Impacts of Wild Indigo Weevil on Seed Production in Longbract Wild Indigo

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Abstract: Seeds of many species of *Baptisia* are eaten by larvae of the wild indigo weevil *Apion rostrum*, impacting plant fitness and compromising prairie restoration activities. We examined the impacts of *A. rostrum* predation on seed output in a commercial seed production population of longbract wild indigo *Baptisia bracteata* in southeastern Minnesota. Predehiscent seed pods (n = 673) were collected from 15 plants in September 2007, measured (total pod length), and examined for intact seeds, damaged seeds, and weevils. Adult weevils were present in 46% of pods examined, averaging 1.53 weevils/predated pod. More than 40% of predated pods contained two or more weevils. Pods contained an average of 9 seeds each, but two-thirds of the seeds failed to develop properly or were damaged by predation and/or fungus (possibly introduced by ovipositing weevils). Non-predated seed pods averaged 10 X more undamaged seeds than did predated seed pods (5.14 vs. 0.48 seeds/pod). Predated pods averaged 0.25 cm larger than non-predated pods, with pods containing two or more weevils > 0.55 cm larger than non-predated pods. *A. rostrum* has a significant impact on longbract wild indigo seed production in this system, preferentially attacking the larger seed pods and damaging either directly or indirectly ~65% of the potential seed crop.

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Introduction

The weevil genus *Apion* contains many serious plant pest species (Tattershall and Davidson 1954, Garza et al. 1996, Deshmukh et al. 2007, Freeman and Wimble 2007, Cockbain et al. 2008, Hansen and Boelt 2008), as well as species important to biological control of invasive plants (Hoddle 1991, Norambuena and Piper 2000, Badenes-Perez and Johnson 2007). Females of several species of *Apion* lay eggs in the developing seed pods of legumes; the weevil larvae then eat the seeds, reducing seed yield by 5 to 90% and adversely affecting seed germination and, in the case of crop plants, market value (Garza et al. 1996, Badenes-Perez and Johnson 2007, Deshmukh et al. 2007, Hansen and Boelt 2008). Ovipositing females also may introduce fungi and viruses into the host plant, potentially causing additional damage to the plant and/or developing seeds (Nepstad 1983, Young et al. 2007, Cockbain et al. 2008).

In North American prairies, the wild indigo weevil *Apion rostrum* Say preys on the seeds of many native species of wild indigo *Baptisia* (Fabales: Fabaceae) (Haddock and Chaplin 1982, Petersen 1989, Petersen and Sleboda 1994, Petersen et al. 1998, 2000, 2006, Horn and Hanula 2004, Young et al. 2007). Although species of *Baptisia* contain alkaloids that can deter potential predators (Cranmer and Turner 1967), *A. rostrum* can induce selective pod abortion as well as consume large portions of potential seed crops (Petersen 1990, Petersen and Sleboda 1994), compromising recovery efforts for endangered species of *Baptisia* (Young et al. 2007).

Longbract wild indigo (*Baptisia bracteata* Muhl. ex Elliott var. *leucophaea* (Nutt.) Kartesz & Gandhi; synonymous with plains wild indigo and cream wild indigo *Baptisia leucophaea* Nutt.) is a common, native legume distributed widely throughout mesic tallgrass prairies in the Midwestern United States, from southern Michigan to Minnesota and Nebraska south to Louisiana and eastern Texas (Venning 1984). The species plays an important role in nitrogen fixation in prairies, so it typically is included in recommended plant lists for prairie restorations throughout this region (Shirley 1994, Kirt 1995, Ladd 1995, Packard and Mutel 1997, Kurtz 2001). Its earlier springtime blooming period may make it less susceptible than other *Baptisia* species to attack by *A. rostrum* (Petersen et al. 2006), but it still can suffer severe seed losses when *A. rostrum* densities are high (Petersen et al. 2000). Nursery populations of *B. bracteata*, with their high plant densities, may be especially vulnerable to attack by *A. rostrum* (WI Department of Agriculture, Trade & Consumer Protection 2005).

The present study examined the impact of the wild indigo weevil on a commercial seed production population of *B. bracteata* in southeastern Minnesota. *B. bracteata* currently is on the Special Concern Species List for the state of Minnesota (http://www.dnr.state.mn.us/ets/vascular_special.html). Specifically, we investigated the effect of *A. rostrum* on *B. bracteata* seed yield and the economic value of this lost production.

Study Area

The study was conducted in a 1.2-hectare commercial seed production field at Prairie Moon Nursery, Wiscoy Township, Winona County, Minnesota (N 43° 53' 19", W 91° 38' 49") during September 2007. The field is located on a hilltop above a wooded hillside, and is divided into five sections by mowed paths. It was originally planted in 1990 as a mixed community production field and it currently supports irregular hand collecting of seeds of the more common species. In addition to *Baptisia bracteata*, the field also contained (among others) the forbs white wild indigo *Baptisia leucantha*, stiff goldenrod *Solidago rigida*, showy goldenrod *S. speciosa*, pale purple coneflower *Echinacea pallida*, yellow coneflower *Ratibida pinnata*, prairie cinquefoil *Potentilla arguta*, wild quinine *Parthenium integrifolium*, round-headed bush clover *Lespedeza capitata*, foxglove beardtongue *Penstemon digitalis*, and the grasses little bluestem *Andropogon scoparius*, Indian grass *Sorghastrum nutans*, and side-oats grama *Bouteloua curtipendula*.

Methods

Fieldwork

Intact, predehiscent seed pods were harvested from *B. bracteata* in late September 2007. Three plant clusters were selected (based on good seed pod production) from within each of five field sections. All predehiscent seed pods were removed from each plant cluster by clipping with a simple garden pruner, and were placed in large, labeled Ziploc bags. Harvested seed pods were then placed in a freezer until they were examined.

Lab work

In the laboratory, seed pod length was measured (nearest mm) with a simple ruler, and pods were opened to expose any seeds and/or weevils present. Adult weevils were counted, and seeds were counted and examined for damage and categorized as viable or not viable (based on presence of holes, shriveling, heavy mold growth, or other damage).

Data analyses

All data analyses were conducted using Microsoft Excel software. Numbers of seed pods per plant cluster, damaged and viable seeds per pod, adult weevils per pod, and pod lengths were compared among sections with single-factor analysis of variance (ANOVA). Simple linear regression was used to examine relationships between 1) seed pod size and numbers of seeds/pod, 2) numbers of *A. rostrum*/seed pod and seed pod length, 3) numbers of weevils/pod and numbers of viable seeds/pod, and 4) numbers of weevils/pod and numbers of damaged seeds/pod. T-tests compared numbers of seeds/pod (total, viable, damaged) between pods with and without weevils, as well as pod size between pods with 0 and 1 weevil and 1 and 2 weevils.

Results

The 15 *B. bracteata* plant clusters sampled produced 673 predihescent seed pods. Plant clusters averaged 45 intact seed pods (range = 17 to 89 pods/cluster), each averaging 43 mm in total length. Neither the number of seed pods/cluster nor seed pod size differed significantly among field sections (Table 1). Seed pods averaged 9 seeds each (3 viable, 6 damaged) and contained 0.7 adult weevils. The total number of seeds/seed pod was significantly correlated (simple linear regression, F = 151.58, P << 0.001) with the size of the seed pod, with one additional seed for every 5.4 mm of additional pod length. Weevil and seed counts did not differ among the five field sections sampled (Table 1). Consequently, data from all field sections were combined for all subsequent analyses.

Of the 673 seed pods examined, 312 (46.4%) contained one or more adult *A. rostrum*. Forty-one percent of these predated pods contained two or more *A. rostrum*, but no pod contained more than four weevils (Figure 1). All field sections displayed similar patterns of pod occupancy by *A. rostrum*. Only 38.6% of all weevils counted (n = 477) were found singly within seed pods; the majority (>61%) were found in pods with one or more conspecific. Overall, predated pods averaged 1.53 weevils each (SD = 0.72 weevil).

The number of weevils/seed pod was significantly correlated (simple linear regression, F = 30.27, P << 0.001) with the size of the seed pod (Figure 2). Predated pods were significantly longer (2.6 mm or 6.2%) than pods lacking weevils (44.4 mm vs. 41.8 mm; t = 3.12, df = 671, P = 0.002), and seed pods with two or more weevils were significantly longer (5.4 mm or 13%) than pods having only a single weevil (47.5 mm vs. 42.2 mm; t = 4.28, df = 310, P << 0.001). However, pods occupied by single weevils were no different in size than those lacking weevils (Figure 2; 42.2 mm vs. 41.9 mm; t = 0.45, df = 543, P = 0.65).

Apion rostrum had a significant, negative effect on the seeds of *B. bracteata* (Figure 3). Seed pods with weevils contained significantly, although only slightly, fewer total seeds (8.4 seeds/pod vs. 9.4

Table 1. Mean (±SD) values for variables associated with *Baptisia bracteata* seed pods in a seed production field at Prairie Moon Nursery, Winona County, Minnesota, in September 2007, and results of single-factor ANOVAs comparing variables among field sections.

Variable	Mean (SD)	n	ANOVA F	P
Seed pods/ plant cluster	44.9 (18.0)	15	2.94	0.08
Seed pod length (mm)	42.9 (10.9)	673	0.28	0.88
Weevils/pod	0.71 (0.91)	673	0.42	0.79
Total seeds/ pod	8.94 (4.70)	673	2.15	0.15
Viable seeds/pod	2.98 (5.15)	673	1.03	0.44
Damaged seeds/pod	5.96 (4.65)	673	0.63	0.65

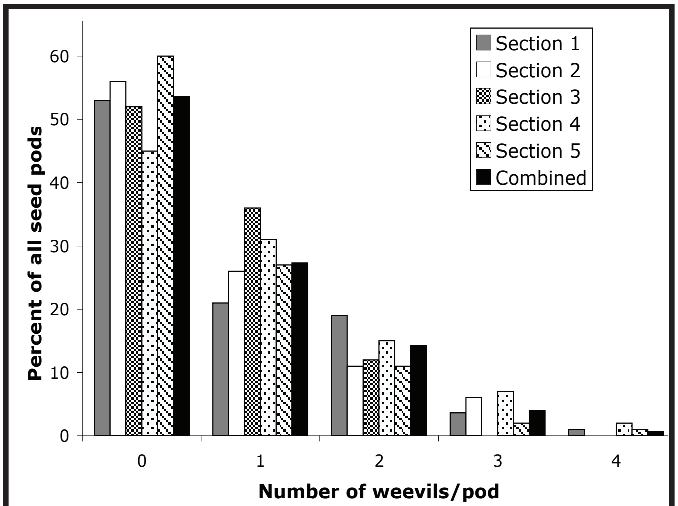

Figure 1. Percentages of *Baptisia bracteata* seed pods (n = 673) (by field section and combined) containing varying numbers of the weevil *Apion rostrum* in a seed production field at Prairie Moon Nursery, Winona County, Minnesota, in September 2007.

seeds/pod; t = 2.74, df = 671, P = 0.006) than did pods without weevils. However, weevil-infested pods contained nearly twice as many damaged seeds (7.9 vs. 4.3 damaged seeds/pod; t = 11.08, df = 671, P <<0.001) as did weevil-free pods, and less than one-tenth as many intact, viable seeds (0.5 vs. 5.1 viable seeds/pod; t = 13.13, df = 671, P << 0.001). The number of *A. rostrum* in a seed pod was correlated negatively with the number of viable seeds in the pod (simple linear regression, F = 128.69, P << 0.001) and positively with the number of damaged seeds in the pod (simple linear regression, F = 117.44, P << 0.001) (Figure 3).

Discussion

Apion rostrum had a significant, negative effect on seed production in a nursery population of *Baptisia bracteata* in southeastern Minnesota. Similar, negative impacts of this weevil have been reported previously on *B. bracteata* and its congenors throughout North America (Haddock and Chaplin 1982, Nepstad 1983, Petersen 1989, Petersen and Sleboda 1994, Petersen et al. 1998, 2000, 2006, Horn and Hanula 2004, Young et al. 2007). Weevil impacts included reduced plant size (Petersen 1989), fewer seed pods per plant (Petersen 1989, Petersen et al. 1998, 2000, Horn and Hanula 2004), increased seed pod abortion (Petersen and Sleboda 1994, Petersen et al. 1998), and reduced seed counts per seed pod and plant (Petersen et al. 1998, 2000, Horn and Hanula 2004). As in the present study, higher infestations (more weevils/seed pod) produced stronger, negative effects, especially on the number of seeds/pod (Nepstad 1983, Petersen 1989, Petersen et al. 1998, 2000, Horn and Hanula 2004).

Nearly 50% of all seed pods examined in the present study contained adult *A. rostrum*, with predated pods averaging 1.53 weevils each. All pods (predated and non-predated) averaged 0.71 weevils/pod. These infestation rates are similar to those reported for several species of *Baptisia* (Petersen et al. 2000, 2006, Young et al. 2007), although rates can vary more than 10-fold at the same site in successive years (Petersen et al. 2000).

Predated pods of *B. bracteata* contained very few intact, mature seeds (average of 0.5 seeds/pod), with 80-100% reduction in viable seeds within predated

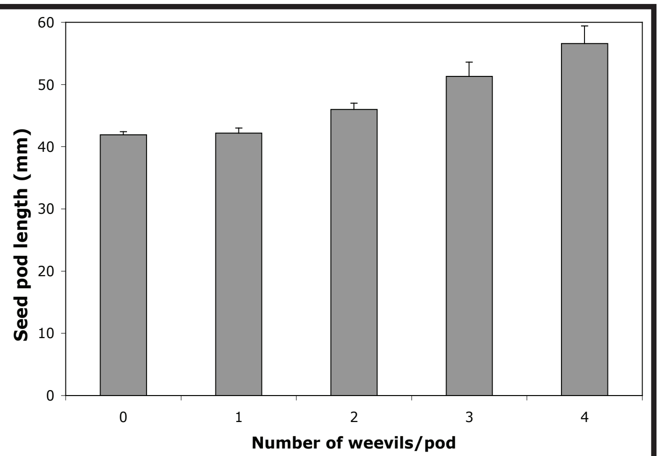

Figure 2. Average length of *Baptisia bracteata* seed pods containing varying numbers of the weevil *Apion rostrum* in a seed production field at Prairie Moon Nursery, Winona County, Minnesota, in September 2007. Error bars represent 1 SE of the mean. Sample sizes for weevil number categories are: 0 weevils – 361, 1 weevil – 184, 2 weevils – 96, 3 weevils – 27, and 4 weevils – 5.

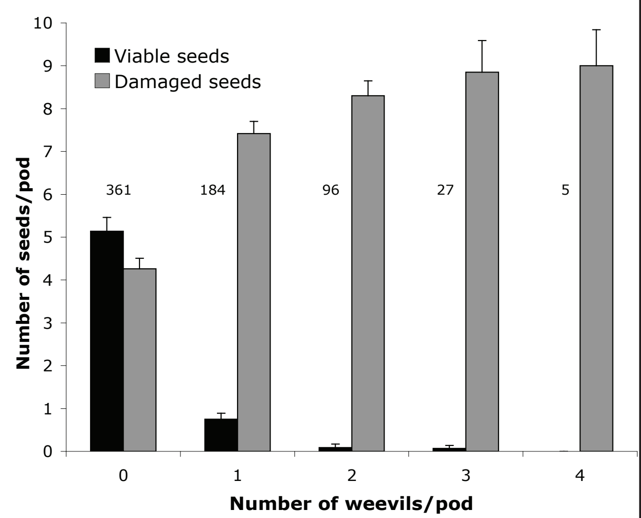

Figure 3. Average numbers of viable and damaged seeds in *Baptisia bracteata* seed pods containing varying numbers of the weevil *Apion rostrum* in a seed production field at Prairie Moon Nursery, Winona County, Minnesota, in September 2007. Error bars represent 1 SE of the mean. Numbers are sample sizes for each weevil number category.

pods. Young et al. (2007) reported that 61% of *B. lanceolata* seed pods and 100% of *B. arachnifera* seed pods attacked by *A. rostrum* contained no intact seeds. Petersen and Sleboda (1994) reported that a single weevil larva can consume 5 or more seeds as it develops. *Baptisia* seed pods in the present study averaged 9 seeds each, and predated pods contained an average of 1.5 weevils, so the lack of intact seeds in predated pods is not surprising.

More than 60% of weevils were found in *B. bracteata* seed pods along with one or more additional weevil. These seed pods were significantly larger than those containing 0 or 1 weevil, and likely contained more seeds than these other pods. More than 15% (56 of 361 pods) of non-predated pods contained >15 seeds each, with a maximum seed count of 23. Seed counts of this magnitude could provide nourishment for two or more *A. rostrum* larvae. Female *A. rostrum* typically oviposit eggs singly into seed pods, but multiple eggs can be laid (Petersen and Sleboda 1994). Female *Apion* may have the ability to decide how many eggs to lay in a pod to maximize offspring fitness (Messina and Renwick 1985, Hoddle 1991a, b), and may deter conspecific females from laying additional eggs into the same pod by depositing a pheromone deterrent (Hoddle 1991a).

Baptisia species are known to contain a variety of secondary chemicals, especially various alkaloids, which may be distasteful or even toxic to herbivores (Cranmer and Turner 1967). While these chemicals may work well as a defense against generalist herbivores (Smith and Smith 2001), they apparently have little effect against the seed predator *Apion rostrum*. Many specialist herbivorous insects are able to breach the chemical defenses of plants by detoxifying the secondary compounds with a mixed function oxidase in their guts (Smith and Smith 2001). It is possible that the specialist *A. rostrum* employs such a detoxifying system to feed specifically on *Baptisia*, resulting in the lost seed production observed in this and earlier studies.

In addition to feeding directly on *Baptisia* seeds, *A. rostrum* may have additional, negative effects on the reproductive output of *B. bracteata*. In the present study, many seed pods with weevils contained fungus-covered seeds in varying stages of decomposition. This fungus, likely introduced into seed pods by ovipositing female weevils (Nepstad 1983), can destroy any uneaten seeds remaining within the pod. Interestingly, this fungus actually may improve *Baptisia* seed germination rates in the short term by acting as a seed-scarifying agent (Nepstad 1983).

Additional indirect seed losses in *Baptisia* may occur when plants selectively abort developing seed pods where seed numbers have been reduced by weevil consumption (Petersen 1989, Petersen and Sleboda 1994, Petersen et al. 1998). Plants with more weevils per pod consistently abort more pods than do plants with lower weevil numbers (Petersen 1989, 1990). Evidence suggests that pods aborted typically were those on the plant that had been attacked first by *A. rostrum*, as development of weevils in attached pods lagged behind development of those in unattached, aborted pods (Petersen and Sleboda 1994). Aborted pods were not assessed in the present study, so the effect of seeds lost via pod abortion to total seed production is unknown. However, pod loss in *B. bracteata* and its congenors frequently exceeds 40%, and can approach 80% under heavy *A. rostrum* infestation (Petersen 1989, Petersen et al. 2000, Young et al. 2007).

Management Implications

Lost seed production in *B. bracteata* can be a significant economic loss. At current market rates ($60/ounce, 1400 seeds/ounce), each longbract wild indigo seed has a value of 4.3 cents. Based on seed pods without weevils, potential total seed production can average 9.40 seeds/pod (value of 40.4 cents). If this population experiences 40% pod loss due to abortion during the growing season, and plant clusters averaged 45 pods in late September, plant clusters likely initiated 75 pods each. Therefore, each plant cluster could have a total seed "starting value" of $30.30. A 40% pod abortion rate would reduce this value by $12.12 per plant cluster. Assuming a 46% rate of infestation of remaining pods by weevils, and a 90.5% loss of seeds within these pods to direct consumption and fungus, seed value per plant cluster would be reduced by an additional $7.64, resulting in a final seed value of

$10.54 per plant cluster. Total estimated losses of *B. bracteata* seed attributable (directly or indirectly) to *A. rostrum* would be approximately $19.76 per plant cluster, a potential loss of value of 65%.

Previous studies have examined the potential for controlling weevils on *B. bracteata* (Petersen et al. 1998), other species of *Baptisia* (Petersen 1989, Horn and Hanula 2004), and a variety of other legumes (Deshmukh et al. 2007, Freeman and Wimble 2007, Hansen and Boelt 2008). Applications of sticky barriers (e.g., Tanglefoot) to plant stems significantly reduced weevil infestations and increased seed yields in relation to untreated control plants (Petersen 1989, Petersen et al. 1998). Treatments of plants with various insecticides also have shown promise, reducing weevil numbers by up to 90% and increasing plant reproductive output and seed yield (Horn and Hanula 2004, Deshmukh et al. 2007, Freeman and Wimble 2007, Hansen and Boelt 2008).

Prescribed burns may be another method to reduce the intensity of seed predation by *A. rostrum*. Fire is an important habitat management tool for many species of *Baptisia*, since it suppresses competition with grasses and increases *Baptisia* stem densities (Carter et al. 2000). Experimental burns have been found to reduce seed predation by moth larvae on northern blazing star *Liatris scariosa* by >30% (Vickery 2002a, b), but similar experiments with *Baptisia* and *A. rostrum* have not been conducted.

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