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Reproductive Biology of American Licorice (Glycyrrhiza Lepidota Pursh) in Western South Dakota with New Seed Insect Associations

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REPRODUCTIVE BIOLOGY OF AMERICAN LICORICE (*GLYCYRRHIZA LEPIDOTA* PURSH) IN WESTERN SOUTH DAKOTA WITH NEW SEED INSECT ASSOCIATIONS

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ABSTRACT

American licorice (*Glycyrrhiza lepidota* Pursh) is a long-lived rhizomatous native legume that is common on moist prairies and meadows in the northern Great Plains and further west. This species is of interest for remediation and conservation because it is a legume that is fairly well adapted to moist saline soils. It is browsed by deer and pronghorn and its seeds are consumed by birds, rodents, and insects. *Acanthoscelides aureolus* (Horn) (Coleoptera: Chrysomelidae)] and *Bruchophagus grisselli* McDaniel & Boe (Hymenoptera: Eurytomidae) can decimate seed production in natural populations. Our objectives were to determine seed yield components (i.e., seeds per pod and weight per seed), frequency of seed predation, seed germination, and parasitoids of *A. aureolus* and *B. grisselli* for 29 natural populations from western South Dakota over a 2-yr period. Seeds per pod, seed weight and frequency of seed predation varied widely among populations and between years. Seed predation was 12% in the first year and 48% in the subsequent year. Germination of normal seeds was not influenced by seeds per pod or seed weight. Seven species of parasitoids representing five taxonomic families (Hymenoptera: Chalcidoidea) were reared from seed samples containing larvae of *A. aureolus* or *B. grisselli*, *Dinarmus acutus* Thomson (Pteromalidae), *Eurytoma tylodermatis* Ashmead (Eurytomidae), *Eupelmus vesicularis* (Retzius) (Eupelmidae), and *Uscana semifumipennis* Girault (Trichogrammatidae) which feed on *A. aureolus* larvae or eggs. *Idiomacromerus perplexus* Gahan and *I. terebrator* Masi (Torymidae), and *Mesopolobus bruchophagi* (Gahan) (Pteromalidae) are parasitoids of *B. grisselli*. A new seed predator, the clover seed caterpillar, *Grapholita interstinctana* (Clemens) (Lepidoptera: Tortricidae), was discovered in a natural population of American licorice at Brookings, SD. The larva completes all instars and consumes the seeds within pods. Percent seed predation was estimated to exceed 60%.

KEYWORDS

Grapholita interstinctana, Acanthoscelides aureolus, Bruchophagus grisselli, Chalcidoidea, parasitoids, seed weight, pod infestation, seed predation, germination

INTRODUCTION

American licorice (*Glycyrrhiza lepidota* Pursh) is a perennial legume native from the Great Plains to the West Coast, but less common and still widespread eastward. It is the only species in its genus in North America. In the northern Great Plains, it is frequently found around mesic environments and riparian ecosystems, such as sloughs, depressions, streams, river bottoms, and roadside ditches (Johnson and Larson 1999; Andersen and Nelson 2014). It is also a common component of halophytic plant communities in grasslands of Saskatchewan (Dodd and Coupland 1966). It is considered to be an important source of nectar and food for native butterflies and other insects (Andersen and Nelson 2014).

American licorice is strongly rhizomatous but also reproduces by seed. It produces pods with hooked prickles that are dispersed through zoochory. Aboveground vegetation is browsed by native ungulates, seeds are eaten by, birds, rodents, and insects (Johnson 1970), and roots and rhizomes are consumed by pocket gophers (*Geomys* sp.). Indigenous Americans used leaves, stems, and roots for food and medicinal purposes (Johnson and Larson 1999). Because of its nitrogen-fixing, soil binding, tolerance to poorly drained saline soils, and forage quality (Fransen and Boe 1981), American licorice has been evaluated for agronomic traits (Boe and Wynia 1985). Initial common garden studies of 25 natural populations from Dakotas indicated that seed predation by bruchid beetles (Coleoptera: Chrysomelidae: Bruchinae) was an impediment to domestication and commercial seed production (Boe and Wynia 1985; Boe et al. 1988). Whitman (1979) concluded that American licorice was one of the best legumes evaluated for revegetation of mine spoil at Dickinson, ND.

Boe and Wynia (1985) found large variation among natural populations of American licorice from eastern North Dakota and eastern South Dakota for seedling vigor and vegetative spread by rhizomes. However, very little is known about the seed production, insect predation, and seed quality of natural populations in the western parts of the Dakotas.

The seed collections from natural populations of American licorice for the current study were made about 30 years ago. At that time there was national interest in collection and evaluation of native North American legumes for forage, conservation, biological diversification, and beautification purposes. Our initial reason for collecting seed from natural populations was to identify seed predators and their impact on seed production and to collect enough seed to conduct preliminary evaluations for vigor and other agronomic traits in a common garden setting (Boe and Wynia 1985). However, since that initial evaluation in a common garden setting at Brookings, SD, indicated very few inflorescences and seed pods were produced under cultivation, no further evaluations have been conducted on natural populations from other regions of the Dakotas.

However, with the recent renewed interest in native legumes for use in habitats to increase populations of native pollinators on land that is not suitable for conventional farming and the recognition of American licorice as a pollinator plant that is well adapted to riparian and moderately saline areas, our objectives were to 1) report seed production components and seed quality characteristics of 29 populations of American licorice in western South Dakota, outside of the Black Hills and 2) determine the biodiversity of parasitoid guilds associated with seed predators, as primary hosts, in the seeds of the plant. In addition, we found another seed predator (Lepidoptera: Tortricidae) that can have a devastating effect on seed production of American licorice in eastern South Dakota. Thus, a secondary objective of this research was to identify that species.

METHODS

Mature pods were collected during August from 12 rangeland sites in six counties in 1986 and from 17 sites in five counties west of the Missouri River in 1987 in western South Dakota. Most of the sites were in ditches or low prairies adjacent to county or state roadways. Sample size (i.e., number of pods) varied among sites due to the fact that the areas covered by the populations ranged from about 2 m^2 to 200 m^2. However, a minimum of 200 pods was collected from each population. Pods were placed in heavy paper bags at room temperature until spring of the following year. Fifty randomly selected pods from each population were dissected and the following data were collected for both 1986 and 1987 pod collections: 1) seeds per pod, 2) number of pods infested by *A. aureolus* (pods with at least one seed that had been infested), and 3) number of seeds infested by *A. aureolus*. Seeds predated by *A. aureolus* were easily identified by the circular exit hole in the testa created by the adult beetles during emergence. Exit holes created by adult chalcidoid parasitoids of *A. aureolus* were more irregular. Since the parasitoids parasitized the bruchid beetle larvae inside the seed, determination of the frequency of seed predation by *A. aureolus* necessarily included counting seeds with either type of exit symptom. However, no attempt was made to capture the emergent insects for identification purposes. To determine if variation occurred among pod sizes and populations for seed weight, we weighed 10 random normal (i.e., uninfested) individual seeds from pod-size classes 2 through 5 (i.e., 2-seeded through 5-seeded pods) at 0.1 mg accuracy using an analytical balance for eight populations (five populations from the 1986 collection and three populations from the 1987 collection) that produced at least 10 normal seeds in each of those pod-size classes.

Seeds obtained from the dissection of 50-pod samples from each population collected in 1987 were scarified for 5 seconds in a Forsberg laboratory scarifier equipped with fine-grit emery cloth. Seeds from each pod-size class from each population were placed on standard germination blotters in 12 cm x 12 cm germination boxes in 2 replications for each location in a germination chamber at 20 °C. Number of seeds in each pod-size x location x replication combination ranged from 1 to 23, depending on number of pods in each pod-size class from each population. Total number of seeds tested was 1839. Totals for each pod-size class ranged from 97 for 7-seeded pods to 388 for 3-seeded pods. Germination (emergence of the radicle) counts were made daily up to 7 days. After 7 days, hard seeds were scratched with a razor blade and returned to the germination chamber. Final germination counts were made at 14 days.

Data analysis consisted of analyses of variance for metrical traits, such as seeds per pod and seed weight, and Chi-squared analyses for frequency data, such as pod predation, seed predation, and germination. The statistical software employed was *Statistix 9* (Analytical Software 2008).

During August 1988 mature pods were collected from natural populations of American licorice in Brookings, Davison, Hamlin, and Mellette Counties in South Dakota and Renville County in North Dakota, all of which are east of the Missouri River, for the purpose of determining species of Chalciodoidea associated with the bruchid beetle (*A. auroleus*) and the phytophagous chalcid wasp (*B. grisselli*) that predate seeds of American licorice in the northern Great Plains. Pods were placed in 1.8-liter paper milk cartons which were wrapped with aluminum foil to occlude light (McDaniel and Boe 1991a). A 5-ml vial was placed in a hole cut in the carton to serve as a trap for positively phototrophic adult chalcids and *A. aureolus*. Cartons were kept at room temperature and insects were collected and placed in 80% ethanol as they emerged. Emergence was highest during April-May 1989. Identifications of species were made by Dr. Burruss McDaniel, South Dakota State University, and verified by the Systematic Entomology Laboratory, USDA ARS, Washington, D.C. Taxonomic names of wasps are from Noyes (2016).

During summer 2015 we observed caterpillars consuming seeds within pods of American licorice in a poorly drained saline area dominated by Kentucky bluegrass (*Poa pratensis* L.) on the campus of South Dakota State University,

Figure 1. American licorice growing in a poorly drained and moderately saline soil dominated by a dense sod of Kentucky bluegrass at Brookings, SD. Photograph was taken July 8, 2016. Note that pods develop and mature in acropetal fashion on individual racemes.

Brookings, SD (Figure 1). We collected and preserved several caterpillars and also reared a single adult moth from infested pods. On June 25 2016 we swept inflorescences in full bloom/early pod development during the evening to collect adult moths. We also dissected pods and collected and preserved several instars of the caterpillar during July and August.

RESULTS AND DISCUSSION

Seeds per pod, percent infested pods, and percent seed predation varied significantly among natural populations of American licorice from western South Dakota in 1986 and 1987 (Tables 1 and 2). Collectively for the two years, 'Dewey 3-86' had the fewest seeds per pod (1.1) and `Perkins 86' had the greatest number of seeds per pod (5.3). Mean number of seeds per pod averaged across populations was similar for the two years (3.0) (Tables 1 and 2). Similarly, Boe et al. (1988) found mean number of seeds per pod ranged from 3.4 to 4.0 for two populations of American licorice in eastern South Dakota.

Percent predated pods was about three times higher in 1987 compared to 1986, and percent seed predation was about four times higher in 1987 compared to 1986 (Tables 1 and 2). Collectively for the two years, the lowest levels of infested pods and seed predation were found for the `Dewey 3-86' population (0% for both pods and seeds); whereas, the highest levels of infested pods and seed predation occurred in the `Pennington 3-87' population (100% and 92% for

Table 1. Seed status data for 50-pod samples from 12 rangeland populations of American licorice collected from six counties in western South Dakota in 1986. Standard error of the mean in parentheses.

County/Site	Location	Seeds per pod (no.)	Infested pods (%)	Seed predation (%)
Dewey 1-86	T16N R28E	4.2	8.0	2.4
Dewey 2-86	T16N R22E	2.3	6.0	4.3
Dewey 3-86	T16N R30E	1.1	0	0
Harding 86	T17N R7E	3.0	17.3	5.1
Meade 1-86	T7N R8E	2.0	22.0	11.0
Meade 2-86	T11N R13E	4.2	18.0	7.2
Meade 3-86	T4N R7E	2.8	0	0
Meade 4-86	T11N R10E	3.5	4.0	1.1
Mellette 1-86	T44N R30W	4.0	68.0	34.0
Mellette 2-86	T41N R28W	2.0	66.0	43.0
Pennington 86	T2N R13E	2.3	18.0	12.0
Perkins 86	T15N R14E	5.3	70.0	22.5
Grand Mean (SE)		3.1 (0.4)	24.8 (7.8)	11.9 (4.1)

Table 2. Seed status data for 50-pod samples from 17 rangeland populations of American licorice collected from five counties in western South Dakota in 1987. *Standard error of the mean in parentheses.

County/Site	Location	Seeds per pod (no.)	Infested pods (%)	Seed predation (%)
Corson 1-87	T20N R18E	3.2	94	42
Corson 2-87	T23N R26E	3.0	84	62
Corson 3-87	T18N R28E	2.7	56	34
Custer 1-87	T6S R8E	2.5	38	21
Custer 2-87	T6S R9E	2.5	56	35
Dewey 1-87	T17N R30E	2.6	64	34
Dewey 2-87	T14N R31E	3.9	48	18
Dewey 3-87	T14N R31E	3.1	78	67
Jones 1-87	T2S R30E	2.5	92	71
Jones 2-87	T2S R28E	2.7	84	60
Jones 3-87	T2S R30E	2.6	96	80
Jones 4-87	T2S R26E	3.8	82	47
Pennington 1-87	T1N R14E	3.3	82	52
Pennington 2-87	T2S R11E	3.6	62	46
Pennington 3-87	T5S R9E	3.7	100	92
Pennington 4-87	T2N R15E	2.1	50	35
Pennington 5-87	T2S R12E	4.0	14	4
Grand Mean (SE)		3.0 (0.1)	69.4 (5.7)	47.1 (5.6)

infested pods and seed predation, respectively) (Tables 1 and 2). Similarly, Boe et al. (1988) found large differences between consecutive years for seed predation (32.6 % in 1986 and 16.6 in 1987) in American licorice populations from eastern South Dakota, and Baskin and Baskin (1977) found that seeds per pod and percentage of pods and percentage of seeds predated by *Sennius abbreviatus* (Say) (Coleoptera: Bruchidae) varied widely among years for the perennial legume Maryland senna (*Cassia marilandica* L.) in Tennessee.

Significant differences were found among pod sizes (seeds per pod) for individual seed weight for the three pod sizes (3-, 4-, and 5-seeded pods) that contributed the greatest number of seeds. Seeds from pods containing 3 or 4 seeds were heavier than seeds from pods containing 5 seeds (Table 3). However, Boe et al. (1988) found differences among pod sizes for individual seed weight was dependent on temporal variation between years.

Significant differences were found among population x year combinations for individual seed weight from the pod sizes (3-, 4-, and 5-seeded pods) that contributed the greatest number of seeds (Table 4). The amount of variation among populations attributed to genetic causes cannot be determined from the data since the seeds were produced in different environments. However, the wide range suggests that a common garden study may be worthwhile for identifying large-seeded populations. Seed size has been associated with seedling vigor in small-seeded forage legumes (Black 1959).

Percent seed predation was not independent of seeds per pod. The tendency was for the largest pod sizes (6 to 7 seeds) to have lower seed predation than the most common pod sizes (3 to 5 seeds). These results were in slight contrast to those from populations of American licorice from eastern South Dakota, where seed predation was in proportion to number of seeds per pod (Boe et al. 1988). However, for the current study, the number of pods that produced 6 or 7 seeds was a small fraction of the total number of pods (Table 5).

Percent germination was not independent of seeds per pod. However, seeds from pods that contained from 1 through 6 seeds had similar percent germination. Seeds from 7-seeded pods had lower germination than seeds from smaller pods. However, 7-seeded pods were rare and thus contributed very few seeds to the total (Table 6).

Table 3. Mean seed weight for seeds from 3-seeded, 4-seeded, and 5-seeded pods, averaged across eight populations of American licorice in 1986 and 1987 in western South Dakota.

Seeds per pod	Seed weight (mg)
3	8.60
4	8.50
5	7.79
LSD (0.05)*	0.14

***F = 3.16, df = 2/288, P < 0.05**

Table 4. Mean seed weight, averaged across 3-seeded, 4-seeded, and 5-seeded pods, for eight populations of American licorice from western South Dakota in 1986 and 1987.

County	Year	Seed weight (mg)
Dewey	1986	6.81
Harding	1986	7.94
Meade	1986	9.32
Mellette	1986	8.77
Pennington	1986	11.00
Pennington	1987	8.26
Custer	1987	9.44
Dewey	1987	7.68
LSD (0.05)*		0.62

***F = 32.01, df = 7/288, P < 0.001**

Table 5. Percent seed predation for 1986 and 1987 combined for seeds from 1-seeded through 7-seeded pods.

Seeds per pod	No. seeds examined	Predation (%)
1	250	30.4
2	696	36.4
3	1,071	35.2
4	1,232	32.6
5	868	28.2
6	373	23.1
7	56	10.7
Chi-squared		44.5***

******Significant at the <0.001 level.***

Table 6. Germination of seeds of American licorice from pods with number of seeds ranging from 1 to 7, bulked across 17 populations collected from western South Dakota in 1987.

Seeds per pod	No. seeds tested	Germination (%)
1	152	95.4
2	251	96.0
3	388	95.4
4	348	95.7
5	316	97.8
6	287	96.2
7	97	84.5
Chi-squared		31.4***

******Significant at the <0.0001 level.***

Parasitoids reared from seeds of American licorice containing larvae of *A. auroleus* and *B. grisselli* are all Hymenoptera and are listed in Table 7. *Dinarmus acutus* Thomson (Pteromalidae), *Eupelmus vesicularis* (Retzius) (Eupelmidae), and *Eurytoma tylodermatis* Ashmead (Eurytomidae) are exotic invasive species that parasitize several species of *Acanthoscelides* native to North America (Johnson 1970; Kingsolver 2004). Boe and Johnson (2008) reared all three parasitoids from pods of Canada milk-vetch (*Astragalus canadensis* L.) containing larvae of *A. perforatus* (Horn) and *Tychius liljebladi* Blatchley (Coleoptera: Curculionidae). Boe et al. (1989) observed that *D. acutus* reduced frequency of seed predation by *A. perforatus* in Canada milk-vetch in spaced-plant nurseries in South Dakota.

Idiomacromerus perplexus Gahan, *I. terebrator* Masi (Torymidae) and *Mesopolobus bruchophagi* (Gahan) (Pteromalidae) are also common invasive parasitoids of the introduced *Bruchophagus gibbus* (Boheman), *B. platypterus* (Walker) and *B. roddi* Gussakovskiy species that attack seeds of alfalfa (Medicago sativa L.), red

Table 7. Parasitoids and a phytophagous seed-feeding chalcid (Hymenoptera: Chalcidoidea†) reared from pods of American licorice from North Dakota and South Dakota.

Family	Species	Behavior
Eurytomidae	*Eurytoma tylodermatis* Ashmead	Parasite of *A. aureolus* larvae
Pteromalidae	*Dinarmus acutus* Thomson	Parasite of *A. aureolus* larvae
Eupelmidae	*Eupelmus vesicularis* (Retzius)	Parasite of *A. aureolus* larvae
Trichogrammatidae	*Uscana semifumipennis* Girault	Parasite of *A. aureolus* eggs[1]
Eurytomidae	*Bruchophagus grisselli* McDaniel & Boe (Fig. 2)	Phytophagous (seed feeder)[2]
Torymidae	*Idiomacromerus perplexus* Gahan	Parasite of *B. grisselli* larvae
Torymidae	*Idiomacromerus terebrator* Masi	Parasite of *B. grisselli* larvae
Pteromalidae	*Mesopolobus bruchophagi* (Gahan)	Parasite of *B. grisselli* larvae

†After: Noyes, J.S. 2016 (April). Universal Chalcidoidea Database. World Wide Web electronic publication. http://www.nhm.ac.uk/chalcidoids
[1]Boe and McDaniel, 1991; [2]McDaniel and Boe, 1991b

Figure 2. Female (left) and male (right) of* Bruchophagus grisselli *McDaniel & Boe (Hymenoptera: Eurytomidae) reared from seeds in pods of American licorice collected in Davison County, South Dakota.

clover (*Trifolium pratense* L.), and birdsfoot trefoil (*Lotus corniculatus* L.) (e.g., Neunzig and Gyrisco 1959). This is the first report of these three parasitoids being associated with *Bruchophagus grisselli* (Figure 2).

Grapholita interstinctana (Clemens) (Lepidoptera: Tortricidae), commonly referred to as the clover seed caterpillar, was identified as a new seed predator at Brookings, SD, in 2015 and 2016. Adults were collected by sweeping inflorescences on 25 June 2016. First instar larvae consistently entered the pods at the proximal end close to its attachment to the rachis, with the entry hole enlarged and closed with frass as the insect grows. Usually there is a single caterpillar per pod and it can consume all of the seeds within a pod during its 4-5 instar stage. We estimated that about 40-60% of the pods were infested and nearly 100% of the seeds were entirely or partially consumed and destroyed in 2015. Larval feeding activity is mostly in early to mid July, but may extend from late June through early August. Larvae exited the pods during late July to early August by reopening the enlarged entry hole.

The clover seed caterpillar is native to North America and is considered a serious pest of seed production in red clover and several other species of *Trifolium*, all of which are important forage crops introduced to North America from Eurasia (Folsom 1909; Wehrle 1924). It evidently does not occur in Eurasia. The plant host range for the clover seed caterpillar is not completely known, but it has been found feeding on native sawtooth sunflower (*Helianthus grosseserratus* M. Martens) and the introduced common sheep sorrel (*Rumex acetosella* L.) (Wehrle 1924). In the late 19th and early 20th centuries, the clover seed caterpillar was considered to be a serious threat to red clover seed production in the eastern US and Canada. However, more recently it was regarded as of little consequence (Manglitz 1985).

This research revealed that seed production in natural populations of American licorice in western South Dakota was highly variable from year-to-year, with variation in level of seed predation by *Acanthoscelides aureolus* an important factor. It also indicated that un-predated seeds in natural populations had high viability and rapid and uniform germination under laboratory conditions, after light scarification.

American licorice has a diverse insect guild associated with seeds. Two phytophgous insects are parasitized by different groups of parasitoids. *Acanthoscelides aureolus* was parasitized by three highly polyphagous introduced species of chalcids, with *D. acutus* the only known one restricted to bruchid beetles. In contrast, the parasitoid guild associated with *B. grisselli* is composed of three introduced species that have been recorded only from the genus *Bruchophagus*, most notably the seed chalcids (*B. gibbus, B. platypterus* and *B. roddi*) that have enormous impacts on seed production of forage legumes worldwide (Peck 1963).

Though little is known about the range of host plants for the clover seed caterpillar, historically it was considered an economic pest only for seed production of red clover. Our preliminary observations indicated it can have a devastating effect on seed production in American licorice. Combs et al. (2013) described a similar seed-feeding guild composed of a bruchid seed beetle (*Acanthoscelides fraterculus* Horn), a seed weevil (*Tychius semisquamosus* LeConte), and a tortricid moth (*Grapholita imitativa* Heinrich) in three species of Astragalus in eastern Washington. The relative impact of the moth vs. the beetles on seed production varied from year to year. Similarly, in native tallgrass prairie in Kansas, Evans et al. (1989) found that pod infestation in the legume blue wild indigo, *Baptisia australis* (L.) R. Br., was from 80 to100% as a result of the combined feeding activity of the moth *Grapholita tristegana* (Clemens) and the seed weevil *Tychius sordidus* LeConte.

The same genus-level taxonomic composition among these associations suggests that further study of native legumes may reveal co-evolutionary patterns not yet elucidated fully. In addition, the sharing of six species of introduced parasitoid wasps among introduced and native host insects is suggestive of an invasive species pattern similar to that indicated by Perilla López et al. (2015) for species of *Aprostocetus* Westwood parasitizing species of *Stenodiplosis* Reuter (Diptera: Cecidomyiidae) in introduced and native grasses. A further similarity is the rarity of native parasitoids on native hosts. We suggest that many, if not most, of the commonly reared chalcidoid parasitoids introduced from Eurasia may be considered invasive as the limited evidence appears to be displacement of native parasitoids that are now rarely reared. If there is a pattern awaiting elucidation, there may well be a cryptic ecological disaster under way that may not be properly documented.

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