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UROPHORA AFFINIS AND U. QUADRIFASCIATA
(DIPTERA: TEPHRITIDAE) RELEASED AND MONITORED BY
USDA, APHIS, PPQ AS BIOLOGICAL CONTROL AGENTS OF
SPOTTED AND DIFFUSE KNAPWEED

R. F. Lang,¹ R. D. Richard¹ and R. W. Hansen¹

ABSTRACT

USDA, APHIS, PPQ has distributed the seedhead gall flies *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae) as classical biological agents of the introduced weeds spotted and diffuse knapweed (*Centaurea maculosa* and *C. diffusa*, respectively) (Asteraceae) in the United States. From 1987 to 1996, *Urophora* spp. have been released in 97 counties in 14 midwestern and western states. Established populations of *U. affinis* and *U. quadrifasciata* are confirmed in 85 and 95 counties, respectively, among all 14 states. These include the first reports of successful establishment of *Urophora* spp. in Arizona (two counties), Colorado (eight counties), Michigan (one county), Minnesota (six counties), Nebraska (four counties), Nevada (two counties), North Dakota (one county), South Dakota (four counties), Utah (three counties), and Wisconsin (two counties). The first confirmed establishment of *U. quadrifasciata* in Indiana and Michigan is also reported.

Spotted knapweed (*Centaurea maculosa* Lam.) and diffuse knapweed (*C. diffusa* Lam.) (Asteraceae) are plants native to Eurasia that have become widespread weeds in North America. Spotted knapweed occurs across southern Canada, the northern United States, and throughout most of the western US, while diffuse knapweed occurs primarily in the western US and southwestern Canada (United States Department of Agriculture 1971). Knapweeds are adapted to a range of habitats and soil types, but appear especially well-suited to relatively dry sites (Watson & Renney 1974). They are aggressive competitors that invade non-cultivated areas and displace native plants and forage grasses (Gardner 1990, Harris & Cranston 1979, Hirsch & Leitch 1996, Watson & Renney 1974). In Montana, more than 2 million acres are infested by spotted, diffuse, and Russian (*Centaurea repens* L.) knapweeds, causing economic losses that exceed \$42 million (US) annually (Hirsch & Leitch 1996).

Spotted knapweed is a short-lived perennial, while diffuse knapweed is a biennial species. Both species reproduce by seed. *C. maculosa* seeds are dispersed by shattering of the seedhead (Watson & Renney 1974), and *C. diffusa* seeds are dispersed when above-ground parts of mature plants break off and tumble with the wind (Strang, et al. 1979). Vehicles, animals, and contami-

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nated hay and crop seed aid in long-distance seed dispersal for both species (Mass 1989, Wallander, et al. 1995).

Because spotted and diffuse knapweeds depend on seeds for reproduction, European seedhead-feeding insects have been released as classical biological control agents in the US and Canada. Among these agents are *Urophora affinis* Frauenfeld and *U. quadrifasciata* (Meigen) (Diptera: Tephritidae). Adult females of both species oviposit under the bracts of developing knapweed flower heads. Newly-hatched larvae burrow into the head and begin feeding on developing seeds and receptacle tissue. Knapweed plants form hard, lignified galls around *U. affinis* larvae, and thin, papery galls around *U. quadrifasciata* larvae (Rees & Story 1991, Zwölfer 1970). Each nonparasitized spotted knapweed seedhead produces an average of 12.6 viable seeds (Harris 1980). *Urophora affinis* and *U. quadrifasciata* galls reduce spotted knapweed seed production by 2.4 and 1.9 seeds, respectively, per seedhead (Harris 1980). Galls also form a metabolic sink and can reduce the number of flower heads produced by diffuse knapweed, but generally not spotted knapweed (Harris 1980). Generally, *Urophora* spp. do not appear sufficient to reduce spotted or diffuse knapweed density in North America (Müller-Scharer 1993). Other biological control agents that contribute more directly to plant mortality will be required (Müller-Scharer 1993).

The first North American releases of *U. affinis* and *U. quadrifasciata* were made in British Columbia, Canada, in 1970 (Harris 1980). In the United States, *U. affinis* was first released in 1973 in Montana and Oregon, with later releases in California, Idaho, and Washington (Maddox 1979). By 1978, *U. affinis* was released in the eastern US and is now established in New York, Pennsylvania, and Virginia (Wheeler & Stoops 1996). *Urophora quadrifasciata* was not released in the western United States but immigrated from Canadian populations, with establishment reported in Idaho in 1980 (Gillespie 1983) and Montana in 1981 (Story 1985). Established populations were later detected in California, Oregon, and Washington. *Urophora quadrifasciata* was also released in Quebec, Canada in 1979 and in Massachusetts and New York in 1983 (Wheeler 1995, Wheeler & Stoops 1996). It is now established in at least 11 eastern states (Hoebeke 1993, Wheeler 1995).

The United States Department of Agriculture, Animal Plant Health Inspection Service, Plant Protection and Quarantine (hereafter referred to as APHIS) began a national redistribution program for knapweed biological control agents in 1987, with *U. affinis* and *U. quadrifasciata* releases beginning in 1987 and 1989, respectively. The purpose of this paper is to document releases and subsequent establishment of *U. affinis* and *U. quadrifasciata* by the APHIS program.

MATERIALS AND METHODS

Potential release sites for biocontrol agents on spotted and diffuse knapweed are located and sampled by state cooperators. Prior to release, these knapweed infestations are sampled between October and May with a collection of 200 randomly selected seedheads. Two seedheads per knapweed plant are collected at intervals of 3–5 feet. The seedheads are placed in a plastic bag and shipped to the Bozeman Biocontrol Facility in Bozeman, Montana. Fifty of the 200 seedheads are randomly selected and examined under a dissecting microscope to record the number of *U. affinis* or *U. quadrifasciata* galls present.

To collect *Urophora* spp. adults for redistribution, spotted knapweed seedheads were collected in April and May from overwintered plants in

southwestern Montana. Seedheads were placed on large screen trays inside screened field cages approximately $3 \times 3 \times 2.1$ m in size. In Bozeman, *U. affinis* and *U. quadrifasciata* adults emerged from seedheads in June and July, and were collected daily from cage walls with an insect vacuum. Groups of 500 flies of both species were placed in 0.95–1 paper containers, to which some excelsior was added as a resting substrate. At least 1000 adults for each release were shipped to cooperators for release within knapweed infestations. The release point was marked with a permanent stake.

At each release site, *Urophora* spp. establishment was monitored by collecting knapweed seedheads between November and May. Two seedheads were collected from randomly selected plants, beginning at the release point and proceeding in expanding circles, until 200 seedheads were collected. Seedheads were sent to the Bozeman laboratory, where 50 of the 200 collected heads were randomly selected and examined under a dissecting microscope. The number of *U. affinis* and *U. quadrifasciata* galls observed in each seedhead was recorded. Galls are readily separated, as *U. affinis* galls are hard and lignified and formed from receptacle tissue (Zwölfer 1970), while *U. quadrifasciata* galls are thin and papery and formed in the ovaries (Rees & Story 1991). One or both *Urophora* spp. were considered established at a site when galls were present for at least two years after the original release or the population had infested 10% of the knapweed seedheads. *Urophora* spp. populations were considered collectable when the average gall density exceeded 1.5 galls per seedhead.

RESULTS AND DISCUSSION

The status of *Urophora affinis* and *U. quadrifasciata* populations released in 14 states by APHIS and cooperating personnel is summarized in Table 1. *Urophora affinis* has been released in 89 counties in 13 states. Of the 85 counties in which post-release sampling was conducted, *U. affinis* is established in 74 (87%). *Urophora quadrifasciata* has been released in 46 counties in 12 states, and established populations are present in 43 of the 46 counties (94%). In addition, established *U. quadrifasciata* populations were present in three counties in Michigan and one county in Indiana before this species was released in these states (Table 1). Both species are established in 32 of the 46 counties (70%) in which they have been released together.

These records describe the first reported establishment of *U. affinis* populations in the following states and counties: Arizona (Coconino), Colorado (Boulder, Douglas, LaPlata, Larimer, and Montrose), Michigan (Isabella), Minnesota (Becker, Beltrami, Clearwater, Ottertail, Polk, and Washington), Nevada (White Pine), North Dakota (Kidder), South Dakota (Pennington and Todd), Utah (Wasatch and Weber), and Wisconsin (Washburn and Waukesha) (Table 1 and Table 2). *Urophora quadrifasciata* was recovered for the first time in Arizona (Coconino), Colorado (Arapahoe, Boulder, Douglas, Jefferson, Larimer, and Montrose), Indiana (Elkhart), Michigan (Delta, Isabella, Dickinson, and Menominee), Minnesota (Becker, Beltrami, Clearwater, Otter Tail, Polk, and Washington), Nebraska (Antelope, Holt, Pierce, and Rock), Nevada (White Pine), North Dakota (Kidder), South Dakota (Pennington, Shannon, Todd, and Tripp), Utah (Wasatch and Weber), and Wisconsin (Washburn and Waukesha) (Table 1 and Table 2). Several *U. quadrifasciata* recoveries from Indiana (Elkhart), Michigan (Delta, Dickson, and Menominee), Minnesota (Washington), and Wyoming (Albany, Bighorn, Carbon, Crook, Laramie, and Sheridan) were detected in prerelease samples (Table 1 and Table 2).

Urophora quadrifasciata adults disperse more rapidly than *U. affinis*

Table 1. Status of *Urophora affinis* and *U. quadrifasciata* populations in the western and midwestern United States. Abbreviation Key: E = Established; NE= Not Established; NR= No Release; R = Recovered; ?= Unknown.

State	County	<i>U. affinis</i>			<i>U. quadrifasciata</i>		
		Yr. rel.	Status	Yr. recov.	Yr. rel.	Status	Yr. recov.
AZ	Coconino	1992-1994	E	1993	1994-1995	E	1993
	Gila	1994-1995	R	1996	1994-1995	NE	-
CO	Arapahoe	1990	NE	-	1990	E	1992
	Boulder	1990-1992	E	1992	1990-1992	E	1992
	Douglas	1989-1993	E	1992	1989-1990	E	1992
	El Paso	1990	NE	-	1990	NE	-
	Jefferson	1992	NE	-	1992	E	1993
	La Plata	1992	E	1993	1992	R	1997
	Larimer	1990	E	1992	1990	E	1992
ID	Montrose	1993	E	1995	1993	E	1995
	Adams	NR	E	1987	NR	E	1987
	Benewah	1987-1989	E	1987	NR	E	1987
	Bingham	1987-1989	?	-	NR	E	1987
	Blaine	1987-1989	?	-	NR	E	1987
	Boise	1987-1989	E	-	NR	E	1987
	Bonner	1987	E	1987	NR	E	1987
	Bonnville	1987-1988	?	-	NR	E	1987
	Butte	1989	E	1987	NR	E	1987
	Camas	NR	E	1987	NR	E	1987
	Cassia	1988-1989	?	-	NR	E	1987
	Clark	1987-1989	?	-	NR	E	1987
	Clearwater	1987	?	-	NR	E	1987
	Custer	1987-1989	?	-	NR	E	1987
	Elmore	1988	?	-	NR	E	1987
	Idaho	1987	?	-	NR	E	1987
	Jefferson	1987-1989	?	-	NR	E	1987
	Kootenai	1987	E	1987	NR	E	1987
	Latah	1987	?	-	NR	E	1987
	Lemhi	1987	E	1987	NR	E	1987
	Lincoln	1987	E	1987	NR	E	1987
	Madison	1989	?	-	NR	E	1987
	Nez Perce	1987	?	-	NR	E	1987
	Power	1989	?	-	NR	E	1987
	Shoshone	1987-1989	E	1987	NR	E	1987
Twin Falls	1987-1989	?	-	NR	E	1987	
IN	Elkhart	1997	NE	-	1997	E	1994
MI	Isabella	1994	E	1995	1994	E	1995
	Delta	NR	NE	-	NR	E	1995
MN	Dickinson	NR	NE	-	NR	E	1995
	Menominee	NR	NE	-	NR	E	1994
	Anoka	NR	NE	-	NR	E	1993
	Becker	1990-1993	E	1991	1990-1993	E	1991
	Beltrami	1992	E	1993	1992	E	1995
MT	Chisago	NR	E	-	NR	E	1993
	Clearwater	1991-1993	E	1992	1991-1993	E	1992
	Otter Tail	1991-1993	E	1992	1991-1993	E	1992
	Polk	1992-1993	E	1993	1992-1993	E	1993
	Washington	1990	E	1991	1990	E	1989
	Big Horn	1990	E	1988	1990	E	1988
	Broadwater	1987-1989	E	1994	NR	E	1994
	Carbon	1988-1991	E	1988	1991	E	1988
	Deer Lodge	1987	E	1987	NR	E	1987
Fergus	1987-1990	?	-	1990	E	1990	

Table 1. Continued.

State	County	<i>U. affinis</i>			<i>U. quadrifasciata</i>		
		Yr. rel.	Status	Yr. recov.	Yr. rel.	Status	Yr. recov.
	Flathead	1987-1989	E	1988	NR	E	1987
	Gallatin	1987-1990	E	1987	1990	E	1987
	Glacier	1987-1989	E	1988	NR	E	1988
	Granite	1987	E	1991	NR	E	1988
	Hill	1989	?	-	NR	E	1988
	Jefferson	1989	E	1991	NR	E	1998
	Lake	1987-1989	?	-	NR	E	1988
	Lewis & Clark	1987-1990	E	1988	1990	E	1988
	Liberty	1989	?	-	NR	E	1988
	Madison	1989	?	-	NR	E	1988
	Missoula	1987-1989	E	1987	NR	E	1987
	Musselshell	1989	?	-	NR	E	1988
	Park	1987-1992	E	1991	1992	E	1991
	Pondera	1987-1989	E	1991	NR	E	1988
	Powder River	1988	E	1988	NR	E	1988
	Powell	1987-1989	E	1991	NR	E	1988
	Ravalli	1989	?	-	NR	E	1988
	Rosebud	1988-1989	E	1988	NR	E	1988
	Saunders	NR	E	1988	NR	E	1988
	Silver Bow	1987	?	-	NR	E	1988
	Sweet Grass	1989-1992	E	1988	NR	E	1988
	Teton	1987-1989	E	1988	NR	E	1988
	Toole	1989	?	-	NR	E	1988
	Wheatland	1992	E	1991	1992	E	1991
NE	Antelope	1990	R	1991	1990	E	1991
	Holt	1991-1992	E	1991	1991-1992	E	1990
	Knox	NR	E	1992	NR	R	1991
	Pierce	1994	R	1991	1994	E	1991
	Rock	1990	R	1991	1990	E	1991
NV	Washoe	1993	NE	-	1993	NE	-
	White Pine	1994-1995	E	1996	1994-1995	E	1996
ND	Kidder	1990	R	1991	1990	R	1991
SD	Davis	NR	NE	-	NR	E	1996
	Pennington	1989-1992	E	1991	1989-1992	E	1991
	Shannon	1994	NE	-	1994	E	1995
	Todd	1991-1992	E	1993	1991-1992	E	1992
	Tripp	1989	NE	1991	1989	E	1991
UT	Grand	1991	NE	-	1991	NE	-
	Wasatch	1993-1994	E	1995	1993-1994	E	1992
	Weber	1992-1994	E	1992	1992-1994	E	1992
WI	St. Croix	NR	NE	-	NR	R	1992
	Washburn	1991	E	1993	1991	E	1992
	Waukesha	1991	E	1992	1991	E	1993
WY	Albany	NR	NE	-	NR	NR	1994
	Big Horn	NR	NE	-	NR	NR	1994
	Carbon	NR	NE	-	NR	NR	1994
	Crook	NR	NE	-	NR	E	1994
	Johnson	1993-1994	E	1994	1993-1994	E	1994
	Laramie	NR	NE	-	NR	NR	1994
	Lincoln	1995	E	1995	1995	E	1995
	Natrona	1991-1992	E	1991	1991-1992	E	1991
	Saunders	NR	NE	-	NR	E	1994
	Teton	1990	E	1995	1990	E	1995
	Uinta	1995	NE	-	1995	E	1995
	Wheatland	NR	E	1991	NR	E	1991

Table 2. *Urophora affinis* and *U. quadrifasciata* infestation rates of spotted and diffuse knapweed seedheads.

State	County and insect	Percent infestation by year						
		1991	1992	1993	1994	1995	1996	1997
AZ	Coconino							
	<i>U. affinis</i>			2		2		
	<i>U. quadrifasciata</i>			4		2		
	Gila							
	<i>U. affinis</i>							6
	<i>U. quadrifasciata</i>							-0-
CO	Arapahoe							
	<i>U. affinis</i>		-0-					
	<i>U. quadrifasciata</i>		4					
	Boulder							
	<i>U. affinis</i>		26					
	<i>U. quadrifasciata</i>		6					
	Douglas							
	<i>U. affinis</i>		44	24				
	<i>U. quadrifasciata</i>		42	68				
	El Paso							
	<i>U. affinis</i>		-0-					
	<i>U. quadrifasciata</i>		-0-					
	Jefferson							
	<i>U. affinis</i>		-0-					
	<i>U. quadrifasciata</i>		48					
	LaPlata							
	<i>U. affinis</i>		6		2	18		
	<i>U. quadrifasciata</i>		-0-		2	-0-		
	Larimer							
	<i>U. affinis</i>		48					
<i>U. quadrifasciata</i>		20						
Montrose								
<i>U. affinis</i>				4	34			
<i>U. quadrifasciata</i>				6	4			
IN	Elkart							
	<i>U. affinis</i>			-0-		-0-	-0-	
	<i>U. quadrifasciata</i>			2		10	48	
MI	Isabella							
	<i>U. affinis</i>					14	80	
	<i>U. quadrifasciata</i>					2	6	
	Delta							
	<i>U. affinis</i>				-0-			
	<i>U. quadrifasciata</i>				10			
	Dickinson							
	<i>U. affinis</i>				-0-			
	<i>U. quadrifasciata</i>				30			
	Menominee							
<i>U. affinis</i>			-0-	-0-				
<i>U. quadrifasciata</i>			36					
MN	Becker							
	<i>U. affinis</i>	26		8	32	26	4	
	<i>U. quadrifasciata</i>	32		-0-	8	10	34	
	Beltrami							
	<i>U. affinis</i>			58	42	68	68	
	<i>U. quadrifasciata</i>			-0-	-0-	8	4	
	Clearwater							
	<i>U. affinis</i>		20	32	38	34	68	

Table 2. Continued

State	County and insect	Percent infestation by year						
		1991	1992	1993	1994	1995	1996	1997
NE	<i>U. quadrifasciata</i>		-0-	-0-	6	2	12	
	Otter Tail							
	<i>U. affinis</i>		12	42	28	54	60	
	<i>U. quadrifasciata</i>		2	22	64	48	30	
	Polk							
	<i>U. affinis</i>			10	6	28	58	
	<i>U. quadrifasciata</i>			2	8	4	14	
	Washington							
	<i>U. affinis</i>		72	74	84	68	68	
	<i>U. quadrifasciata</i>		10	38	20	22	48	
	Antelope							
	<i>U. affinis</i>			-0-	4	-0-		
	<i>U. quadrifasciata</i>			84	34	58		
	Holt							
	<i>U. affinis</i>		6	-0-	6			
	<i>U. quadrifasciata</i>		30	60	66			
	Knox							
	<i>U. affinis</i>		2					
	<i>U. quadrifasciata</i>		32					
	Pierce							
<i>U. affinis</i>					-0-	-0-		
<i>U. quadrifasciata</i>					52	46		
Rock								
<i>U. affinis</i>	2		-0-					
<i>U. quadrifasciata</i>	2		26					
NV	White Pine							
<i>U. affinis</i>						26		
<i>U. quadrifasciata</i>						-0-		
ND	Kidder							
<i>U. affinis</i>	6	-0-						
<i>U. quadrifasciata</i>	-0-	2						
SD	Pennington							
<i>U. affinis</i>			6	34	66			
<i>U. quadrifasciata</i>			10	50	10			
Shannon								
<i>U. affinis</i>				-0-	-0-			
<i>U. quadrifasciata</i>				54	34			
Todd								
<i>U. affinis</i>		-0-	-0-	4				
<i>U. quadrifasciata</i>		22	32	78				
Tripp								
<i>U. affinis</i>			-0-		-0-			
<i>U. quadrifasciata</i>			34		46			
UT	Wasatch							
<i>U. affinis</i>			-0-	-0-	6	8		
<i>U. quadrifasciata</i>			-0-	4	60	78		
Weber								
<i>U. affinis</i>		12	6	4	28			
<i>U. quadrifasciata</i>		30	18	44	16			
WI	St. Croix							
<i>U. affinis</i>			-0-					
<i>U. quadrifasciata</i>			2					

Table 2. Continued

State	County and insect	Percent infestation by year						
		1991	1992	1993	1994	1995	1996	1997
WY	Washburn							
	<i>U. affinis</i>		-0-	26	4	2	-0-	
	<i>U. quadrifasciata</i>		4	4	18	30	16	
	Waukesha							
	<i>U. affinis</i>		2	10	60			
	<i>U. quadrifasciata</i>		-0-	30	26			
	Albany							
	<i>U. affinis</i>					-0-		
	<i>U. quadrifasciata</i>					10		
	Bighorn							
	<i>U. affinis</i>				-0-			
	<i>U. quadrifasciata</i>				6			
	Carbon							
	<i>U. affinis</i>					-0-		
	<i>U. quadrifasciata</i>					2		
	Crook							
	<i>U. affinis</i>				-0-			
	<i>U. quadrifasciata</i>				58			
	Johnson							
	<i>U. affinis</i>			-0-	6			
	<i>U. quadrifasciata</i>			52	50			
	Laramie							
	<i>U. affinis</i>				-0-			
	<i>U. quadrifasciata</i>				12			
	Lincoln							
	<i>U. affinis</i>					90		
	<i>U. quadrifasciata</i>					12		
	Natrona							
<i>U. affinis</i>			6	30				
<i>U. quadrifasciata</i>			32	8				
Sheridan								
<i>U. affinis</i>				-0-				
<i>U. quadrifasciata</i>				78				
Teton								
<i>U. affinis</i>				20				
<i>U. quadrifasciata</i>				2				
Uinta								
<i>U. affinis</i>				-0-				
<i>U. quadrifasciata</i>				18				

adults, and quickly migrate into new knapweed-infested areas (Harris 1980, Roitberg 1988). This is supported by the detection of *U. quadrifasciata* in prerelease samples from Indiana, Michigan, Minnesota, and Wyoming as mentioned above.

These recoveries of *U. affinis* and *U. quadrifasciata* help to complete the known distribution of these two *Urophora* flies in the United States. The APHIS distribution program has extended the documented range of *U. affinis* and *U. quadrifasciata* into knapweed-infested areas of the western and midwestern US. *Urophora quadrifasciata* will probably continue to spread on

its own throughout these regions. *Urophora affinis* does not disperse as readily, and will require collection and distribution from established populations to facilitate spread.

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