Seasonal phenology and impact of *Urophora sirunaseva* on yellow starthistle seed production in California

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**Abstract**

The gall fly, *Urophora sirunaseva*, is one of six insect species released as classical biological control agents to control the invasive weed, yellow starthistle. Two study sites were established in Northern California to evaluate the *per capita* impact of galls on seed production. Evaluations during two years at each site used small cloth bags placed over developing seedheads to contain developing seeds and insects. Larger seedheads produced more seed but also supported more galls. Within-seedhead gall densities as high as 15 were detected. The impact of a single gall was estimated to reduce seed number by between 2.1–2.9 seeds per gall. A regression model was developed that estimated percentage seed loss as a function of seedhead size and number of galls. Individual galls were estimated to cause a 5–11% decrease in seed production compared to ungalled seedheads. The impact of the gall fly was greatest in smaller seedheads at both sites. Gall densities did not reach levels needed to exert significant control of seed production. Seed production in non-galled seedheads was not affected by the presence of galls in seedheads elsewhere on the plant. Gall flies were more likely to attack plants already supporting galls. Two generations of the fly were detected at both sites. The occurrence of overwintering larvae began in mid- to late-July depending on site. By early-August, all new galls held only overwintering larvae. Follow-up samples at one location eight years later showed the gall fly still present but at less than half of the population level observed earlier.

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1. Introduction

Yellow starthistle (*Centaurea solstitialis* L., Asteraceae), an invasive, exotic winter annual weed in California and other western states, has been the target of biological control efforts since the 1960s (Turner et al., 1995). The guild of insects initially selected for biological control consisted solely of capitulum-impacting species, one of which was the gall forming fly, *Urophora sirunaseva* (Hering) (Diptera: Tephritidae).

Tephritid flies have been utilized as biological control agents for several exotic weeds with varying degrees of success (White et al., 1990; Turner, 1996a). In particular, *Urophora* species have been selected as host-specific biological control agents for many of the Asteraceae (Harris, 1980; Freidberg, 1984; Turner, 1996a,b). Adult *Urophora* females oviposit within the host plant where the developing larvae stimulate the production of gall tissue. Eggs are usually placed in developing capitula but in some species, such as *U. cardui* in Canada thistle (Lalonde and Shorthouse, 1984), galls are produced in stems. In spite of their host specificity and relative ease of establishment, few detailed studies have been published on the impact that *Urophora* spp. have on their hosts. In one well-studied system, the knapweed gall flies, *U. affinis* and *U. quadri fasciata*, are believed to impact their host on two levels: a direct reduction of total seed number by physical displacement of achenes (hereafter seeds) by the developing galls, and an indirect impact on seed numbers by disruption of resource partitioning within the plant (Harris, 1980).

The yellow starthistle gall fly, *U. sirunaseva*, was first introduced into North America in 1984. Extensive host specificity testing (Clement and Sobhian, 1991; Sobhian, 1993; Turner, 1994) demonstrated a high-level of host specificity in this insect and a federal permit was granted. For the first year of releases, gall flies collected in northern Greece were released in California while others collected in Turkey were released in Idaho. Additional collections from Greece, in 1985, 1990 and 1991, were released in California, Idaho, Oregon, and Washington (Turner et al., 1995). The fly was
established at several locations by 1989 and an extensive distribution campaign was initiated in California (Villegas, 1996). Currently the fly is widely distributed throughout the range of yellow starthistle in California (Pitcairn et al., 2008).

Adult female flies oviposit in closed flower buds of starthistle and developing larvae stimulate the formation of lignified, unilocular galls, which are partially submersed in the receptacle. Previous laboratory studies showed the fly to be bivoltine and to overwinter as mature larvae within galls (Zwölfer, 1969; Turner, 1994; Turner et al., 1994). The initial presumption was that the flies, free from their natural parasites, would increase to high-population levels and substantially reduce seed production of their host plant in the western United States.

Here we report on a field study to examine the impact of *U. sirinaseva* on yellow starthistle seed production. The impact of an exotic species results from its geographic distribution, its population density, and its *per capita* amount of damage (Parker et al., 1999). In this study, we estimate the suppressive effect of individual galls on seed production and examine the within-season variation in the activity of the fly relative to the production of seed heads by its host plant. The study was performed at two distinctly different locations where the gall fly was established in California. At the time, the bud weevil, *Bangasternus villosus*, another exotic biological control agent, was present at low levels at both sites, but no other biological control agents were present.

2. Materials and methods

2.1. Study sites

Two ungrazed field sites with populations of yellow starthistle were selected as study sites. The ‘Ukiah’ site (39° 4.40’N, 123° 12.30’W) was a steep, starthistle-infested grassy hillside adjacent to a grape vineyard near the town of Ukiah in Mendocino County. Most rain falls in California during the winter, when yellow starthistle grows through the seedling and rosette stages. The summer flowering season of yellow starthistle in Ukiah is hot (maximum daily temperatures average 30–33 °C) with an average cumulative summer rainfall of only 12 mm. In 1990, this site received one of six releases of *U. sirinaseva* obtained from foreign material with 372 adult flies reared from galls imported from Greece. Our studies at this site occurred in 1993 and 1994.

The ‘Winters’ site (38° 28.87’N, 122° 2.35’W) was a dry hillside overlooking the Sacramento Valley near the town of Winters in Solano County. It was distinctly warmer and drier than the Ukiah site with daily summer high-temperatures averaging 34–36 °C and an average cumulative summer rainfall of only 5 mm. Gall flies released at this site were locally collected as galled capitula (hereafter seedheads) from established populations near Newcastle in Placer County, approximately 90 km distant. The galled seedheads were placed in screen-topped containers and adult flies were allowed to emerge on-site. Based on laboratory rearing of subsamples, over 1300 flies were released during 1993 and 1994 at this site. Our studies took place in 1995 and 1996.

Plant and seedhead densities were estimated at Ukiah in fall 1994 and at Winters in fall 1995 by counting all the seedheads on all plants rooted in 40, quarter square meter frames along transects at each site.

2.2. Study plants

Four 20-m transects were established at each site. The transects were placed to represent the primary variation in yellow starthistle populations at each site. At Ukiah, two transects were located on the upper ridge of the hillside where plants were small and produced few seedheads, and two were located near the base where plants were larger and produced many seedheads. The four transects at Winters were placed parallel across the hillside with the lowest transect near the base of the hillside and the other transects placed every 2 m up the hillside. Metal rods (n = 40) were placed along each transect in a stratified random method (each rod was randomly located with a random-number table within each half-meter section) for a combined total of 160 rods per site. The nearest flowering plant to each rod was selected as a study plant. As each seedhead on the selected plant reached maturity and the post-pollination florets began to oxidize, a small cotton bag was tied over the seedhead to confine developing seeds and any emerging insects. Sites were visited weekly to monitor plants and all post-pollination seedheads were bagged. To provide a better estimate of the attack rate, additional seedheads on nearby plants were bagged to increase the weekly sample size to 100 when the weekly total of bagged seedheads dropped below 100 seedheads.

The yellow starthistle plants growing at the Winters site were particularly small. Large plants (having more than three seedheads) were under-represented in the regular transects. Therefore, in 1995, at the season end, an additional set (n = 80) of non-bagged plants, each with at least four seedheads, ‘large’ plants were selected from every fourth rod and harvested. Seed production could not be evaluated from these plants so during the second year (1996), an additional four transects were established and ten large plants per transect (n = 40) were selected. These were monitored and bagged along with the regular plants throughout the season.

2.3. Estimating seed loss due to *U. sirinaseva*

Each study plant was harvested upon death (August–October), brought to the laboratory and each seedhead on every plant was evaluated. External diameters of the intact seedheads were measured and recorded in 1-mm size classes. Seedheads were then carefully dissected for evidence of insect damage and the number and status of galls (empty or with larva), and the number of pappus-bearing and non-pappus-bearing seeds were counted. All mature seeds were weighed, then germinated in controlled environmental chambers at 20 °C on wet blotter paper with an 8/16 h light/dark cycle to determine viability. Seeds not germinating by seven days were cut open and those filled with healthy embryo tissue were also considered viable. Seed production was evaluated as the sum of germinated seed and ungerminated viable seed. All seedheads and plant parts were oven dried at 60 °C and weighed separately. A total of 4029 seedheads were bagged and evaluated during the two-year study (1993–94) at Ukiah and 1783 during the two years (1995–96) at Winters.

The impact of galls on seed production was examined in three ways. First, the direct impact of individual galls was calculated using multiple linear regression with seedhead size and number of galls as independent variables and the number of seed per seedhead as the dependent variable. Each year was analyzed separately. Secondly, the potential maximum direct impact of galls was evaluated by similar analysis using only maximumly-producing seedheads. In this case, for each seedhead size and gall number combination, the number of seeds produced by three seedheads with the highest number of seeds was regressed against seedhead size and gall number. These results estimated the loss in maximum seed production compared to the loss of seed averaged across all seedheads. Lastly, indirect impact of galls on seed production was estimated as the proportional loss of seed compared to ungalled seedheads. Mean seed number was calculated for all combinations of the seedhead size and gall number. Proportional seed loss was estimated by dividing each combination mean by the mean number of seeds for
that size seedhead with no galls. For example, for all seedheads 4 mm in diameter, the mean number of seeds produced in seedheads with one-gall, two-galls, etc., were each divided by the average number of seeds for 4 mm seedheads without galls. The proportion of seed destroyed, S, within a seedhead due to the presence of galls was described using the equation:

\[ S = a \times H + b \times G + \text{intercept} \]

where \( H \) is the diameter of the seedhead (mm) and \( G \) is the number of galls. To increase sample size, data from both years was combined for each site.

### 2.4. Impacts beyond the attacked seedhead

In order to evaluate the impact of galls to other parts of the plant beyond the attacked seedhead, we compared ungalled seedheads on ungalled plants to ungalled seedheads on galled plants. Plants were placed into two groups: plants with at least one gall and those without galls. Within each year and bagging date, we compared seed production by ungalled seedheads from ungalled plants to seed production by ungalled seedheads in the same size class that developed on galled plants. Mean seed production was compared only where three or more seedheads were produced on both galled and ungalled plants within each sampling date.

### 2.5. Seasonal activity of the gall fly

Two analyses were made on the seasonal activity of the gall fly. In order to evaluate the bivoltine nature of the gall fly, bagged samples for the second year at each site (1994 and 1996) were processed within six months of collection. The developmental stage of the flies (larva or adult) and their health (dead or alive) were noted for each individual gall. Empty galls represented flies that emerged during the summer generation, while those remaining in the galls as mature larvae represented the overwintering generation.

The plant preference of the gall flies was examined by sorting plants into four groups based on number of seedheads. We compared those groups in which the first three seedheads were galled to those whose first three seedheads were not galled. Groups included: small plants having 4–10 seedheads; medium plants having 11–19 seedheads; large plants having 20–29 seedheads; and huge plants having over 30 seedheads. Plants with mixed results for the first three seedheads were excluded from this analysis. The attack rate on subsequently produced seedheads of each plant was evaluated for each plant group. The Winters site had very few large plants so only the data for Ukiah was analyzed. Plants from both years at Ukiah were combined in order to accumulate a large enough sample size in each category.

### 2.6. Long-term follow up

The Ukiah site was again sampled in 2000 to assess any long-term changes in the population density of the gall fly. Twenty plants were collected at the end of the summer, (closest plant to every eight rod of pre-existing transects) and processed as above to evaluate attack by any of the yellow starthistle biological control agents. Seed production was not evaluated. The Winters site had been repeatedly grazed and was not sampled.

### 3. Results

#### 3.1. Weed and insect populations

Environmental conditions differed substantially between the two study sites. The Winters site was an exposed hillside with shallow soil that dried out rapidly in the summer, in contrast to the deeper soil and cooler temperatures at Ukiah. Plant density at Ukiah was considerably lower and, consequently, plants were much larger than those at the Winters site, both in weight and number of seedheads (Table 1). The flowering season at the Winters site was roughly half the duration of the Ukiah site (Table 1). Larger plants at each site produced larger seedheads than smaller plants (at Ukiah, \( y = 0.49
\ln x + 6.92 \)), \( r^2 = 0.316 \); at Winters, \( y = 0.89 \ln x + 6.55 \), \( r^2 = 0.63 \). The seed weevil, *B. villosus*, damaged less than 1% of seedheads over both years at Ukiah and approximately 1% and 5% of the seedheads at Winters during 1995 and 1996.

### 3.2. Distribution of galls among plants and seedheads

Gall fly populations, estimated by the percent of seedheads with galls, were much higher at Ukiah than at Winters (Table 2). Gall flies did not attack all seedheads or all plants. When present, most galls occurred singly or in small groups of 2–5 galls per seedhead. These clusters represented 86% and 73% of the galled seedheads during the two years at Ukiah and 94% and 96% of the galled seedheads at Winters. The frequency distribution of galls in galled seedheads for Ukiah in 1993 and Winters in 1996 is shown in Fig. 1 which typified both years at each site. Gall density in terms of galls per galled seedhead and the maximum number of galls per seedhead was much higher at Ukiah (Table 2). Large plants with many heads were more likely to be attacked by *U. sirunaseva* than the smaller plants (Fig. 2). For example, 72% of the large plants collected in 1995 from Winters had at least one galled seedhead compared to 19% on the smaller plants.

### 3.3. Direct impact of galls on seed production

Seed production by yellow starthistle was strongly correlated with seedhead size (at Ukiah \( y = 5.39x - 12.86 \), \( P < 0.001 \) in 1993; \( y = 7.61x - 29.75 \), \( r^2 = 0.970 \), \( P < 0.001 \) in 1994; at Winters, \( y = 4.94x - 12.27 \), \( r^2 = 0.991 \), \( P < 0.001 \) in 1995; \( y = 6.22x - 33.12 \), \( r^2 = 0.967 \), \( P < 0.001 \) in 1996). Linear regressions showed that each mm increase in size accounted for an additional 4.9–7.6 seeds in non-galled seedheads, depending on the site and year. Seedhead size varied from 3–12 mm in diameter with a median of 7 mm. Most (95%) seedheads were in the 5–9 mm size classes. Some seedheads without galls produced no seed while the largest seedheads produced up to 88 seeds. The seedheads that produced no seeds were excluded from further analysis.

Larger seedheads were more likely to have galls than the smaller seedheads (Fig. 3A), particularly at Ukiah where there were both more gall flies and a higher number of large seedheads. Large seedheads did not however, always support a higher number of galls per seedhead (Fig. 3B). The exception was Ukiah in 1994 and, to a lesser degree, in 1993. The difference may be due to the higher density of gall flies relative to the availability of seedheads and, thus, higher oviposition pressure at Ukiah. Thus, larger seedheads, which have the potential to produce more seed per seedhead, could support a larger number of galls per seedhead.

The direct impact of individual galls on the average number of seeds per seedhead is presented by seed type in Table 3. The presence of each gall caused a reduction of between 2.1 and 2.9 seeds per seedhead depending upon the year. The impact of each gall under maximum seed production conditions increased to between 4.0 and 5.4 seeds in an individual seedhead. Galls appear to have a slightly greater impact on pappus-bearing seed than non-pappus seed, both on average and in the largest seedheads.
Losses of pappus-bearing seed accounted for between 78% and 92% of the total seed loss depending on the year, while pappus-bearing seed made up 70.6% of the total seed produced in non-galled seedheads during the four years of our study.

Percent seed destruction was estimated as the proportional decrease in average seed number per seedhead compared to ungalled seedheads. The linear model explained 59% and 51% of the variance in seed destruction for Ukiah and Winters, respectively (Table 4). More complex non-linear models did not significantly increase the amount of explained variance. The regression equations estimated an 11% (Winters) and 5% (Ukiah) decrease in seed production with the addition of each gall to a seedhead. According to the fitted equations, 100% seed destruction was not expected to occur at Ukiah, even at the highest densities of galls observed per seedhead (Fig. 4). At Winters, 100% seed destruction was estimated for seedheads with more than seven galls in smaller seedheads and more than 10 galls in the larger seedheads.

3.4. Impacts beyond attacked heads

Seed production in ungalled seedheads produced on galled plants at Ukiah was slightly higher (102% S.D. = 34), but not significantly different from seed production in similarly sized ungalled plants. At Winter, seed production was higher still (118% S.D. = 35) of that in ungalled plants.

3.5. Seasonal activity of U. sirunaseva

The production of new post-pollination seedheads by yellow starthistle began in late-June (Winters) and early-July (Ukiah) and continued through August and into September (Winters) and through October (Ukiah) (Fig. 5). For three years (1994–1996), seedhead production showed a single peak in mid season. In 1993 at Ukiah, seedhead production occurred in two peaks, one

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**Table 1**

Characteristics of yellow starthistle plants at two sites over two years in California

<table>
<thead>
<tr>
<th></th>
<th>Ukiah</th>
<th>Winters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1993</td>
<td>1994</td>
</tr>
<tr>
<td>Population density (plants/m²)</td>
<td>8.6</td>
<td>77.7</td>
</tr>
<tr>
<td>Mean plant dry wt. g (S.E.)</td>
<td>3.3 (0.7)</td>
<td>0.5</td>
</tr>
<tr>
<td>Mean # seedheads/plant (S.E.)</td>
<td>12.1 (1.5)</td>
<td>1.4 (0.1)</td>
</tr>
<tr>
<td>Flowering season (weeks)</td>
<td>13</td>
<td>5</td>
</tr>
</tbody>
</table>

<sup>a</sup> Second set of large plants (>3 seedheads) harvested at end of summer but not bagged.

<sup>b</sup> From extra transects of large (>3 seedheads) plants.

**Table 2**

Gall distribution in yellow starthistle plants monitored over two years at two sites in California

<table>
<thead>
<tr>
<th></th>
<th>Ukiah</th>
<th>Winters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1993</td>
<td>1994</td>
</tr>
<tr>
<td>% Plants w/galls</td>
<td>61.9</td>
<td>46.5</td>
</tr>
<tr>
<td>% Seedheads w/galls</td>
<td>46.4</td>
<td>55.7</td>
</tr>
<tr>
<td>Mean galls per sampled seedhead (S.E.)</td>
<td>1.5 (0.1)</td>
<td>2.4 (0.1)</td>
</tr>
<tr>
<td>Mean galls per galled seedhead (S.E.)</td>
<td>3.1 (0.1)</td>
<td>4.1 (0.1)</td>
</tr>
<tr>
<td>Maximum # galls per seedhead</td>
<td>14</td>
<td>15</td>
</tr>
</tbody>
</table>

<sup>a</sup> Second set of large plants (>3 seedheads) harvested at end of summer but not bagged.

<sup>b</sup> From extra transects of large (>3 seedheads) plants.

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Fig. 1. Frequency distribution of galls in galled seedheads at Ukiah 1993 (solid bars) and Winters 1996 (shaded bars).

Fig. 2. Relationship of plant size, estimated by number of seedheads, to attack by Urophora sirunaseva. Plants were grouped into categories based on the number of seedheads per plant. The Ukiah data is based on bagged plants along the transects. The Winters data includes the regular transects and the large plants to increase representation in the large categories.
early-August and the other in mid-September. Adult flies were already present in the field at both sites when the first plants began to flower and were also present when flowering ceased at the end of summer. Oviposition occurred throughout the summer as fresh galls could be detected for each sample date (Fig. 5). High-oviposition rates were observed among the early seedheads (Fig. 6) then declined approximately 2–3 weeks later during both years at Ukiah and in 1995 in Winters. A second, more protracted peak of activity occurred in August. High-oviposition rates were absent among the early seedheads at Winters in 1996 where only one distinct peak of activity was observed. The largest peak of gall formation at the Ukiah site was the second generation. In contrast, the largest peak at the Winters site is in the early part of the year with a very small peak in mid summer. This single peak of *U. sirunaseva* gall formation is closely timed to yellow starthistle development which also had a short season at this site (Fig. 6).

Rapid processing of the samples shortly after harvest in 1994 and 1996 allowed an evaluation of development of the overwintering stage of the gall fly. The presence of empty galls indicated summer emergence while individuals remaining as larvae represented the overwintering generation. Galls produced in early-July resulted almost exclusively (90%) in summer emergence of gall flies (Fig. 7). The proportion shifted from summer emergence to an overwintering stage during July, with 50% of galls producing overwintering larvae in mid-July at Winters and late-July at Ukiah. By mid-August, all new galls produced only overwintering larvae.

Plants whose first three seedheads were attacked by *U. siruras-eva* were far more likely to attract gall flies in future seedheads than plants not galled in the first three seedheads (Fig. 8). Subsequently produced seedheads on each plant tended to follow the pattern of the first three heads. On average, subsequently-produced seedheads were seven times more likely to remain non-galled if the first three heads were non-galled.

### 3.6. Observations at Ukiah six years later

The gall fly was present at the Ukiah site six years after the impact study was completed. Galls were found in 65% of the Ukiah

<table>
<thead>
<tr>
<th>Location</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ukiah</td>
<td>−0.0236</td>
<td>0.0548</td>
<td>0.1552</td>
<td>0.51</td>
</tr>
<tr>
<td>Winters</td>
<td>−0.0421</td>
<td>0.1068</td>
<td>0.3505</td>
<td>0.59</td>
</tr>
</tbody>
</table>

See text for function equation.
Fig. 5. Yellow starthistle seedhead production and gall development at Ukiah 1993 (A), Ukiah 1994 (B), Winters 1995 (C), and Winters 1996 (D). The total number of seedheads and galled seedheads developing on all transect plants were divided by the number of days since the last sampling interval to calculate the number of new seedheads (closed squares) and galled seedheads (open circles) produced on the sampled plants per day during the sampling interval.

Fig. 6. Seasonal distribution of yellow starthistle galls at two sites in California. A total of 160 plants were bagged each week in 1993–1995 and 200 in 1996. The final weeks of bagging at Winters included three or fewer seedheads so the percent attack is not shown.

Fig. 7. Developmental stage of Urophora sirunaseva in flowerheads of yellow starthistle at two sites in California. Galls either had overwintering larva at time of bagging or were empty (adults emerged). Heads with dead larva were excluded.
plants collected in 2000, but in only 21% of the seedheads. This was less than half of the attack rate observed in 1994. The false peacock fly, *Chaetorellia succinea*, a common insect of yellow starthistle accidentally introduced in the early 1990s (*Balcunas and Villegas, 1999*) had invaded the site and occurred in 55% of the heads. No other biological control agents (including *B. orientalis*) were recovered.

4. Discussion

During host testing, *Turner (1994)* felt that, in the absence of its own natural enemies, *U. sirunaseva* would become a better biological control agent of yellow starthistle once insect populations increased to their full potential. The gall fly has proven to be fairly easy to establish and to distribute throughout California. A massive distribution program (*Villegas, 1996*) introduced the gall fly throughout the state and it established well in most locations (*Pitcairn et al., 2008*). The Ukiah site was established in 1990 and by 1992, 44% of seedheads were infested (*Turner et al., 1994*). Our results show that the gall fly population rose to 46% in 1993 and to 56% in 1994 but declined by October 2000 (10 years after the first release) when galls were found in only 21% of the seedheads.

We cannot explain why *U. sirunaseva* has not increased to levels which would control the weed, but competition with other introduced biological control agents is possible. The successful establishment of at least three other insect species at most sites in California creates competition for a limited resource (*Pitcairn et al., 2003, 2008*). The recent immigration of *C. succinea* is particularly important. In 2000, over 50% of the seedheads at the Ukiah site were infested with *C. succinea*, replacing *U. sirunaseva* as the most common biological control insect at the site. In a 1985 field study, *Clement and Sobhian (1991)* found that *U. sirunaseva* attacked only 2.6% of the capitula in a garden plot in Greece. With ten species of insects attacking yellow starthistle in that study, *U. sirunaseva* faced substantial competition. Apparently, as more insects fill this niche in California, we might expect *U. sirunaseva* to decline to a minor role. The gall fly does not appear to have progressed distinctly better at other sites in California. A state-wide survey in 2001/2002 found *U. sirunaseva* galls at 61% of the 421 sites surveyed and only eight sites had greater than 25% of the seedheads with galls (*Pitcairn et al., 2003, 2008*).

In our study, the maximum galls per seedhead (15) was higher than previously reported (nine in Greece and 12 in California) (*Turner et al., 1994*). There was also a substantial increase in gall density: 1.9 galls per galled seedhead in 1992 (*Turner, 1994*) which increased to 3.1 and 4.6 in 1993 and 1994, respectively. Overall, 68% of the galled seedheads at the Ukiah site evaluated in our study had more than one gall. This is a substantial increase over the 56% found by *Turner (1994)* for his best site in 1992. Gall densities have not maintained statewide as we have only detected in-head gall densities of greater than eight on one other occasion out of 46,555 seedheads dissected statewide through 2004 (personal observations).

Even if the gall fly had maintained populations at the higher Ukiah levels, *U. sirunaseva* does not appear to have the potential to have a major impact on seed production by yellow starthistle in California as individual galls have a limited impact. Quantifying the impact of galls in yellow starthistle provided some challenges due to the increased seed production in larger seedheads. By comparing gall effects within seedhead size classes, we estimated the impact of a single gall as 2.1–2.9 seeds per gall. The impact may be somewhat larger (4.0–5.4 seeds per gall) when comparisons are made of the effect that single galls can have on maximally producing heads. Still, much higher population densities of *U. sirunaseva* are needed to significantly impact total seed production at the population level.

Reduction of seed by *U. sirunaseva* is fairly similar to other *Urophora* species in other systems. *Harris (1980)* found that each *U. affinis* reduced production by 2.4 seeds per seedhead in spotted knapweed and each *U. quadrifasciata* reduced production by 1.9 seeds per seedhead. *Mays and Kok (1986)* calculated similar values and noted that substantial reduction in seed production did not occur until there were at least four galls in a spotted knapweed seedhead.

Yellow starthistle also seems to have a threshold necessary for impact, however, the substantially larger seedhead size and per-head seed production of yellow starthistle diminished the relative impact of single galls even further. Smaller seedheads were more affected by the presence of 1–3 galls than were the larger seedheads in terms of seed production. For seedheads larger than 7 mm, a single gall or two appeared to have little impact on total seed production. Yet a single gall in a size 5 mm seedhead reduced seed production by over 25%. However, for all head sizes when gall density reached four or more per seedhead, seed production was dramatically impacted. This was particularly acute at Winters where no seedhead with more than six galls had over three seeds (15% of normal for unattacked heads). Seedheads size 6 mm and smaller seldom supported more than six galls. Larger seedheads can handle increasingly more galls without an apparent loss of seed numbers, perhaps due to a greater capacity to accept physical distortion of the receptacle. Unfortunately, highly concentrated galls were not common and seedheads with more than four galls occurred less than a fourth of the time for any given year.

The larger seedheads of yellow starthistle will require extremely high-levels of attack by *U. sirunaseva* to cause significant reduction in seed production on the population level. With an average reduction of 2.1 seeds per gall, an average of 14 galls per head would be necessary to achieve a 90% seed reduction at Ukiah and 11 galls per head at Winters. In contrast, our field sample average of 1.9 and 0.5 galls per head and would account for only 7.6% and 2.6% reduction of the seed produced at the Ukiah and Winters sites, respectively.

The phenology of the yellow starthistle flowering season was not always synchronized with activity by *U. sirunaseva* as in the knapweed system in the northern parts of the continent. Spotted knapweed in much of North America has a reasonably short flowering period and activity by *U. affinis* is well timed to exploit this. In the drier portions of the Central Valley of California, yellow starthistle behaves much as it does at Winters, with a short flowering season but also limiting *U. sirunaseva* to a single generation per year. How-
ever the deeper soils infested by yellow starthistle through other parts of the state provide adequate moisture for an extended season that supports new bud formation over several months as it did at Ukiah. In spite of the gall fly remaining active over the entire summer flowering period in our study, attack levels did vary over the season, dropping between generations.

_Urophora sirunaseva_ has a distinctly different mode of impact (seed displacement) than the other yellow starthistle seedhead biological control agents which feed directly on developing seeds. Shorthouse (1989), in his study of the hard galled biological control agents which feed directly on developing seeds. (seed displacement) than the other yellow starthistle seedhead attack levels did vary over the season, dropping between generations.

References


