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Density and Survival of Introduced Populations of *Urophora stylata* (Diptera: Tephritidae) in *Cirsium vulgare* (Compositae) in Canada, Compared with Native Populations

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Abstract

Flower heads of the introduced thistle *Cirsium vulgare* were studied in British Columbia, where the gall fly *Urophora stylata* has been introduced as a biological control agent. Overall levels of infestation in Canada were high. Mortality of *U. stylata* was due mainly to larvae shrivelling, rather than to parasitism and predation as in Europe. In spite of this difference, incidence of mortality in relation to flower head size and area of gall-tissue per larva was similar: larvae are safest in large heads and when surrounded by ample gall-tissue, these two factors being largely independent and additive in effect. In Europe, mortality caused by ectoparasitoids seemed influenced more by head size than packing density. Caterpillars, though eating more crowded larvae, when common showed a preference for large heads. In both native and introduced populations, deaths due to shrivelling were greater in small heads with crowded larvae. Flower heads at the tips of shoots are destined to be the largest and produce the largest number of seeds. Biological control will be most effective when these apical heads are heavily infested, both because the proportion of seeds destroyed will be high and because larval mortality will be low. In our Canadian samples, from one year only, a high proportion of apical heads escaped infestation. If common, such failure of synchrony would limit the effectiveness of the fly as a biological control agent.

Introduction

The spear or bull thistle, *Cirsium vulgare* (Savi) Tenore (Compositae) is a weed of pastures, both in its native range in Europe and western Asia, and in areas where it has been introduced accidentally, especially northern North America (Moore and Frankton 1974, Harris and Wilkinson 1984). Within its natural range, the flower heads of *C. vulgare* may be infested by larvae of the gall fly *Urophora stylata* (F.) (Diptera: Tephritidae) which, in a single head, form individual galls which coalesce, resulting in hard, multilocular growths (Redfern 1968, 1983). The resulting multiple gall may contain between 1 and 40 or more gall-cells. Infestation has a considerable impact on seed production (Zwölfer 1972, Michaelis 1984) and for this reason *U. stylata* was released at a number of sites in Canada as a biological control agent for *C. vulgare* (Harris and Wilkinson 1984). Within its natural range, levels of infestation of *C. vulgare* by *U. stylata* vary considerably, but only rarely do they approach levels found in some of the introduced populations in Canada (Zwölfer 1972, Harris and Wilkinson 1984, Redfern and Cameron 1985).

The principle causes of mortality in native *U. stylata* populations are insect parasitism, consumption by browsing lepidopteran caterpillars or carnivorous Diptera and shrivelling or disappearance in early larval life (Redfern 1968, 1983, Zwölfer 1972, Michaelis 1985, Redfern and Cameron 1985). Other causes of mortality are generally trivial in effect.

Overall mortality rates and the contributions of different causes vary considerably, both between populations and between generations in the same population (Redfern and Cameron 1985, Redfern, unpubl. data). There are no clear connections between mortality and population density (Michaelis 1985), although there is some indication of delayed density-dependence shown by the parasitoids (Michaelis 1984). Within populations, risk of mortality varies with circumstances. Larvae in large flower heads are safer than those in small heads (Redfern and Cameron 1985) and mortality, due to both parasitoids and predators, is lowest in galls in which each larva has a large amount of gall-tissue around it (Michalis 1985). In

some populations at least, *U. stylata* larvae tend to be concentrated in the safest locations (Redfern and Cameron 1985), but interpretation of this is complicated. The ultimate size of flower heads is partly determined by position on the plant but, in addition, infestation leads to sequestration of resources, increasing the size and weight of infested heads possibly at the expense of uninfested ones (Zwölfer 1985). Further, although the size of the gall is clearly limited by the size of the head in which it develops, it may be considerably smaller and its occupants more crowded than in galls in smaller heads.

In any particular thistle population, the size and number of heads infested and the density of gall-cells in each head depend not only on the density of *U. stylata* and on the effects of their larvae on the growth of the heads, but also on the synchronization of oviposition by *U. stylata* with the development of the plant (Michaelis 1985, Zwölfer, pers. comm.).

We compare the density and mortality in some introduced populations of *U. stylata* in Canada with populations within the natural range. Introduced populations achieve high densities (Harris and Wilkinson 1984) but mortality, its causes and its distribution between larvae in different situations has not been recorded. The insect parasites present in Europe are absent in Canada, as are the lepidopteran caterpillars and predatory maggots of *Palloptera* spp. (Diptera: Pallopteridae).

Materials and Methods

Samples of *C. vulgare* flower heads were taken from three infested populations south of Vancouver, British Columbia, in 1984 (Table 1). From small plants, all heads were removed. Where plants were large, all heads were removed from between 9 and 16 branches on each plant. Each head diameter was measured (maximum distance between outer bracts) and, for infested heads, the diameter of the gall, the number of cells in it and the fate of the contained larvae were recorded. Gall-cells are generally arranged in one plane and so the area of gall-tissue per larva was estimated by dividing the cross-sectional area of the gall by the number of cells contained (Michaelis 1985).

For comparison, we have data from three populations within the natural range, for which more details are given in Redfern and Cameron (1985). Two come from West Germany (sampled in 1982) and one from England (sampled in 1986); one, from Oberwaiz near Bayreuth, West Germany, was selected because the density of *U. stylata* approaches that found in the introduced populations. Other more general comparisons are considered in the discussion.

Results and Discussion

The number and sizes of plants sampled varied between sites but, as in European populations, no evident correlations between size of plant and infestation by or mortality in *U. stylata* were found. All plants sampled at each site have been combined. Levels of infestation may be found in Table 1 and details of mortality and its causes, arranged by size of head and by degree of crowding (gall-tissue per larva), are given in Appendix 1. Due to the scarcity of *C. vulgare*, particularly at Ladner, some samples of *U. stylata* are relatively small so that some classes of head size or level of crowding are represented by few gall-cells. These are noted in the figures.

Overall levels of infestation in the introduced populations were high (Table 1), although the occurrence of high populations of uninfested large heads at Cloverdale 168 compared with some European examples at high density suggests a failure in synchronization of oviposition with growth of buds (see below).

As expected, no mortality from insect parasites was recorded for the Canadian populations (Appendix 1), the overwhelming cause of death being shrivelling or cells empty for reasons unknown. The contrast with European populations is marked. In spite of this contrast, the incidence of mortality in relation to flower head size and gall-tissue per larva is similar (Fig.

Table 1. Degree of infestation by *Urophora stylata* in heads of different sizes at three sites in British Columbia.

Head dia (mm)	Parameter	Cloverdale 168 168St./96 Ave.	Cloverdale 184 184 St./88 Ave.	Ladner Husband Farm Tamboline Rd. Westham I.
< 16	No. heads	149	13	56
	% infested	54.4	30.8	9.8
16 - 19	No. heads	78	13	38
	% infested	89.7	92.3	10.5
20 - 23	No. heads	150	16	34
	% infested	65.3	100.0	58.8
> 23	No. heads	38	22	25
	% infested	63.2	95.4	88.0
	Total no. of heads	415	64	153

1). Both in Europe and Canada, larvae are safest in large heads and when surrounded by ample gall-tissue, and these two factors are partially independent and additive in effect. Although infestation rates in Canada vary, survival in large heads, with much gall-tissue per larva, is better in the Canadian populations, especially when contrasted with the population at Oberwaiz where comparable density was achieved.

Analysis of particular causes of death (Fig. 2) shows that, in Europe, patterns are not always consistent with those found overall. Where caterpillar damage is high (Oberwaiz), crowded larvae are more at risk than those with more gall-tissue, but those in large heads suffer more than those in small heads. Where such damage is less, no clear pattern is found. Deaths caused by the endoparasitoid *Eurytoma tibialis* Boheman (Hymenoptera: Eurytomidae) are similarly without consistent pattern, but those caused by ectoparasitoids are more frequent in small heads than in large, with crowding appearing to be irrelevant. The pattern of death by shrivelling, however, does match that for overall mortality and also resembles that seen in the Canadian populations (exceptions being due to small sample sizes at Ladner). Where there is more than 15 mm^2 of gall-tissue per larva, differences in mortality between sites and areas are slight and inconsistent. However, amongst the most crowded larvae, death by shrivelling is significantly more frequent at both Cloverdale sites than at any European site in both large and small heads ($P < 0.05$ in 10 out of 12 comparisons, X^2 tests, the two failing to reach significance involving the sample of only 7 larvae in heads 20+ mm^2 at Rupertskapelle). Within the crowded category (< 15 mm^2/ larva), the mean amounts of gall tissue per larva are less at Cloverdale than in the European sites. Thus, heavier mortality may merely reflect a greater degree of crowding. Overall mortality due to shrivelling is far greater in the Canadian populations than in those from Europe because a much higher proportion of larvae have less than 15 mm^2 of gall tissue (see Appendix 1).

The causes of shrivelling are not known, but the strong association with small heads and larval crowding in both native and introduced populations suggests that, at least in part, it is due to insufficient resources for the larvae involved.

Assessment of the reasons why other causes of mortality are non-randomly distributed within populations are complicated by different methods of data analysis used in various studies of native populations. Redfern and Cameron's (1985) analysis did not consider larval crowding in terms of gall-tissue rather than head size, and Michaelis (1984, 1985) did not include head size in his analysis. The evidence presented here suggests that both head size and crowding

can influence mortality, but to different degrees in different populations. Caterpillar-caused mortality, at least where it is high (at Oberwaiz), is greater for crowded than uncrowded larvae and is greater in large heads than in small ones, which may reflect a preference by the caterpillars for large heads (Michaelis 1985, Redfern and Cameron 1985). In Michaelis' (1985) study, both the endoparasitic *E. tibialis* and the commonest ectoparasitoid, *Eurytoma robusta* Mayr, caused heaviest mortality amongst crowded larvae, but in this study only the ectoparasitoids show such a trend and flower head size appears to be of more importance. Both the size of head and amount of gall-tissue around the *U. stylata* larva may affect ease of oviposition by parasitoids, on which more information is needed.

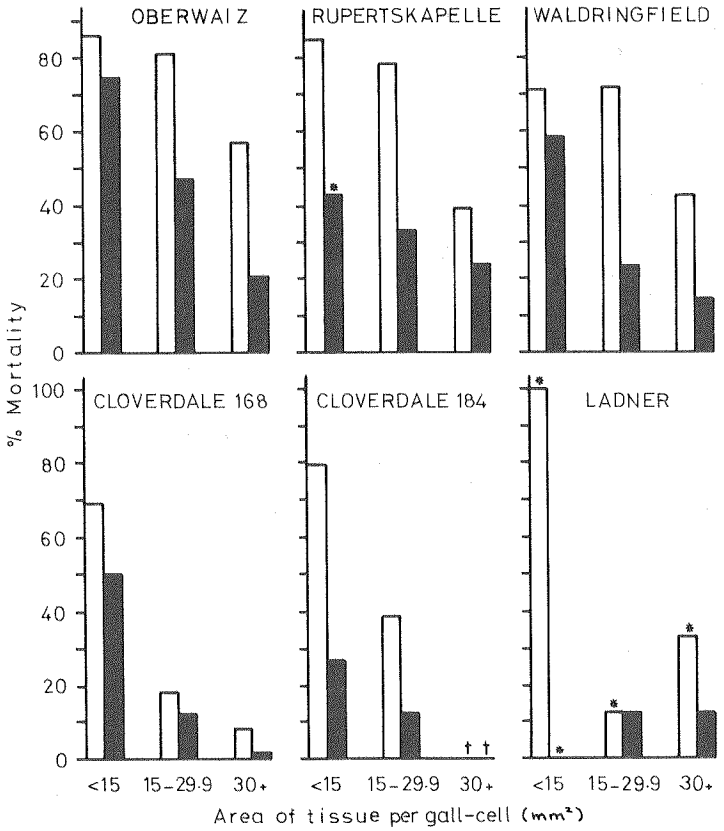

Figure 1. Total mortality (%) of *Urophora stylata* (Savi) Tenore larvae in relation to area of gall-tissue per cell in small heads (open bars; dia < 20 mm) and large heads (closed bars; dia 20 + mm); * = sample of < 10 gall-cells, † = no sample (see Appendix 1).

Flower head size clearly influences survival of *U. stylata* in both native and introduced populations. It does so both directly and in relation to the maximum size of gall contained. Also, however, head size is profoundly influenced by the presence of *U. stylata*. Zwölfer (1985, and pers. comm.) has shown that while position on the plant and, in particular, distance from the apex of the stem, affects head size, the effect of infestation is greater and increases as the number of larvae in the gall increases. The activities of the larvae create a nutrient sink and the diversion of resources may not only increase the size of galled heads, but reduce both the size and number of those uninfested. As in other metabolic sinks (Harris pers. comm.), resources are taken first from new small buds rather than existing apical heads. In heavily-infested plants, this could account for the greater mortality due to shrivelling of *U. stylata* in small heads (usually lower down the stem) independent of larval crowding in relation to gall-tissue.

In the absence of predators and parasitoids, the success of *U. stylata* larvae, both in avoiding mortality and in achieving high levels of infestation and consequent seed destruction in *C. vulgare*, depends very much on synchronization. If the earliest developing (usually apical) flower heads are heavily infested, not only is mortality least but destruction of seeds is greatest, both directly by larval activity inside heads which would otherwise be the most productive, and indirectly by the sequestration of resources which would otherwise go to other heads. In our Canadian samples of 1984, there is evidence of a failure to infest all of the early developing heads, despite high overall levels of infestation. However, data from Cloverdale in 1977 (Harris pers. comm.) show no such effect; the largest heads were nearly all infested and, presumably, seed destruction was high. Further studies are needed both in Canada and in native populations to discover whether lack of synchrony is common and whether this limits the effectiveness of *U. stylata* as a seed-destroyer.

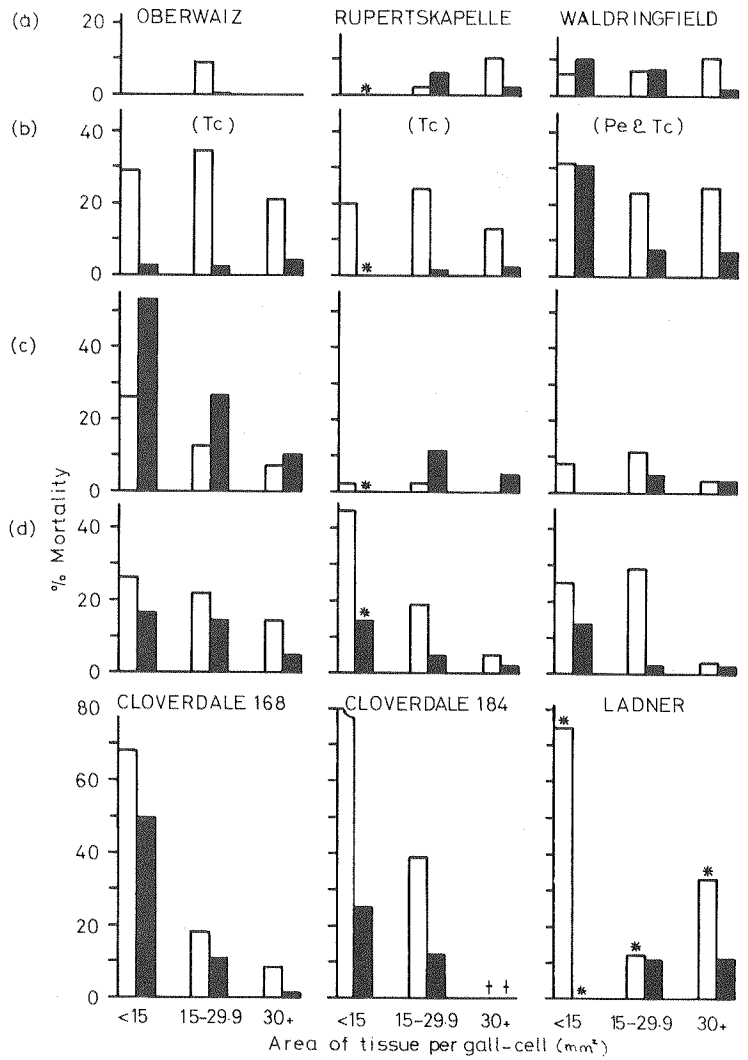

Figure 2. Mortality (%) of *Urophora stylata* (Savi) Tenore larvae caused by: (a) *Eurytoma tibialis* Boheman; (b) ectoparasitoids (the commonest species noted: Tc = *Torymus chloromerus* [Walker], Pe = *Pteromalus elevatus* [Walker]); (c) caterpillars; and (d) shrivelling. Relationship to area of gall-tissue per cell in small heads (open bars; dia < 20 mm) and large heads (closed bars; dia > 20 mm) is included; * = sample of < 10 gall-cells, † = no sample (see Appendix).

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Appendix 1. Causes of death (% of gall-cells) of *Urophora stylata* (F.) larvae in Europe and Canada in relation to area of gall-tissue per cell in small and large heads of *Cirsium vulgare* (Savi) Tenore. Sample size (no. of gall-cells) is included; * = includes empty cells.

Site	Mortality factor (%)	Head dia < 20 mm Gall area per larval cell (mm)			Head dia 20 + mm Gall area per larval cell (mm)		
		< 15	15 - 29	30 +	< 15	15 - 29	30 +
Oberwaiz	Total dead	86.8	81.2	57.1	74.8	47.1	21.0
	Endoparasitoid	0.0	9.4	0.0	0.0	0.4	0.0
	Ectoparasitoids	28.9	34.4	21.4	2.8	2.4	3.9
	Caterpillars	31.6	12.5	7.1	53.2	26.2	10.2
	Larvae shrivelled *	26.3	21.9	14.3	16.4	14.6	4.9
	Other deaths	0.0	3.1	14.3	2.4	3.5	1.9
	No. gall-cells opened	38	32	14	250	507	205
Rupertskapelle	Total dead	85.0	78.4	39.5	42.9	33.3	23.8
	Endoparasitoid	0.0	2.7	10.5	0.0	6.4	2.9
	Ectoparasitoids	20.0	24.3	13.2	0.0	1.5	2.5
	Caterpillars	2.5	2.7	0.0	0.0	11.3	5.0
	Larvae shrivelled *	45.0	18.9	5.3	14.3	4.9	1.9
	Other deaths	17.5	29.7	10.5	28.6	9.3	11.6
	No. gall-cells opened	40	37	38	7	204	524
Waldringfield	Total dead	71.4	72.1	42.9	58.6	23.3	14.8
	Endoparasitoid	6.3	7.3	10.7	10.3	7.7	2.1
	Ectoparasitoids	31.7	33.5	25.0	31.0	7.4	7.0
	Caterpillars	7.9	11.8	3.6	0.0	5.0	3.7
	Larvae shrivelled *	25.4	29.4	3.6	13.8	2.6	2.1
	Other deaths	0.0	0.0	0.0	3.4	0.8	0.0
	No. gall-cells opened	63	68	28	29	339	243

Appendix 1. Continued.

Site	Mortality factor (%)	Head dia < 20 mm Gall area per larval cell (mm)			Head dia 20 + mm Gall area per larval cell (mm)		
		< 15	15 - 29	30 +	< 15	15 - 29	30 +
Cloverdale 168	Total dead	69.2	18.5	8.3	50.0	12.5	1.8
	Larvae shrivelled *	68.5	18.5	8.3	49.7	10.9	1.8
	Other deaths	0.7	0.0	0.0	0.3	1.7	0.0
	No. gall-cells opened	601	168	48	334	359	274
Cloverdale 184	Total dead	79.8	38.9	-	27.0	12.4	-
	Larvae shrivelled *	79.8	38.9	-	25.4	12.4	-
	Other deaths	0.0	0.0	-	1.6	0.0	-
	No. gall-cells opened	124	18	0	441	185	0
Ladner	Total dead	100.0	12.5	33.3	0.0	12.6	12.8
	Larvae shrivelled *	75.0	12.5	33.3	0.0	11.0	11.8
	Other deaths	25.0	0.0	0.0	0.0	1.6	1.0
	No. gall-cells opened	4	8	3	8	127	102