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Establishment and Dispersal of *Urophora affinis* (Diptera: Tephritidae) and *Metzneria paucipunctella* (Lepidoptera: Gelechiidae) in Southwestern Virginia

W. T. MAYS AND L. T. KOK

Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

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Two European gall-producing insects, *Urophora affinis* Frfld. (Diptera: Tephritidae) and *Metzneria paucipunctella* (Zeller) (Lepidoptera: Gelechiidae) were introduced into Virginia in 1986 for biological control of spotted knapweed (*Centaurea maculosa* Lam.). Adults of *U. affinis* (*n* = 2625) and *M. paucipunctella* (*n* = 450) were released at two sites in Montgomery County, Virginia, and their populations were monitored yearly by dissecting spotted knapweed flower heads. Beginning in 1992, knapweed samples collected at various distances from the release sites were checked for dispersal. *U. affinis* is well established and is spreading slowly. The number of larvae per flower head and the seed numbers are inversely related as plants with the greatest number of larvae per spotted knapweed head had the lowest number of seeds. Knapweed density has declined at one of the release sites which had the highest rate of infestation by *U. affinis*. Establishment of the moth, *M. paucipunctella*, is less certain as it has been recovered at a very low level from only one site.

KEY WORDS: *Urophora affinis; Metzneria paucipunctella; Centaurea maculosa;* spotted knapweed; classical biological control; insect dispersal; weed control.

INTRODUCTION

Spotted knapweed (*Centaurea maculosa*) is one of several *Centaurea* species of Eurasian origin (Moore, 1972) infesting rangelands and pastures in the United States and Canada. It was first reported in North America at Victoria, British Columbia, Canada, in 1893 (Groh, 1944). Due to allelopathic properties (Fletcher and Renney, 1963) and drought resistance (Watson and Renney, 1974), it has displaced more desirable herbaceous plants over large areas, especially in the drier rangelands of western Canada and the northwestern United States (Müller-Schärer and Schroeder, 1993). By 1988, spotted knapweed infested more than 2.8 million ha in nine western states and two western Canadian provinces (Lacey, 1989). Spotted knapweed is also widespread in the eastern United States (Reed and Hughes, 1970; Gleason and Cronquist, 1991) and is the most dominant of eight species of *Centaurea* in Virginia (Johnson, 1974; Harvill *et al.*, 1992). It is common along weedy roadsides, in abandoned fields, and in poorly managed pastures, especially in the western portion of the state.

Information on the biology and taxonomy of spotted knapweed has been well documented (Fernald, 1950; Radford *et al.*, 1968; Reed and Hughes, 1970; Watson and Renney, 1974). Reproduction is primarily by seeds (500 to 25,000 per plant) although vegetative reproduction also occurs from lateral shoots (Watson and Renney, 1974). In Virginia, flowering is from June through August or even November when conditions are right. Fruiting is from mid June to November. Spotted knapweed overwinters as rosettes or as seeds that may be dormant for a number of years (Davis and Fay, 1989).

Various methods have been used to control spotted knapweed (Watson and Renney, 1974; Müller-Schärer and Schroeder, 1993). Herbicides such as 2,4-D, dicamba, and picloram can successfully control spotted knapweed (Fay *et al.*, 1989) but cost, inaccessibility, and chemical persistance in soil make this method impractical (Harris and Cranston, 1979). Cultivation, mowing, and fire can also be effective but terrain and cost greatly limit these practices.

Biological control has received more attention in recent years (Schroeder, 1985; Müller and Schroeder, 1989). Zwölfer (1965) published a list of insects that attack spotted knapweed in central Europe. Biological control of the spotted knapweed in North America began with release of the seed-head gall fly, *Urophora affinis,* in British Columbia, Canada, in 1970 (Harris, 1980b) and subsequently in the United States in 1973 in Montana and Oregon (Story and Anderson, 1978; Maddox, 1982). A second seed-head gall fly, *Urophora quadrifasciata,* released in Canada in 1972 spread to the United States (Montana) on its own (Story, 1985). Both flies have become widely established in the Pacific

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Northwest and in western Canada. The release, establishment, distribution, and biology of these two insects on spotted and diffuse knapweed (*Centaurea diffusa*) in western North America are well documented (Story and Anderson, 1978; Berube, 1980; Harris, 1980a,b, 1989; Myers and Harris, 1980; Maddox, 1982; Story, 1985; Story *et al.*, 1987; McCaffrey *et al.*, 1988; Müller-Shärer and Schroeder, 1993).

A third seed-head feeding insect that attacks spotted knapweed is the moth *Metzneria paucipunctella*. First released in British Columbia, Canada, in 1973, it had spread to the Pacific northwestern United States by 1980. Its impact on spotted knapweed and on the two *Urophora* seed-head flies is reported in several studies (Englert, 1971; Harris and Myers, 1984; Harris, 1986; Story *et al.*, 1989; Müller-Schärer and Schroeder, 1993).

U. affinis and *M. paucipunctella* were introduced into Virginia in 1986. Their subsequent establishment and dispersal are monitored and reported here.

MATERIALS AND METHODS

Spotted knapweed flower heads infested with *U. affinis*, *U. quadrifasciata*, and *M. paucipunctella* from British Columbia, Canada, were received courtesy of Dr. Peter Harris, Agriculture Canada, in spring 1986. The heads were placed in 1-liter clear plastic cylindrical containers and held at room temperature (25 ± 2°C) for adult insects to emerge. Each container, with 100 heads, had several openings (3 × 3 cm) covered with 18 × 16 mesh aluminum screening. *U. affinis* and *M. paucipunctella* adults that emerged between May and July 1986 were released at two sites in Montgomery County, Virginia, but *U. quadrifasciata*, which was not approved for release in Virginia, was separated out. Releases at two sites (Rich Hill, $n = 525$ *U. affinis* and 50 *M. paucipunctella;* Hospital, $n = 2{,}100$ *U. affinis* and 400 *M. paucipunctella*) have been monitored yearly since 1987.

The Rich Hill site had a knapweed infestation (5 ± 0.4 plants/m^2) of approximately 1.0 ha intermixed with grasses and other weedy plants. The Hospital release site is a steep road bank of about 2.0 ha. At the time of insect release at this site, knapweed density exceeded 40 ± 4.6 plants/m^2 and was devoid of other vegetation. Density of the knapweed plants was measured from 11 permanent plots of 1 m^2.

Beginning in late February 1987, whole plants chosen at random were sampled once at each site, and all heads were removed from the plants and thoroughly mixed in plastic containers. In the lab, 500 heads from each site were placed in ventilated containers as described above. Each contained 100 heads and adult insect or parasite emergence was observed at room temperature. The number and sex of emerging insects were recorded. Sample size was increased to 1000 flower heads per site between 1988 and 1994.

Dispersal studies were initiated in 1992 by collecting samples from five sites that were 1.6 to 3.2 km radiating in different directions from the release sites, and from a sixth site, Vicker, which was midway (6.4 km) between the two release sites. From each of these sites, 1000 flower heads were collected in late February and observed for adult emergence in the laboratory. In 1993, four additional sites (3.2 to 6.4 km from the release sites) and in 1994, 13 new sites (6.4 to 12.8 km from the release sites) were sampled.

All new sites sampled are either highway or railroad embankments covering an area of about 0.5 to 1.0 ha each. At all of these sites, the knapweed population was at least 35 (±4.5) plants/m^2 and the sites were almost devoid of other vegetation.

To quantify larval infestation, spotted knapweed flower heads were collected on July 20, 1993 from 11 of the 12 sites that had been sampled for adults in February 1993. One hundred mature heads, which had completed flowering but had not shed their seeds, from each site were dissected to record the number of larvae and seeds per head and the diameter of each involucre. The 12th site (Airport) could not be sampled because the knapweed plants had been mowed. On July 29, 1994 spotted knapweed heads (100 per site) from all 25 sites sampled in February 1994 for adults were dissected to determine larval infestation, involucre diameter, and seed number.

RESULTS AND DISCUSSION

U. affinis was recovered at both release sites from 1987 through 1994 (Table 1). The mean number of adult *U. affinis* per head increased from 0.07 in 1987 to 1.45 in 1994 at the Hospital site. A slower rate of increase was seen at the Rich Hill site, where the mean number of adults was low through 1992. However, there was a 6-fold increase in 1993 followed by another 1.8-fold increase in 1994. The slower initial rate of increase is likely a reflection of the smaller number of insects released at this site and a lower host density.

Dispersal was evident as *U. affinis* was detected at three of six additional sites sampled in 1992. At two of these sites, Yellow Sulphur and VPI Airport, the mean number of adults per head (0.51 and 0.37, respectively) in 1993 was comparable to the 0.49 adults per head at the Rich Hill site. Insect numbers increased at all sites by 1994 except at the Airport site, which was mowed. The latter is the only case in all the years of sampling where *U. affinis* infestation declined, indicating that mowing or site disruption can adversely affect the population of *U. affinis*. At Merrimac, *U. affinis* which was found in low numbers in 1992 and 1993 increased dramatically in 1994. Of the four additional sites

TABLE 1

Mean ± SE of Adult *U. affinis* per Spotted Knapweed Head at Sites with Insect Recovery[a]

Site	1987	1988	1989	1990	1991	1992	1993	1994
Hospital[b]	0.07 ± .02	0.08 ± .01	0.18 ± .02	0.52 ± .05	0.74 ± .06	0.97 ± .04	1.2 ± .06	1.45 ± .09
Rich Hill[b]	0.004 ± .002	0.02 ± .002	0.04 ± .005	0.04 ± .01	0.06 ± .01	0.08 ± .01	0.49 ± .03	0.89 ± .05
Merrimac	—[c]	—	—	—	—	0.005 ± .002	0.007 ± .002	1.63 ± .09
Yellow Sulphur	—	—	—	—	—	0.15 ± .01	0.51 ± .02	0.54 ± .02
VPI Airport	—	—	—	—	—	0.30 ± .02	0.37 ± .03	0.12 ± .01
Vicker	—	—	—	—	—	0	0	0.02 ± .002
Plum Creek	—	—	—	—	—	0	0	0.01 ± .002
Ellett	—	—	—	—	—	—	0.22 ± .01	0.58 ± .03
NRV Mall	—	—	—	—	—	—	0.01 ± .002	0.17 ± .02
Whitethorne	—	—	—	—	—	—	0	0.08 ± .005
Round Meadows	—	—	—	—	—	—	0	0.02 ± .002
Riverview	—	—	—	—	—	—	—	0.58 ± .04
West Christiansburg	—	—	—	—	—	—	—	0.06 ± .01
Falls Ridge	—	—	—	—	—	—	—	0.01 ± .002
St. Michaels Church	—	—	—	—	—	—	—	0.01 ± .002

[a] All sites in Montgomery County, VA.; 10 other sites that showed no recovery of *U. affinis* are not included in this table; based on sample size of 500 heads/site in 1987 and 1000 heads/site from 1988–1994. SE, standard error of the mean.
[b] Release sites.
[c] — Not sampled.

sampled in 1993, *U. affinis* was recovered in low numbers at the NRV Mall and Ellett sites.

By 1994, *U. affinis* was recovered from 13 sites which had no insect releases, including 4 sites where it was not detected in 1993. As these are 1.6 to 9.6 km from the release sites, *U. affinis* has not only become well established on spotted knapweed in Montgomery County, Virginia, but it is dispersing steadily. Ten other sites sampled in 1994, ranging from 1.6 to 12.8 km away from the original release sites, showed no recovery of *U. affinis*.

The sex ratio (0.90) of *U. affinis* has been quite constant through the years, with slightly more males than females at all sites combined (Table 2). There was little difference in sex ratio between sites where the recovery was made.

M. paucipunctella does not appear to have become well established. Recovery was low and inconsistent at the Hospital release site. Two adults were recovered in 1989, five in 1990, three in 1991, none in 1992 or 1993, and four in 1994. It has not been recovered from the Rich Hill release site or at any of the additional sites sampled in the dispersal study. Failure to become well established could be due to the low numbers of adults released, low temperature mortality, or to interspecific competition with *U. affinis* for the same head.

TABLE 2

Sex Ratio of *U. affinis* (All Sites Combined)

Year	Female	Male	Female:Male
1987	16	19	0.84
1988	53	50	1.06
1989	98	119	0.82
1990	258	297	0.87
1991	393	408	0.96
1992	713	801	0.89
1993	1341	1446	0.93
1994	2891	3292	0.88
Total/mean	5763	6432	0.90

Mean ± SE of knapweed density at the Hospital site was 39.8 ± 4.3 plants/m^2 through 1991. By 1994, density had decreased slightly to 31.6 ± 5.4 plants/m^2. How much of this can be attributed directly to *U. affinis* is not known but several of the plots have been invaded by fescue and other grasses. Infestation by *U. affinis* could have decreased knapweed competitiveness and allowed invasion by other vegetation.

The highest number of *U. affinis* larvae per head in 1993 was 1.7 at the Hospital site (Table 3). Three sites had more than 1.0 larva per head, and four others had ≤0.5 larva per head. Four sites with no larvae also did not have adult emergence during the previous sampling in February (Table 1). At the Vicker site, no adults emerged from flower heads collected in February 1993 (Table 1), but larvae (0.03 per head) were found in heads collected in July 1993 (Table 3). This indicates that the site was newly infested by immigrating adults. Although this site is approximately midway between the two release sites, the insect is more likely to have spread from the Hospital site which had a higher infestation rate than that at the Rich Hill site. Adults were recovered for the first time from the Vicker site in February 1994 (0.02 per head). Larvae from heads collected in July 1994 (0.2 per head) confirms establishment and suggests an increasing population when

TABLE 3

Mean ± SE of *U. affinis* Larvae, Knapweed Seeds, and Involucre Diameter for 1993 and 1994[a]

Site	No. larvae/head		No. seeds/head		Involucre diameter (mm)	
	1993	1994	1993	1994	1993	1994
Hospital[b]	1.7 ± 0.1	1.8 ± 0.1	16.2 ± 0.5	15.7 ± 0.5	6.8 ± 0.04	6.8 ± 0.04
Rich Hill[b]	0.5 ± 0.06	0.9 ± 0.08	20.6 ± 0.7	19.6 ± 0.8	6.9 ± 0.05	6.9 ± 0.05
Merrimac	0.4 ± 0.05	1.7 ± 0.09	31.6 ± 0.7	24.5 ± 0.7	7.3 ± 0.05	7.3 ± 0.05
Yellow Sulphur	1.4 ± 0.1	1.7 ± 0.1	16.0 ± 0.6	14.8 ± 0.6	6.7 ± 0.04	6.7 ± 0.04
VPI Airport	—[c]	0.7 ± 0.09	—	19.0 ± 0.6	—	6.9 ± 0.04
Vicker	0.03 ± 0.02	0.2 ± 0.05	24.2 ± 0.7	24.0 ± 0.9	6.8 ± 0.04	6.8 ± 0.04
Plum Creek	0	0.2 ± 0.05	25.1 ± 0.7	23.3 ± 0.8	7.0 ± 0.05	7.0 ± 0.05
Walton	0	0	22.9 ± 0.6	24.3 ± 0.6	6.8 ± 0.04	6.9 ± 0.05
Ellett	1.2 ± 0.09	1.6 ± 0.1	21.3 ± 0.5	19.5 ± 0.7	7.0 ± 0.06	7.0 ± 0.06
NRV Mall	0.3 ± 0.05	0.9 ± 0.08	21.4 ± 0.7	20.0 ± 0.7	6.7 ± 0.04	6.7 ± 0.04
Whitethorne	0	0.3 ± 0.06	22.0 ± 0.5	21.8 ± 0.5	6.9 ± 0.05	6.9 ± 0.05
Round Meadows	0	0.1 ± 0.3	24.1 ± 0.7	24.0 ± 0.9	7.1 ± 0.05	7.1 ± 0.05
Riverview	—	1.4 ± 0.1	—	18.1 ± 0.6	—	7.0 ± 0.06
West Christiansburg	—	0.4 ± 0.06	—	23.3 ± 0.7	—	7.1 ± 0.05
Falls Ridge	—	0.2 ± 0.04	—	21.9 ± 0.6	—	6.9 ± 0.04
St. Michaels Church	—	0.2 ± 0.04	—	27.5 ± 0.6	—	7.4 ± 0.05
Price's Fork	—	0	—	28.1 ± 0.6	—	7.3 ± 0.05
Ironto	—	0	—	24.0 ± 0.7	—	6.9 ± 0.05
East Christiansburg	—	0	—	24.7 ± 0.7	—	6.8 ± 0.05
Bethyl Elem. School	—	0	—	23.8 ± 0.7	—	6.8 ± 0.05
Pepper's Ferry Br.	—	0	—	26.6 ± 0.6	—	7.0 ± 0.05
Luster's Gate	—	0	—	26.0 ± 0.7	—	7.0 ± 0.06
Childress	—	0	—	24.3 ± 0.7	—	6.9 ± 0.05
Ingles Ferry Br.	—	0	—	24.2 ± 0.7	—	7.0 ± 0.05
Montgomery Tunnels	—	0	—	23.4 ± 0.7	—	6.9 ± 0.05

[a] Sample size of 100 heads/site.
[b] Release site.
[c] — Not sampled.

compared with the lower corresponding data from 1993.

In 1994, 60% of the sites sampled ($n = 25$) had *U. affinis* larvae. Of these, one-third had more than 1 larva per head and two-thirds had <1 larva per head. Three of the sites with no larvae in 1993 had low numbers in 1994. One site (Riverview), which was not sampled earlier, had 1.4 larvae per head in 1994, indicating that the insect was present at this site for a number of years before sampling began.

The Hospital and Yellow Sulphur sites with the highest number of larvae per head (1.7 and 1.4, respectively) in 1993 also had the lowest number of seeds per head (16.2 and 16.0, respectively) (Table 3). In 1994, with more larvae per head at these two sites, the seeds continued to decrease. Although there were more than 1 larva per head at the Ellett site in 1993 and 1994, and at the Merrimac site in 1994, the number of seeds per head did not decline to the same level at these two sites. This could be due to the larger mean involucre diameter ($\geq 7.0 \pm 0.06$ mm) at these sites. Merrimac, which had the highest mean number of seeds per head (31.6 ± 0.7) and the largest mean involucre diameter (7.3 ± 0.05 mm) in 1993 was unchanged in involucre diameter in 1994, but seed number decreased to 24.5 per head. This was likely the result of more feeding as larval density increased from 0.4 in 1993 to 1.7 per head in 1994.

The impact of larval feeding is shown by the inverse relationship of larval density and seed number (Fig. 1). Multiple regression analysis ($y = 97.1 - 3.6x_1 - 10.5x_2$, $r^2 = 0.98$) of mean seeds per head against number of larvae per head and involucre diameter showed significant ($P < 0.05$) impact of larval density. There was a linear reduction of seed number as larval density increased (regression equation for seed number and larval density for all knapweed heads is $24.64 - 4.55x$, $r^2 = 0.97$). Heads with no larvae averaged 25 seeds but those with four larvae had only 5 seeds. Of 3600 heads dissected, 70.3% had no larva, 15.7% had one larva, 9.6% had two larvae, 3.9% had three larvae, and only 0.5% had four larvae. It was only at the sites where *U. affinis* had the highest infestation rates (Hospital, Yellow Sulphur, Ellett, and Merrimac) that four larvae per head were found. This indicates that substantial seed reduction is not likely until high insect population levels are reached.

The mean involucre diameter at all sites for both

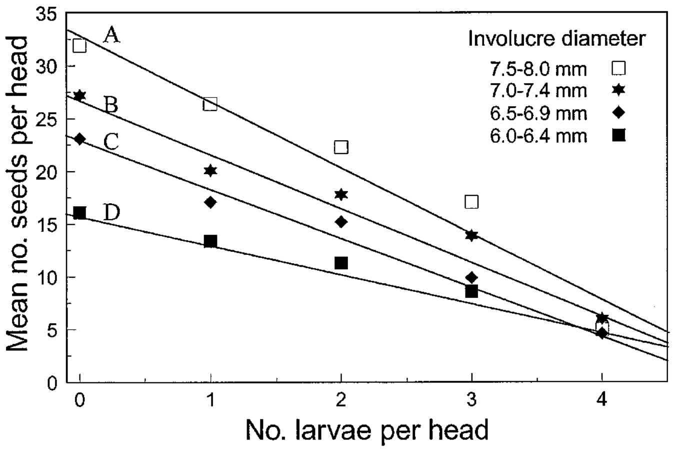

FIG. 1. Number of knapweed seeds per flower head in relation to larval density for all sites and years combined. Regression equation for all flower heads is $24.64 - 4.55x$ ($r^2 = 0.968$). When grouped by involucre size, regression equations for the four involucre diameter classes are: (A, 7.5–8.0 mm) $33.14 - 6.30x$ ($r^2 = 0.948$); (B, 7.0–7.4 mm) $26.71 - 4.85x$ ($r^2 = 0.964$); (C, 6.5–6.9 mm) $22.82 - 4.42x$ ($r^2 = 0.982$); and (D, 6.0–6.4 mm) $16.05 - 2.50x$ ($r^2 = 0.997$). The multiple regression equation of mean no. seeds/head against no. of larvae/head and involucre diameter is $97.1—3.6x_1 - 10.5x_2$ ($r^2 = 0.98$; r^2 is 0.97 for larvae/head and 0.81 for involucre diameter).

years was 7 ± 0.08 mm, which is the middle to low end of measurements for spotted knapweed heads (Moore and Frankton, 1974; Radford *et al.*, 1968). As diameter of the insect puparium was only 1.9 ± 0.3 mm ($n = 50$), the small knapweed heads in Montgomery County, Virginia, can support the development of at least several more larvae before space and nutritional supply become restrictive.

When comparing adult emergence data with larval data in dissected heads (Table 4), the ratio of larvae to adults per head ranged from 1 to 5.5 at four sites in 1993. However, high ratios were observed at two sites; at the Merrimac site the larva/adult ratio was about 57 and at NRV Mall site it was about 30. These high larva/adult ratios may indicate an increasing insect population or it may suggest high adult overwintering mortality due to adverse environmental factors such as moisture and cold temperatures at these sites. Subsequent sampling in 1994 confirmed that the insect population was increasing rapidly at the Merrimac site which showed a dramatic increase from 0.007 adults per head in 1993 to 1.6 per head in February 1994. By July 1994, the larva/adult ratio of 1.1 indicated that the population was probably leveling off and future increases will not be as dramatic. At the NRV Mall site, the increase in adult population in 1994 was moderate.

At the 15 sites where *U. affinis* was recovered in 1994, the larva/adult ratio per head ranged from 1 to about 5, and at 3 of the sites the ratio was 20. This indicates that the *U. affinis* population at most sites is stable or increasing slightly, with moderate increases at a few sites.

No parasites were recovered. This suggests that parasitism is not a limiting factor. How much of the *U. affinis* population is affected by predation is not known as this was not part of the study. Since the insect overwinters in exposed knapweed heads, abiotic factors

TABLE 4

Mean ± SE and Ratio of Larvae vs. Adults of *U. affinis* for 1993 and 1994[a]

Site	Feb. '93 A/head	July '93 L/head	'93 Ratio L/A	Feb. '94 A/head	July '94 L/head	'94 Ratio L/A
Hospital[b]	1.19 ± 0.06	1.7 ± 0.1	1.4	1.45 ± 0.09	1.8 ± 0.1	1.2
Rich Hill[b]	0.49 ± 0.03	0.5 ± 0.06	1.0	0.89 ± 0.05	0.9 ± 0.08	1.0
Merrimac	0.007 ± 0.002	0.4 ± 0.05	57.1	1.63 ± 0.09	1.7 ± 0.09	1.1
Yellow Sulphur	0.51 ± 0.02	1.4 ± 0.1	2.8	0.54 ± 0.02	1.7 ± 0.17	3.1
VPI Airport	0.37 ± 0.03	—[c]	NA	0.12 ± 0.01	0.7 ± 0.09	5.8
Vicker	0	0.03 ± 0.02	NA	0.02 ± 0.002	0.2 ± 0.05	10.0
Ellett	0.22 ± 0.01	1.2 ± 0.09	5.5	0.58 ± 0.03	1.6 ± 0.1	2.8
NRV Mall	0.01 ± 0.002	0.3 ± 0.05	30.0	0.17 ± 0.02	0.9 ± 0.08	5.3
Whitethorne	0	0	0	0.08 ± 0.005	0.3 ± 0.06	3.8
Plum Creek	0	0	0	0.01 ± 0.002	0.2 ± 0.05	20.0
Round Meadows	0	0	0	0.02 ± 0.002	0.1 ± 0.03	5.0
Riverview	—[d]	—	—	0.58 ± 0.04	1.4 ± 0.1	2.4
West C'burg	—	—	—	0.06 ± 0.01	0.4 ± 0.06	6.7
Falls Ridge	—	—	—	0.01 ± 0.002	0.2 ± 0.04	20.0
St. Michaels Church	—	—	—	0.01 ± 0.002	0.2 ± 0.04	20.0

Note. A, adult; L, larva.
[a] Sample size of 100 heads/site.
[b] Release site; 10 other sites sampled showed no recovery of *U. affinis*.
[c] Data not available due to site disruption.
[d] — Not sampled.

such as severe winter weather could be a major cause of mortality.

Although *U. quadrifasciata* has been reported as established and is spreading rapidly in Pennsylvania and New York (Hoebeke, 1993), none was recovered in our study. However, since its dispersal rate is much greater than that of *U. affinis* (Harris and Myers, 1984), as it moves south, it will probably be in southwest Virginia before long.

We have determined that *U. affinis* and possibly *M. paucipunctella* are established in Montgomery County, Virginia. Their impact on spotted knapweed populations will probably be similar to that observed in Canada or the northwestern United States (Harris and Cranston, 1979; Story *et al.*, 1989). Over the long term, biological control combined with other stress factors could help to reduce knapweed plant densities. One possible approach may be the use of plant competition in conjunction with the insects to reduce knapweed populations. Tall fescue (*Festica arundinacea* Schreb.) in combination with insect biological control agents has been shown to be successful in controlling musk thistle (*Carduus nutans* L. = *thoermeri* Weinmann) (Kok *et al.*, 1986) and Canada thistle (*Cirsium arvense* Scop.) (Ang *et al.*, 1994). This approach could produce results in a much shorter time in the eastern United States, where spotted knapweed stands are less extensive than those in the west.

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REFERENCES

Ang, B. N., Kok, L. T., Holtzman, G. I., and Wolf, D. D. 1994. Competitive growth of Canada thistle, tall fescue, and crownvetch in the presence of a thistle defoliator, *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae). *Biol. Control.* **4,** 277–284.

Berube, D. E. 1980. Interspecific competition between *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae) for oviposition sites on diffuse knapweed (*Centaurea diffusa:* Compositae). *Z. Angew. Entomol.* **90,** 299–306.

Davis, E. S., and Fay, P. K. 1989. The longevity of spotted knapweed seed in Montana. *In* "Proceedings of the 1989 Knapweed Symposium" (P. K. Fay and J. R. Lacey, Eds.), pp. 67–72. Montana State Univ., Bozeman, MT.

Englert, W. 1971. "*Metzneria paucipunctella* Zel. (Gelechiidae, Lepidoptera): A Potential Insect for the Biological Control of *Centaurea stoebe* L. in Canada." CIBC Prog. Rep. No. 28.

Fay, P. K., Davis, E. S., Chicoine, T. B., and Lacey, C. A. 1989. The status of long term chemical control of spotted knapweed. *In* "Proceedings of the 1989 Knapweed Symposium" (P. K. Fay and J. R. Lacey, Eds.), pp. 43–46. Montana State Univ., Bozeman, MT.

Fernald, M. L. 1950. "Gray's Manual of Botany," 8th ed. Am. Book Co., New York.

Fletcher, R. A., and Renney, A. J. 1963. A growth inhibitor found in *Centaurea* spp. *Can. J. Plant Sci.* **43,** 475–481.

Gleason, H. A., and Cronquist, A. 1991. "Manual of Vascular Plants of Northeastern United States and Adjacent Canada," 2nd ed. N. Y. Botanical Garden, Bronx, New York.

Groh, H. 1944. "Canadian Weed Survey," 2nd Annu. Rep. Can. Dept. Agric.

Harris, P. 1980a. Effects of *Urophora affinis* Frlfd. and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) on *Centaurea diffusa* Lam. and *C. maculosa* Lam. (Compositae). *Z. Angew. Entomol.* **90,** 190–201.

Harris, P. 1980b. Establishment of *Urophora affinis* Frlfd. and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) in Canada for the biological control of diffuse and spotted knapweed. *Z. Angew. Entomol.* **89,** 504–514.

Harris, P. 1986. "Biological Control of Spotted Knapweed by *Metzneria paucipunctella* (Zeller). Canadex 641:613. Agric. Canada.

Harris, P. 1989. Feeding strategy, coexistence and impact of insects in spotted knapweed capitula. *In* "Proc. 7th Int. Symp. Biol. Control Weeds, 6–11 March 1988, Rome, Italy" (E. S. Delfosse, Ed.), pp. 39–47. 1st Sper. Patol. Veg. (MAF).

Harris, P., and Cranston, R. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in western Canada. *Can. J. Plant Sci.* **59,** 375–382.

Harris, P., and Myers, J. H. 1984. *Centaurea diffusa* Lam. and *C. maculosa* Lam., diffuse and spotted knapweed (Compositae). *In* "Biological Control Programmes Against Insects and Weeds in Canada 1969–1980" (J. S. Kelleher and M. A. Hulme Eds.), pp. 127–137. CAB, Slough, England.

Harvill, A. M., Jr., Bradley, T. R., Stevens, C. E., Wieboldt, T. F., Ware, D. M. E., Ogle, D. W., Ramsey, G. W., and Fleming, G. P. 1992. "Atlas of the Virginia Flora," Va. Botanical Associates, Farmville, VA.

Hoebeke, E. R. 1993. Establishment of *Urophora quadrifasciata* (Diptera: Tephritidae) and *Chrysolina quadrigemina*) (Coleoptera: Chrysomelidae) in portions of the Eastern United States. *Entomol. News* **104,** 143–152.

Johnson, M. F. 1974. Cynareae (Asteraceae) in Virginia: *Arctium, Centaurea, Cnicus. Castanea* **39,** 63–73.

Kok, L. T., McAvoy, T. J., and Mays, W. T. 1986. Impact of tall fescue grass and *Carduus* thistle weevils on the growth and development of musk thistle (*Carduus nutans*). *Weed Sci.* **34,** 966–971.

Lacey, C. 1989. Knapweed management: a decade of change. *In* "Proceedings of the 1989 Knapweed Symposium" (P. K. Fay and J. R. Lacey, Eds.), pp. 1–6. Montana State Univ., Bozeman, MT.

Maddox, D. M. 1982. Biological control of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*C. maculosa*). *Weed Sci.* **30,** 76–82.

McCaffrey, J. P., Wight, R. P., Stoltz, R. L., Callihan, R. H., and Kidder, D. W. 1988. "Collection and Redistribution of Biological Control Agents of Diffuse and Spotted Knapweeds." Univ. Idaho Coop. Ext. Serv. Bull. No. 680.

Moore, R. J. 1972. Distribution of native and introduced knapweeds (*Centaurea*) in Canada and the United States. *Rhodora* **74,** 331–346.

Moore, R. J., and Frankton, C. 1974. "The Thistles of Canada." Can. Dept. Agric. Monograph No. 10.

Müller, H., and Schroeder, D. 1989. The biological control of diffuse and spotted knapweed in North America—What did we learn?, *In* "Proceedings of the 1989 Knapweed Symposium" (P. K. Fay and J. R. Lacey, Eds.), pp. 151–169. Montana State Univ., Bozeman, MT.

Müller-Schärer, H., and Schroeder, D. 1993. The biological control of *Centaurea* spp. in North America: Do insects solve the problem? *Pestic. Sci.* **37,** 343–353.

Myers, J. H., and Harris, P. 1980. Distribution of *Urophora* galls in flower heads of diffuse and spotted knapweeds in British Columbia. *J. Appl. Ecol.* **17,** 359–367.

Radford, A. E., Ahles, H. E., and Bell, C. R. 1968. "Manual of the Vascular Flora of the Carolinas." Univ. North Carolina Press, Chapel Hill, NC.

Reed, C. F., and Hughes, R. O. 1970. "Selected Weeds of the United States." USDA Agric. Handbook 366.

Schroeder, D. 1985. The search for effective biological control agents in Europe 1. Diffuse and spotted knapweed. *In* "Proceedings of the 6th Int. Symp. Biol. Control Weeds (E. S. Delfosse, Ed.), pp. 103–119. Agric. Canada.

Story, J. M. 1985. First report of the dispersal into Montana of *Urophora quadrifasciata* (Diptera: Tephritidae), a fly released in Canada for biological control of spotted and diffuse knapweed. *Can. Entomol.* **117,** 1061–1062.

Story, J. M., and Anderson, N. L. 1978. Release and establishment of *Urophora affinis* (Diptera: Tephritidae) on spotted knapweed in western Montana. *Environ. Entomol.* **7,** 445–448.

Story, J. M., Boggs, K. W., Good, W. R., and Nowierski, R. M. 1989. The seed head moth, *Metzneria paucipunctella:* its impact on spotted knapweed seed production and the two seed head flies, *Urophora* spp. *In* "Proceedings of the 1989 Knapweed Symposium" (P. K. Fay and J. R. Lacey, Eds.), pp. 172–174. Montana State Univ., Bozeman, MT.

Story, J. M., Nowierski, R. M., and Boggs, K. W. 1987. Distribution of *Urophora affinis* and *U. quadrifasciata,* two flies introduced for biological control of spotted knapweed (*Centaurea maculosa*) in Montana. *Weed Sci.* **35,** 145–148.

Watson, A. K., and Renney, A. J. 1974. The biology of Canadian weeds. 6. *Centaurea diffusa* and *C. maculosa. Can. J. Plant Sci.* **54,** 687–701.

Zwölfer, H. 1965. Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) in Europe. *CIBC Tech. Bull.* **6,** 81–154.