of a milligram. If a pod contained less than ten seeds, all seeds were weighed. Comparisons of components of plant reproductive yield, plant size, and number of *A. rostrum*/pod were done using the Mann-Whitney test. Coefficients of variation (CV) were also computed from data to test which component (or components) were least variable. The *a priori* prediction was that if trade-offs occur, a component which benefits should also be the least variable since it is being buffered from the effects of seed predation.

Selective pod abortion can provide a means for nutritional trade-offs among components of reproductive yield to occur. For example, by nonrandomly aborting pods having fewer seeds, more seeds may be maintained than if pods were randomly aborted. To determine if pods having fewer seeds/pod are selectively aborted, comparisons were made between aborted pods and those not aborted. Because predation by *A. rostrum* affects seed numbers/pod and thereby possibly pod abortion, a similar comparison between pods was made considering counts of *A. rostrum*/pod. Between July 21 and 27, 1988, three pods if possible were randomly removed from all racemes of each of seven plants other than the 33 plants used in the seed predation experiment. If racemes had fewer than three pods, all pods were collected. Mean plant counts of seeds/pod and *A. rostrum*/pod from aborted pods found beneath each of the seven plants during the same time period were compared to those from pods that were removed using the Mann-Whitney test.

RESULTS

No herbivores and seed predators other than *A. rostrum* were observed feeding on *B. leucantha*. Trends between data from Tanglefoot and control treatments were similar (Table 1). Tanglefoot treated plants had lower grand mean numbers of *A. rostrum*/pod ($\bar{X}$ number · pod^{-1} · plant^{-1}) than control plants for both 1985 and 1988, although the difference was only significant ($p < 0.001$) during 1988 (See

Table 2 for all results of the Mann-Whitney tests). In relation, the grand mean numbers of seeds/plant ($\bar{X}$ numbers · pod^{-1} · $plant^{-1}$) from Tanglefoot treated plants were significantly higher during both years. Thus, Tanglefoot was effective in reducing seed predation. The mean numbers of pods/plant and BD's of plants were higher, while the grand mean masses/seed ($\bar{X}$ mg seed · pod^{-1} · $plant^{-1}$) were lower, in the Tanglefoot treatments compared with the control treatments. However again significant differences were only found for one of the two years for each type of comparison (Table 2). The rankings of the CV's that were computed from data in Table 1 were the same between treatments and years of the study: Mass/seed <BD< Seeds/pod<Pods/plant (Table 3).

Aborted pods contained significantly ($p < 0.001$) fewer seeds than pods not aborted ($U = 146$; $n_1 = n_2 = 7$; Table 4), thus providing evidence that *B. leucantha* selectively aborts pods. Nonsignificant ($p > 0.05$) differences were found in counts of *A. rostrum*/pod ($U = 32$; $n_1 = n_2 = 7$; Table 4).

DISCUSSION

Seed predation was the major factor causing differences in components of *B. leucantha* reproductive yield between control and Tanglefoot treatments. For the year 1988, it was possible that the significant difference in plant size between treatments existed from the beginning of the growing season and that this caused significant differences in the other plant components instead of predation. However if such conditions existed, mean counts of pods/plant measured early in the growing season should have been different between treatments. On the contrary, no significant difference was found. Also, no significant difference in BD's was noted between treatments in 1985, nonetheless trends in data between years were identical.

The overall impact of seed predation on components of reproductive yield was negative with less grand mean seeds/pod, pods/plant, and smaller BD's measured from the more heavily infested *B. leucantha* of the control treatments. However, there was evidence that trade-offs among components of *B. leucantha* reproductive yield may occur that buffer against losses to seed predation by *A. rostrum*. The relative consistency in grand mean mass/seed among plants and the contrasts in grand mean mass/seed between Tanglefoot treated plants and the control plants provided the evidence. Harper et al. (1970) state that the relatively low variability in mass/seed commonly observed among plants is due in part to stabilizing selection pressure for a mass great enough to support sufficient nutrition for successful seed germination and seedling survivorship. This can explain why grand mean mass/seed was relatively invariable between treatments and among plants within a treatment, while other components of reproductive yield, including basal diameters, were lower in the control treatment and always more variable. Mass/seed was maintained, and perhaps promoted, at the expense of other components of reproductive yield. Heavier mass/seed, as was experienced from the control treatments, has been shown to promote successful germination and seedling survivorship especially under shaded conditions such as would be found on the floor of a densely populated tall-grass prairie (Howe and Richter, 1982; Stanton, 1984; Winn, 1985). It is interesting to speculate whether *A. rostrum* might also promote the population growth of *B. leucantha* if it does affect mass/seed.

In addition, *A. rostrum* predation of seeds may affect seed abortion which in turn can account for the heavier mass/seed in the control treatments. The fact that pods are aborted as seeds develop, and apparently selectively so, suggests that other factors, such as nutrient limitations, may also limit reproductive yield. However, despite the nonsignificant difference in counts of *A. rostrum* /pod between aborted pods and those not aborted, seed predation should still affect seed number and therefore pod abortion. Seed predation's effect on pod abortion can explain why the control plants, which matured fewer pods, yielded heavier seeds. Nutrients could be reallocated from lost components of reproductive yield to those maintained.

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Table 1. Mean counts ±s of *Apion rostrum*/pod and components of *Baptisia leucantha* yield for the control (C) and Tanglefoot (T) treatments. Mass/seed, counts of *A. rostrum*/pod and seeds/pod are grand means ($\bar{X} \bullet pod^{-1} \bullet plant^{-1}$) ±s.

Date (Treatment)	*Apion* pod	Mg mass/ seed	BD	Seeds/ pod	Pods/ plant
1985(C)	1.4 ±1.1	15.1 ±1.4	12.6 ±3.3	15.9 ±5.4	19.2 ±22.2
1985(T)	0.7 ±0.7	13.6 ±1.2	12.8 ±2.2	16.3 ±5.5	34.9 ±33.4
1988(C)	1.9 ±0.8	14.1 ±1.6	14.8 ±3.1	13.3 ±4.0	35.8 ±43.5
1988(T)	0.4 ±0.5	13.2 ±2.3	15.2 ±2.8	15.9 ±6.6	66.3 ±60.3

Table 2. Values of U by year from the Mann-Whitney tests between control and Tanglefoot treatments. The headings to the columns name the variables compared.

Year	*Apion*/ pod	Mg mass/ seed	BD	Seeds/ pod	Pods/ plant
1985	142	***190	128	*167	141
1988	***430	272	***411	**336	**332

*denotes significance: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Table 3. Variability (%CV) in the components of *Baptisia leucantha* yield according to year and treatment. (C) = Control treatment and (T) = Tanglefoot treatment.

Year (Treatment)	Mass/ seed	BD	Seeds/ pod	Pods/ plant
1985(C)	9.1	26.4	34.2	115.6
1985(T)	8.7	17.5	34.0	96.7
1988(C)	12.2	20.7	29.8	121.5
1988(T)	17.6	18.3	41.4	90.9

Table 4. Counts of seeds/pod and *Apion rostrum*/pod from aborted pods and pods not aborted. Data are expressed as grand means ($\bar{X} \bullet pod^{-1} \bullet plant^{-1}$) ±s.

	Seeds/pod	*Apion*/pod
Aborted pods	18.4 ±3.1	1.0 ±0.4
Pods not aborted	22.4 ±3.3	1.1 ±0.5