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Influence of Biocontrol Insects on Canada Thistle: Seed Production, Germinability, and Viability

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ABSTRACT -- We conducted surveys of thistle-feeding insects on Canada thistle [*Cirsium arvense* (L.) Scop.] during the 2000 and 2001 growing seasons at Lacreek National Wildlife Refuge (LNWR), South Dakota, and analyzed their impact on thistle seed production, germination, and viability. Insects included Canada thistle stem weevil [*Hadroplontus litura*, formerly *Ceurtorhynchus litura*, (Coleoptera: Curculionidae)], introduced at LNWR as a biocontrol agent, plus two seed head parasites, the thistle head weevil [*Rhinocyllus conicus* (Coleoptera: Curculionidae)] and the seed head fly [*Terellia ruficauda* (Diptera: Tephritidae)]. Infestation by these insects caused no significant reduction in per-head seed yield, with means ranging from 82.5 seeds per head, when both Canada thistle stem weevil and seed head parasite(s) were present, to 85.7 seeds per head with no parasites present. Average per-head seed yield was found to decline from 86.3 to 81.3 between our 12 to 14 July 2000 and 26 to 27 July 2000 sampling periods, but the decline was not attributable to seed head parasites. Infestation by seed head fly occurred at a rate of 14.7% of open female heads; male heads were not attacked by seed head fly. Thistle head weevil infested both female and male heads with 10.8% of female heads in pre-flowering condition infested compared to 7.8% in flowering or post-flowering stage; about 7% of male heads were infested in both pre-flowering and flowering/post-flowering stages. Germination testing suggested some reduction in germination rates due to seed head parasites, but high variability among replicates

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often obscured the source of differences. Seed viability, as revealed by germination and tetrazolium testing, was reduced by about 2% by either seed head parasite and by about 4% when both the seed head fly and thistle head weevil were present. The impact of these insects on the potential for Canada thistle to spread by seed appeared to be negligible.

Key Words: biocontrol insects, Canada thistle, *Cirsium arvense*, germination, Lacreek National Wildlife Refuge, seed production, South Dakota.

Canada thistle (*Cirsium arvense* (L.) Scop.) is a perennial weed of Eurasian origin that was introduced into eastern North America in the early 1600's and has since spread throughout the northern United States and southern Canada (Hodgson 1968, Moore 1975). In the northern Great Plains, Canada thistle has become one of the most serious weed pests in agricultural, rangeland, and wetland environments (Nuzzo 1997). In 2000, the South Dakota Department of Agriculture reported that Canada thistle infested over 485,623 ha in the state, giving South Dakota the distinction of having the largest acreage impacted by Canada thistle of any state in the United States.

The invasive nature of Canada thistle is due mainly to extensive vegetative reproduction involving development of new shoots from a spreading, ramifying root system. Canada thistle forms dense patches, with up to 39 stems per m² (Bakker 1960), and spreads by lateral expansion of the root system. Rates of lateral root spread of up to 6 m in a single growing season have been reported (Rogers 1928), although patch expansion is typically on the order of 1 to 2 m per year (Amor and Harris 1975).

While clonal growth accounts for local spread and increase of Canada thistle, invasion of new areas or new habitats typically requires establishment of new clones by seed. Long-distance seed dispersal by Canada thistle has been shown to be effective in colonization of new habitats (Bakker 1960). However, the amount of seed dispersed from established colonies to new areas is limited by a number of factors. First, Canada thistle is dioecious and therefore seed is produced solely by female colonies. [Gynodioecious populations of Canada thistle, with flower heads of some otherwise male plants producing some fruits, are yet to be discovered in the United States though they occur in Eurasia (Heimann and Cussans 1996) and New Zealand (Lloyd and Myall 1976).] Furthermore, good seed set requires that male plants be in close proximity to females to ensure pollination, so distance between male and female plants has been proven to affect seed production (Hay 1937, Lalonde and Roitberg 1994). Secondly, most seeds produced by female Canada thistle plants do not escape the parent colony. The plume of bristles (the pappus) atop each achene (the one-seeded fruit) usually separates and blows away, leaving the achene inside the flower head or very near the parent plant.

Heimann and Cussans (1996) found that only 10% of trapped thistle plumes bore an achene at about 10 m from source plants. Bakker (1960) reported that only 3.4% of plumes bore an achene at 27 m from source plants, and just 0.2% of plumes retained an achene at 1000 m away from the source. Long-distance wind dispersal of Canada thistle seed is evidently a low-probability event.

The percentage of seeds escaping female Canada thistle colonies might be low, but a new colony can be established with a single seed. Consequently, poor efficiency in seed dispersal by wind is probably not a major issue in long-term spread of the species. Further, other agents besides wind, such as wildlife and humans, might be vectors for transporting Canada thistle seeds away from existing populations.

A third factor affecting Canada thistle reproduction by seeds is the loss or reduction of seed crop to insects feeding on thistle plants, especially those that feed within the flower head. A number of insects attack Canada thistle, including some that were introduced intentionally in efforts to achieve some measure of biological control over the weed. Other insects were introduced accidentally but have nonetheless been promoted as potential biological control agents. Whether or not thistle-feeding insects are effective in reducing or inhibiting the spread of Canada thistle by seed is unclear as studies have yielded conflicting results (Maw 1976, Peschken and Wilkinson 1981, Peschken et al. 1982, Forsyth and Watson 1985a, b, Rees 1990, Lalonde and Roitberg 1992, Peschken and Derby 1992, Youssef and Evans 1994, Liu et al. 2000).

Lacreek National Wildlife Refuge (LNWR) is a 6,641-ha complex of artificially controlled impoundments and surrounding grasslands, located near Martin, Bennett County, South Dakota (Fig. 1). LNWR has battled Canada thistle infestation for over two decades by using a combination of spraying, mowing, intensive cattle grazing, and biological control insects (Rolf Kraft, United States Fish & Wildlife Service, personal communication). Our purpose was to learn which thistle-feeding insects are established on the refuge and to determine whether they have any measurable impact on the yield, germinability, and viability of Canada thistle seed, thereby potentially reducing sexual reproduction and establishment of new patches by seed. Biocontrol insect releases at LNWR for Canada thistle control are summarized in Table 1.

METHODS

During 7 to 9 June 2000, we surveyed Canada thistle stands at eight sites at LNWR (Fig. 1) for the presence of Canada thistle stem weevil [*Hadroplontus litura* (= *Ceutorhynchus litura*), Coleoptera: Curculionidae] larvae. With two exceptions, stands were located on or adjacent to dikes separating wetland pools on the refuge. The two other sites (4 and 7, Fig. 1) were associated with wetland borders.

Canada Thistle Sampling Sites at Lacreek National Wildlife Refuge

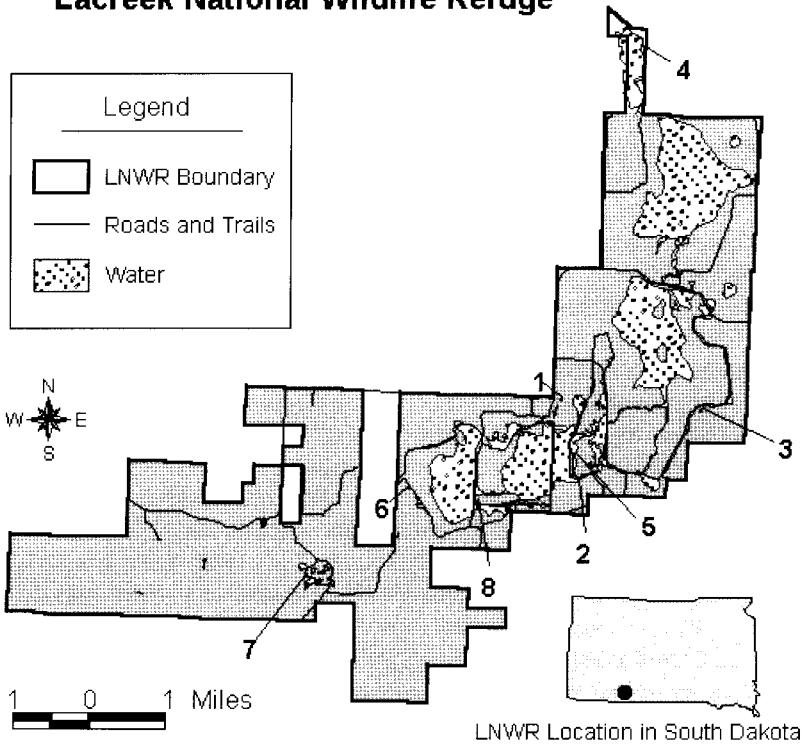


Figure 1. Map of Lacreek National Wildlife Refuge showing locations of Canada thistle (*Cirsium arvense*) sampling sites.

The oldest flower heads of the season were in the bud (pre-flowering) stage. We randomly selected one hundred stems within each stand by tossing a 15-cm diameter plastic hoop within Canada thistle patches and selecting the Canada thistle stem nearest to the hoop. We cut off each sampled stem at ground level and then sectioned it longitudinally from the base upward to check for tunneling and presence of Canada thistle stem weevil larvae. Boring by Canada thistle stem weevil larvae started near the stem base and progressed upward within the stem pith. Tunnels were well marked by dark staining from larval frass. We recorded height and basal diameter of all sampled stems in order to identify relationships between stem size and presence of Canada thistle stem weevil.

We revisited five sites (1, 2, 5, 7, and 8) during 12 to 14 July 2000 and three sites (1, 2, and 5) during 26 to 27 July 2000. Sites omitted during each revisit had

Table 1. Canada thistle (*Cirsium arvense*) biocontrol insect releases at Lacreek National Wildlife Refuge.

Biocontrol insect	Year released	Number released	Detected during 2000-2001
Canada thistle stem weevil (<i>Hadroplontus litura</i>) (Coleoptera: Curculionidae)	1989	500	Yes
	1995	800	
Canada thistle bud weevil (<i>Larinus planus</i>) (Coleoptera: Curculionidae)	1993	300	No
	1994	300	
Canada thistle gall fly (<i>Urophora cardui</i>) (Diptera: Tephritidae)	1993	300	Yes, but very low frequency
Green tortoise beetle (<i>Cassida rubiginosa</i>) (Coleoptera: Chrysomelidae)	1995	400	No
	1996	600	

been herbicide-treated and rendered unusable. Again, we randomly sampled 100 stems and recorded presence/absence and extent of tunneling (distance up the stem) by Canada thistle stem weevil larvae for each sampled stem, along with stem height and diameter. Additionally, we harvested four mature seed heads per plant from 25 randomly selected (again by using the hand-tossed hoop) female plants at each site to assess seed head parasite activity and to obtain per-head seed counts. We determined seed head maturity by elongation of pappus bristles and avoided seed heads already releasing pappus. The four seed heads we excised from the same plant were bagged and sealed together and kept refrigerated (4°C) prior to lab analysis. We gathered and bagged bulk samples of mature seed heads at each site for use in germination and viability tests. We also gathered in bulk mature head samples from male plants to ascertain whether seed head parasites also were using male flower heads.

In 2001, we obtained bulk collections of male and female flower heads from sites 1, 2, and 5 during 17 to 19 July. In addition, we collected all flower heads (from bud to fruiting stage) from randomly selected male and female plants (50 plants of each sex) to measure head parasitism rates among flower heads of different ages and sexes. No Canada thistle stem weevil data were collected in 2001.

We wanted to determine baseline infestation rates of the two seed head parasites and to see if they differentially were parasitizing flower heads based

on sex and developmental stage of the heads. For our analysis, all flower heads (in all developmental stages) were removed from 50 each of male and female Canada thistle plants from site 2 (Fig. 1) and checked for the presence of the seed head parasites. Thistle head weevil infestation of pre-flowering heads was detected by a small cap covering the egg on the involucre of the flower head.

We analyzed Canada thistle head collections within four weeks after collection to determine infestation rates and seed yield. We removed achenes from individual heads and separated them from their plumes. We also removed and preserved the larvae and/or pupae (or occasionally a metamorphosed adult) of seed head parasites in alcohol. We used an illuminated magnifier (3X) in sorting and counting achenes on a per-head basis to determine seed yield. Only plump, undamaged achenes were counted toward the total seed yield. We placed achenes from each head in envelopes and categorized them into four groups according to infestation status as follows: 1) those lacking all target insect parasites, 2) those with Canada thistle stem weevil damage in the stem but without seed head parasites, 3) those with one or both seed head parasites but without Canada thistle stem weevil damage, and 4) those with both Canada thistle stem weevil damage and one or both seed head parasites. Seed counts were done on 200 seed heads of each infestation category to measure any effect parasites might have on seed yield. We also enumerated on a per-head basis insect-damaged achenes and undeveloped achenes (often the result of incomplete pollination of the flower head) but did not include them in germination tests. We conducted germination tests on seed collections within a year after collection, prior to which we kept seed packets refrigerated (4°C).

For germination and viability testing, we placed 40 seeds in clear plastic germination boxes on moistened blotter paper and subjected them to a 14 day pre-chill without light at 5°C. After the pre-chill, we transferred germination boxes to a germinator with a constant temperature of 25°C and a light/dark cycle of 8 hr light/16 hr dark. We added distilled water to blotter paper as needed to maintain moisture. Seed boxes remained in the germinator for 28 days during which we recorded germinations daily and tallied germinations weekly. Nearly all germinations occurred within the first 14 days; very few occurred during the third and fourth weeks. At the end of the 28 day germination period, dormancy of remaining seeds was determined by using a tetrazolium (TZ) test (Association of Official Seed Analysts 2000). Viability percentage was determined from the number of seeds that germinated plus those that tested alive (but dormant). Nonviable seeds included not only those that failed to stain with TZ, but also achenes found to contain no embryo.

We performed germination and seed viability tests on seed lots categorized strictly on the basis of head infestation status as follows: 0 – no seed head parasites, 1 – thistle head weevil [*Rhinocyllus conicus* (Coleoptera:

Curculionidae)], 2 – seed head fly [*Terellia ruficauda* (Diptera: Tephritidae)], 3 – both seed head parasites. We did not consider stem weevil infestation status in germination and viability tests because we had found that Canada thistle stem weevil had no discernible effect on per-head seed production or plant vigor, and because the locus of feeding was distant from the flower heads. We tested seeds (= achenes) in three separate runs by using 10 replicates of 40 seeds per germination box for each infestation category (i.e., 400 seeds per category per run). The limited number of heads containing both seed head parasites permitted only one test run with seeds of category 3. Also, the final run included only six replicates (240 seeds) of category 1, again limited by seed quantity. We determined seed viability versus head infestation status by combining germination and tetrazolium testing results from all three germination trials. We analyzed all data by using SAS/STAT (SAS Institute 1989).

RESULTS

Of the intentionally released species, only the Canada thistle stem weevil and gall fly [*Urophora cardui* (Diptera: Tephritidae)] were detected at LNWR during 2000 and 2001 (Table 1). The gall fly appeared at very low frequency, with stem galls observed on only three Canada thistle stems of over one thousand sampled during the project. The Canada thistle stem weevil was well established at LNWR, although highest infestation levels (34% to 54%) were at or near the 1989 Canada thistle stem weevil release site (site 1). Infestation levels at sites 4 and 6 were 11% and 4%, respectively, and two of the eight Canada thistle stands (sites 3 and 7) examined in 2000 had no evidence of Canada thistle stem weevil, which indicated that Canada thistle stem weevil was dispersing outward from release sites. Numbers of larvae were usually one to few per stem, but occasionally more than 10 larvae were observed inside a stem.

Stem measurement data showed a positive relationship between stem basal diameter and boring by Canada thistle stem weevil. The mean diameter of stems bored by Canada thistle stem weevil (6.8 mm, SE \pm 0.2, n = 179) was significantly greater (t-test, $t = -6.60$, d.f. = 267, $P < .0001$) than the mean diameter of uninfested stems (5.2 mm, SE \pm 0.1, n = 489). In contrast, stem height data analyzed on a site-by-site basis showed no significant relationship with Canada thistle stem weevil activity with the exception of Site 5, where mined stems averaged 6.6 cm shorter (ANOVA, $F = 4.58$, d.f. = 1, 48, $P = 0.04$) than uninfested stems.

Other insect predators of Canada thistle at LNWR were two seed head parasites with the potential to affect thistle seed production and viability directly through their feeding activity. The larvae and pupae of seed head weevil and seed head fly were found commonly within Canada thistle flower heads.

Mean number of seeds per head ranged between 82.5, when both Canada thistle stem weevil and seed head parasite(s) were present, and 85.7, with no insect parasites present (Fig. 2), but differences were not significant (ANOVA, $F = 0.51$, d.f. = 3, 792, $P = 0.68$). We found that average per-head seed yield declined (t-test, $t = -1.87$, d.f. = 196, $P = 0.06$) between sampling periods. Seed heads collected 12 to 14 July 2000 from sites 1, 2, and 5 averaged 86.3 seeds/head (SE ± 2.0 ; $n = 124$), whereas seed heads collected during 26 to 27 July 2000, from the same sites, averaged 81.3 seeds/head (SE ± 1.7 ; $n = 75$).

The seed head fly was found strictly in female heads and only in the open (flowering or post-flowering) condition. The rate at which seed head fly larvae or eggs were found in flowering/post-flowering female heads ($n = 1954$) was 12.8% (Table 2). In contrast, the thistle head weevil infested flower heads of both sexes and was detectable in both pre- and post-flowering condition (Table 2). Maximum likelihood ANOVA (PROC CATMOD) of the thistle head weevil head infestation data revealed significant interactions between head sex and weevil infestation ($\chi^2 = 4.3$, $P = 0.04$), and head developmental stage and thistle head weevil infestation (χ^2

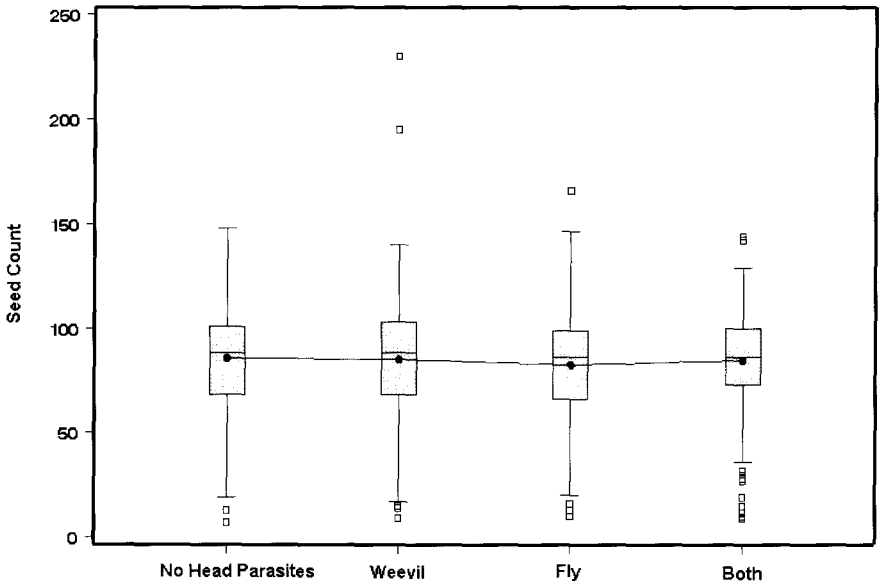


Figure 2. Seed yield of Canada thistle (*Cirsium arvense*) infested by thistle head weevil (*Rhinocyllus conicus*), seed head fly (*Terellia ruficauda*), both parasites, or no parasites. Means are indicated by solid circles in boxplots.

Table 2. Infestation of male and female Canada thistle (*Cirsium arvense*) flower heads in pre-flowering and flowering/post flowering condition (collected 17 to 19 July 2001) by thistle head weevil (*Rhinocyllus conicus*), and seed head fly (*Terellia ruficauda*) at Lacreek National Wildlife Refuge.

Head status and sex (n)	No. infested by thistle head weevil (%)	No. infested by seed head fly (%)
Pre-flowering male (394)	28 (7.1%)	0
Flowering/post flowering male (2822)	192 (6.8%)	0
Pre-flowering female (673)	73 (10.8%)	0
Flowering/post flowering female (1848)	144 (7.8%)	237 (12.8%)

= 4.25, $P = 0.04$); however, three-way interaction was not significant ($\chi^2 = 1.54$, $P = 0.21$). Infestation rate was highest (10.8%) for female heads in the pre-flowering condition compared to an average infestation rate of 7.8% for open female heads. Male flower heads were infested by thistle head weevil at a lower rate (about 7%) than female flower heads (Table 3).

Germination trials yielded differing results (Table 4). Germination trial 1 showed a mean germination rate that was higher for seeds from non-infested seed heads than for those containing one or both of the seed head parasites; however, the differences were not significant ($F = 0.48$, d.f. = 3, 36, $P = 0.70$). Trial 2 (Table 4) also showed a higher mean germination rate for seeds from non-infested seed heads, with some significant differences ($F = 2.91$, d.f. = 3, 36, $P = 0.048$). In particular, seeds from heads infested with the thistle head weevil and those from heads infested with seed head fly showed depressed germination relative to seeds from non-infested heads, although those from heads containing both insects had a mean germination rate that was not significantly different from either of the other infestation categories. For Trial 3 (Table 4), no more seeds from heads containing both head parasites were available, and those from heads infested with thistle head weevil were limited to six, rather than ten, replicates of 40 seeds. Analysis of these results showed a significantly lower ($F = 3.58$, d.f. = 2, 23, $P = 0.044$) germination rate for seeds from thistle head weevil-infested heads compared to those with seed head fly or with no parasites. Tetrazolium testing suggested a slight loss (about 2%) of seed viability due to infestation by the two seed head parasites separately and about a 4% reduction when these two insects co-occurred (ANOVA, $F = 55.86$, d.f. = 3, 4291, $P < 0.0001$, Fig. 3).

Table 3. Frequency of infestation by thistle head weevil (*Rhinocyllus conicus*) versus sex of flower heads and stage of flower head development.

Infestation status	Male heads (n = 3216)	Female heads (n = 2521)	Flowering/ postflowering (n = 4670)	Preflowering (n = 1067)
Infested	220 (6.8%)	217 (8.6%)	336 (7.2%)	101 (9.5%)
Noninfested	2996 (93.2%)	2304 (91.4%)	4334 (92.8%)	966 (90.5%)

Table 4. Mean percent germination from three germination trials of Canada thistle (*Cirsium arvense*) seeds obtained from heads containing no parasites, heads with thistle head weevil (*Rhinocyllus conicus*), heads with seed head fly (*Terellia ruficauda*), and heads with both parasites. Each trial tested 10 lots of 40 seeds per infestation category; however, only 6 lots (240 seeds) from thistle head weevil-infested heads and no seeds from heads containing both parasites were available for trial 3.

Trial No.	No head parasites	Thistle head weevil	Seed head fly	Both parasites
Mean percent germination*				
1	42a	34a	32a	31a
2	47a	28b	24b	37ab
3	25a	7b	31a	—

*Means in the same row followed by different letters are significantly different.

DISCUSSION

Of insects intentionally released at LNWR to attack Canada thistle, only Canada thistle stem weevil has become well established. Canada thistle stem weevil was abundant in the vicinity of original releases, infesting 32 to 54% of stems sampled, but was absent or at considerably lower levels (4 to 11% of stems infested) at sites up to 5 km from original release sites. We detected no obvious inhibition of thistle growth or vigor caused by Canada thistle stem weevil, although refuge personnel perceived some stand reduction at the earliest release site, i.e., site 1 (Rolf Kraft, United States Fish & Wildlife Service, personal communication). Peschken and Wilkinson (1981) suggested that declines in Canada thistle stand density also might be attributable to natural degeneration that accompanies aging

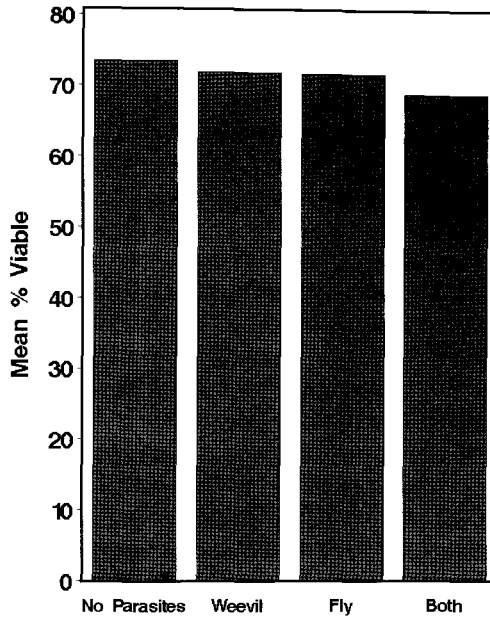


Figure 3. Mean percent viable seed for four categories of seed head infestations. Percentages represent tetrazolium and germination test results from three germination trials.

of stands. Detailed, long-term studies are needed to ascertain whether the Canada thistle stem weevil truly affects plant survival (and thus seed production) within Canada thistle clones.

The larger diameters of weevil-infested stems compared to non-infested stems might have resulted from adult weevils selecting the largest Canada thistle rosettes when ovipositing in the spring. Larger rosettes would be expected to produce stouter shoots. Some basal enlargement of the stem also might have been caused by the injury of stem penetration and mining by larvae. Our finding of no relationship between stem height and infestation status contradicts the findings of Peschken and Derby (1992) and Zwolfer and Harris (1966) who noted positive correlations between Canada thistle stem weevil infestation and stem height.

The Canada thistle stem weevil has been described variously as being effective in reducing Canada thistle stands to having virtually no impact. Rees (1990) reported that Canada thistle stem weevil caused elevated winter mortality of Canada thistle plants in the Gallatin Valley of Montana (12% or less survival of infested plants versus 93% or greater survival of non-infested plants). He

attributed this effect to Canada thistle stem weevil injury that allowed secondary invasion of underground stems and roots by nematodes and small arthropods. Studies by Peschken and Derby (1992) and Liu et al. (2000) detected declines in nonstructural carbohydrate root reserves in Canada thistle due to Canada thistle stem weevil, although the former authors described this effect as temporary and disappearing six to eight weeks after boring activity ceased. Peschken and Wilkinson (1981) reported no measurable reduction in Canada thistle stands infested with Canada thistle stem weevil at sites in British Columbia, Alberta, and Saskatchewan. Such variable results obtained with Canada thistle stem weevil might be attributed to interactions between environmental factors and genetic variation in Canada thistle populations.

Thistle head weevil and seed head fly commonly infested seed heads of Canada thistle at LNWR, even though neither of these insects were introduced intentionally at LNWR. The thistle head weevil was introduced originally in Canada (Ontario and Saskatchewan) in 1968, and hence to Virginia and Montana in 1969, California in 1971, and Nebraska in 1972, with subsequent redistribution from those areas (Louda et al. 1997). Weeds originally targeted by thistle head weevil introduction were plumeless thistle (*Carduus acanthoides*) and musk thistle (*C. nutans*) and milk thistle (*Silybum marianum*) (Boldt and Kok 1982); however, the insect also has been found to infest heads of Canada thistle (Rees 1977, Peschken 1984, Youssef and Evans 1994) as well as many nontarget native species of *Cirsium* spp. (Louda 1998). The seed head fly was introduced accidentally to North America long ago and is now widespread in Canada and the United States where it is known to feed only on Canada thistle.

Infestation levels for thistle head weevil and seed head fly on a per-flower head basis were low, and seed yield on a per-head basis was not reduced by infestation. Variability in seed set caused by incomplete pollination and natural abortion of achenes appeared to outweigh any reduction in seed yield caused by the insects. Our results indicated that thistle head weevil egg-laying activity might have been intensifying with time, probably due to a growing thistle head weevil population, with 7.2% of flowering/post-flowering heads infested compared to 9.5% of heads in pre-flowering condition. Also, female heads were infested at slightly higher rates than male. While our data analysis showed a statistically significant interaction between thistle head weevil infestation and sex of flower heads, and also between infestation and head developmental stage, this result is attributable to large sample size and is doubtfully of any biological significance.

The restriction of the seed head fly to mature female flower heads is explainable by the fact that they feed strictly on achenes (Forsyth and Watson 1985b). In contrast, thistle head weevil larvae were observed to feed mostly on soft tissues of the receptacle beneath the flowers, in both male and female flower heads, and were not reliant on developing achenes. Our findings regarding seed head fly agree with Lalonde and Roitberg (1992) who describe egg-laying activity of the

seed head fly as focused on flower heads one day prior to their flowering, and with Angermann (1986) who likewise found seed head fly eggs and larvae restricted to female flower heads. Lalonde and Roitberg (1992) also reported that seed head flies avoid ovipositing on heads in which eggs had been laid, and that seed head size and achene number had no influence on whether a seed head was used for ovipositing. Our observed rates of seed head fly infestation of seed heads were far below 70%, the highest seed head infestation rate of seed head fly reported by Forsyth and Watson (1985a).

The amount of seed produced per head was highly variable (Fig. 2), likely due to incomplete pollination (Hay 1937) or natural abortion of achenes (Lalonde and Roitberg 1994). Thus, there was no statistical basis to indicate that infestation by Canada thistle stem weevil, seed head parasites, or both together had any measurable effect on seed yield. At least in the case of the seed head fly, these results contrast sharply with Forsyth and Watson (1985a) who reported about a 21.5% reduction in seed yield per head caused by seed head fly infestation. A variety of environmental factors could have caused the decline in per-head seed yield we observed from the mid to the late July sampling periods, including hotter, drier growing conditions and the need for plants to allocate resources to more numerous heads, but there was no evidence that seed head parasites played a role.

Three separate germination trials yielded mixed results when comparing seeds from infested versus non-infested seed heads. While the results of all three germination trials suggest some decline in germinability due to seed head parasitism, the relationship is supported weakly because of considerable variability in germination rates among the replicates. Seed head parasites, and especially the thistle head weevil, might cause some suppression of seed germinability, most likely due to the loss of resources for achene development caused by larval feeding on receptacle tissues. Tetrazolium testing indicated a slight loss of seed viability from heads containing parasites. The suggestion that seed head parasites caused a real loss of seed viability is not supported strongly, however, because germination replicates were combined for TZ testing and results were thus weighted by high numbers of seeds. If seed viability had been determined on a replicate by replicate basis for each trial, differences between infestation classes might not have tested statistically significant.

The effects of Canada thistle parasites on production, germinability, and viability of Canada thistle seed appear to be of little consequence to overall reproduction and spread of the weed. Relatively little seed travels far from Canada thistle stands to establish new colonies so that any influence these insects might have in reducing seed yield in existing colonies would have negligible impact on establishment of new ones. Results of our study and many others (e.g., Donald 1990) suggest that control of Canada thistle solely through the use of insects is unattainable. The fact that Canada thistle remains a problematic weed in its home range in Europe (Schroeder et al. 1993), where it coexists with these same insects,

points to their ineffectiveness as control agents. Further, integrated approaches to Canada thistle control are difficult because herbicide use interferes with the life cycles of would-be control agents. Hence, reliance on biocontrol insects to control Canada thistle in natural areas appears impractical, and herbicide treatment remains the most effective management tool.

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