TOADFLAX, FIRE, *MECINUS JANTHINUS*,
AND COMPENSATORY GROWTH

by

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July 7, 2005

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ABSTRACT

Dalmatian toadflax is a noxious weed of the western United States. In western Montana it invades in the foothills zone where bunchgrasses (*Agropyron spicatum* and *Festuca idahoensis*) meet low forests (*Pinus ponderosa* and *Pseudosuga menziesii*). Our results show that wildfire strengthens toadflax, probably at the expense of native grasses. The stem boring weevil, *Mecinus janthinus*, is being tested as the most likely biocontrol agent for the weed. On our toadflax infested sites in the *Agropyron spicatum*/*Pinus ponderosa* zone *Mecinus* established, survived, and spread slowly (2-4m/yr) for two years following introduction. At the low initial densities *Mecinus* induced compensatory growth in toadflax i.e. stem density, plant height, branch number, and seed capsule number all increased. In a garden experiment, we exposed plants to *Mecinus* at increasingly higher densities (0-32 insects per plant) to measure the effect of a higher attack rate. With exposure rates of 2-4 insects per plant compensatory growth occurred. With exposure rates greater than 8 insects per plant total biomass and especially flower biomasses were reduced. If *Mecinus* densities in the field exceed eight weevils per plant this may indicate eventual exhaustion and decline of the weed.

CHAPTER 1

INTRODUCTION

Toadflax, both Dalmatian (*Linaria dalmatica*) and yellow (*Linaria vulgaris*), are noxious weeds in Montana (Montana Department of Agriculture 2003) and the prairie forest border of the northern plains. It may be encouraged by fire if burning weakens it less than its native competitors, such as native grasses. I develop these statements in the following “literature review” section.

Toadflax might conceivably be contained by quarantine, chemical treatment, natural enemies, or a combination of these agents. This statement is also developed in the literature review section. If species specific natural enemies can be found, they offer the advantages of low cost and high persistence. *Mecinus janthinus* appears to control toadflax in cool moist segments of its ‘noxious’ range (DeClerck-Floate 2002). We consider its efficacy in a colder drier environment of Montana, both as a test of its effectiveness here and to further outline the parts of toadflax’s range in which *Mecinus* might provide useful control.

We report here on five aspects of toadflax control in Montana. 1) Under natural conditions does fire encourage Dalmatian toadflax. In a field experiment (chapter 2) we considered use of *Mecinus* to control toadflax in the field. 2) Can the insect survive in our cold dry climate. 3) How rapidly does the insect spread from inoculation points. 4) What impact does the insect have at initial field densities. In a separate garden experiment we compared plant performance (total, stem, leaf, and flower biomass) when it was exposed to *Mecinus* numbers ranging from initial field densities to abnormally higher rates (0-32 insects per plant). 5) And, in Appendix 1, we outline a failed experiment in which the effects of rest, light grazing, fire, and cultivation on the competitive status of toadflax were to have been observed in *Pinus ponderosa*/ *Agropyron spicatum* savanna.

Dalmatian toadflax, *Linaria dalmatica*

History and distribution

Dalmatian toadflax, *Linaria genistifolia* ssp. *dalmatica* (L.) Maire & Petitmengin is an invasive weed in North America. It was introduced as an ornamental plant from Mediterranean Europe and western Asia in about 1874. *L. dalmatica* is named for the Dalmatian coast of former Yugoslavia. Its native range extends from Yugoslavia eastward into northern Romania and southeastward into northern Syria, northern Iraq and northern Iran (Alex 1962; Vujnovic and Wein 1996). The latitudinal range of Dalmatian toadflax in Eurasia is from 35^{o} to 47^{o} N, as compared to a range of 33^{o} to 56^{o} N in North America (Alex 1962). Within fifty years of its arrival to North America Dalmatian toadflax had escaped cultivation and was found in 7 Canadian provinces and 22 US states, with its largest populations found in the western parts of the United States (Figure 1**)** and Canada (Lajeunesse et al. 1993). The spread of toadflax was facilitated by its many uses, not only as an ornamental, but also as a medicinal and dye plant. Its unintentional spread, was aided by railway corridors, roads, and crop impurities. By the

1940's, this invasive had become established in south central Montana, and within 40 years it was found in 24 counties. Today's records indicate that *L. dalmatica* occurs in 43 Montana counties.

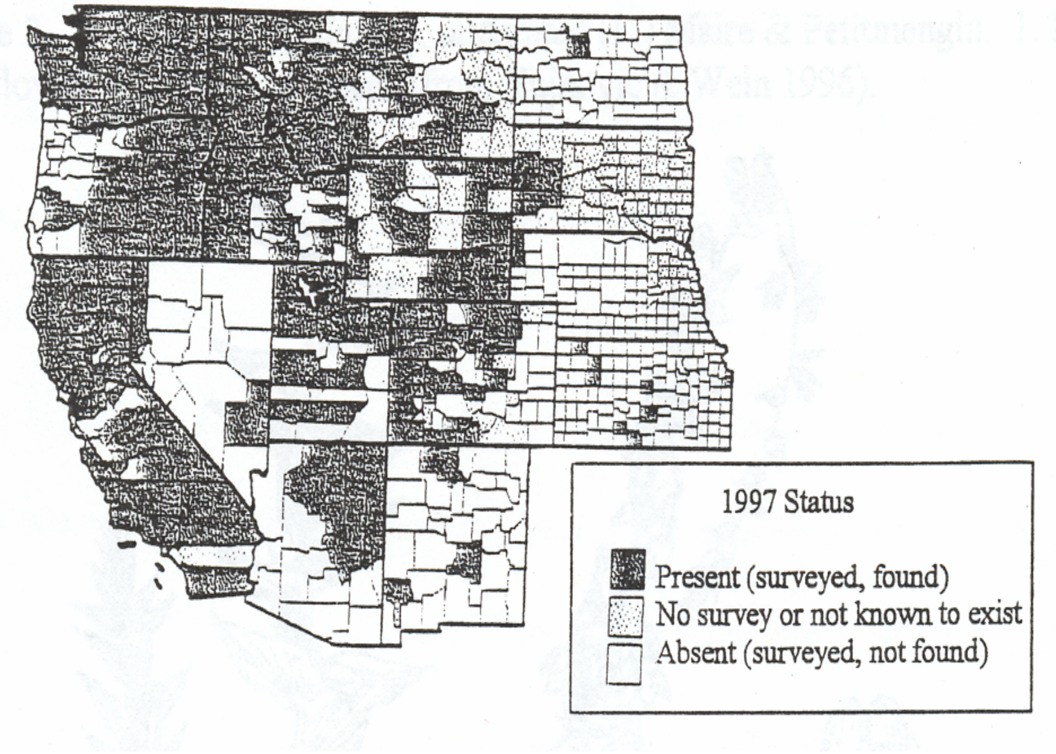

Figure 1. Distribution of *L. genistifolia* ssp. *Dalmatica* in the Western US (Montana CAPS, 1999).

<u>Biology</u>

Dalmatian toadflax, a member of the family Scrophulariaceae, is a "robust perennial herb with attractive yellow flowers and glaucous green foliage" (Alex 1962). It has broad leaves that are heart-shaped and usually wrap alternately around the stem (Nowierski 1996). Mature toadflax plants range in height from 0.3 to 0.9 m and have extensive root/rhizome systems reaching depths of 1.3 to 3.3 m and a lateral range of 3.6

m. Lateral roots/rhizomes support vigorous clonal expansion. The flowers are yellow with orange centers and resemble those of snapdragons. The plant blooms from May-June through September-October, and disperses seeds from June throughout the winter (Lajeunesse et al. 1993). Toadflax produces up to 500,000 seeds per year (Robocker 1970). It is well adapted to a variety of climatic ranges and soil types, but it grows best in coarse textured soils.

Impacts

Dalmatian toadflax has become an important weed in pastures, cultivated fields and disturbed rangelands throughout the northern and western United States and Canada (Coupland and Alex 1954, Lange 1958, Montgomery 1964, Reed and Hughes 1970, Nowierski 1995, 1996). Invasion is feared in the grassland/low forest zone of western Montana. It is an aggressive competitor due both to an expansive root system allowing for more efficient exploitation of water resources and emergence earlier in the spring than most natives, thus giving it a competitive edge. As it displaces native species, wildlife and livestock forage is reduced. In addition, Dalmatian toadflax contains chemicals that make it toxic to livestock (Nowierski 1996). Weed infestations, including toadflax, reduce grazing capacity of rangelands by up to 75% and are the factor accounting for the largest portion of total annual losses in agricultural production (Rao 2000, Sheley et al. 1999).

Weed Control

Methods

Manual and mechanical methods of weed control may be viable practices in cultivated systems. When they are used with herbicides, overall weed management efficiency may be enhanced. Weeds are as problematic in forest systems as in agricultural systems, however historically less attention is paid to them as their economic impact is less significant (Rao 2000).

Due to the plants high genetic variability that allows for its adaptiveness, and broad tolerance which allows it to flourish and spread in diverse environments, management of Dalmatian toadflax is particularly important and troublesome. Prescribed burning has little effect on toadflax root buds or seeds buried in the soil, therefore rendering it ineffective for weed control. Powerful roots provide an anchor that prevent grazing animals and cultivation from dislodging or destroying plants. Chemical control of Dalmatian toadflax is also very difficult due to its extensive root system and waxy leaves. Duncan (1999) found, however, that applying Picloram during the bloom growth stage for two years results in 81-99% control. Where toadflax is present in remote locations in forest and grassland systems, chemical and mechanical means of control are impractical options.

Biological Control

Biological control has become an important tool in weed management. It involves introducing enemy insects found in the plant's native range to control the weed in its new range. The goal of bio-control is not to eradicate, but to put additional pressure on the target weed in order to reduce its dominance in the invaded ecosystem and cause a decline in weed population density to a level that is non-damaging/acceptable (Wilson and McCaffrey 1999). Once a biological control agent is established, it self-perpetuates and provides a more cost-effective solution than repeated application of classical control methods. Although a bio-control agent commonly takes several years to establish and its effects are not immediate, biological control agents contribute to long term weed control and lend themselves well to integrative weed management.

Several bio-control agents, natural enemies of Dalmatian toadflax, have successfully passed rigorous host specificity testing and have been approved for introduction in the US by USDA-APHIS-PPQ. These include a defoliating moth (*Calophasia lunula*), a root-boring moth (*Eteobalea intermediella*), a seed-feeding weevil (*Gymnetron antirrhini*), and a stem-boring weevil (*Mecinus janthinus*). *C. lunula* is widely established in northeastern Washington, as well as in parts of a few places in Idaho and Montana. However, the moth has difficulty surviving at higher elevations and is presumably intolerant of cold climates (McClay and Hughes 1995). Saner et. al. (1994) found *E. intermediella* not to have statistically significant effects on Dalmatian toadflax performance.

Two other enemies of toadflax, *Brachypterolus pulicarius* and *Gymnetron antirrhini*, gained access into North America accidentally while accompanying an introduction of toadflax for ornamental purposes. The impact of *Brachypterolus* on Dalmatian toadflax is not clear, however research shows the beetle reduces yellow toadflax seeds by 80-90%.It is hoped that a strain of *B. pulicarius* adapted to Dalmatian toadflax will perform similarly (Nowierski 2004). A strain of *G. antirrhini* adapted to Dalmatian toadflax was released in Wyoming in 1998, but whether it has established is unknown (Nowierski 2004).

Stem-miners are expected to have more of an impact on toadflax than either defoliators or seed-feeders (Jeanneret and Schroeder 1992). No stem-mining weevils native to North America are known to attack Dalmatian toadflax (Jeanneret and Schroeder 1992). Saner et. al. (1994) reports decreased shoot biomass resulted from *Mecinus* attack. Therefore *Mecinus janthinus* appears to be the most promising bio-control agent for Dalmatian toadflax.

Mecinus janthinus

Biology

Mecinus janthinus Germar is a stem-mining weevil in the family Curculionidae. Its native range extends from central and southern Europe to the former southern USSR. *Mecinus* occurs just below the subalpine zone in the Alps (Hoffmann 1959). The weevil occurs in regions representing a wide range of ecological conditions. Additionally, soil type does not limit *Mecinus* distribution (Jeanneret and Schroeder 1992).

Mecinus janthinus over-winters in the stems of Dalmatian toadflax**.** Adult weevils feed sparingly on leaves and, after a short period of feeding and mating, lay eggs in host stems in late spring. Females chew holes in toadflax stems and ovipost eggs singly into each hole, with approximately 2-100 eggs per stem (DeClerck-Floate 2002). Larvae emerge from eggs after about 1 week and tunnel in the stem while feeding, thereby creating a chamber. Over the summer, the larvae go through 3 instars before pupation occurs. Adults are fully formed by early fall and remain in the senesced toadflax stalks through the winter, only to emerge the following spring leaving one emergence hole per adult weevil. *Mecinus* produces one generation each year (Jeanneret 1992).

We optimistically hypothesize that *M.janthinus* will serve as a control agent for Dalmatian toadflax in Montana, based on its performance in British Columbia (De Clerck-Floate and Miller 2002). In 1996, *Mecinus janthinus* was approved for release against Dalmatian toadflax in the United States by the Animal Plant Health Inspection Service – Plant Protection & Quarantine. The stem-boring weevil was introduced at six places in Montana between 1997 and 2001 and has been present at all these sites each year since its introduction (Table 1, Nowierski personal communication, Anthony and Weaver this document).

Table 1. First releases of *Mecinus janthinus* in Montana
(Nowierski personal communication, Anthony and Weaver this document).

Year of release	Location	
1997	Crow reservation	Hardin, MT
	BLM site	south of Townsend, MT
1998	Bison Range	Ronan, MT
	Mt. Helena	Helena, MT
2001	BLM site	near Melstone, MT
	USFS sites	Helena National Forest, MT

CHAPTER 2

FIELD EXPERIMENT

Introduction

Our field experiment investigated control of toadflax in *Pinus ponderosa*/ *Agropyron spicatum* environments of Montana. It measured the initial (immediate) capacity of *Mecinus janthinus* to survive, spread, and impact toadflax. Toadflax's compensatory growth is of special interest.

A separate experiment, the garden experiment (Chapter III) tests the impacts of higher density *Mecinus* populations than may appear when the insect becomes well established.

Methods

Study sites

Study sites were located in the Rocky Mountain vegetation most commonly invaded by toadflax, i.e. found where forests replace grasslands on the altitudinal gradient. The grasslands at lower elevations are dominated by *Agropyron spicatum / Festuca idahoensis* (Mueggler 1980). These grasses form understories in open forests of *Pinus ponderosa* or *Pseudotsuga menziesii* above the grasslands (Pfister 1977). Environments of these sites have been described with respect to climate by Weaver (1980, 1994), Mueggler (1980), and Pfister (1977). And with respect to soils by Weaver

(1979), Mueggler (1980), and Pfister (1977).

Our eight experimental sites were located in the Helena National Forest, 27 to 45 miles southeast of Helena, Montana. All sites were dominated by *Agropyron spicatum* grassland at the margin of *Pinus ponderosa* forests. Their location, environmental types, slope/aspect, and elevation are described in Table 2. Most sites were south facing at elevations of 4500-5500 feet. Most sites have sandy to cobbly foothill soils. The locations (lat/long) and local names locate them approximately. Sites were burned (B) or not (-) in 2000.

Climate of the study area is described in Table 3. Spring rains (approximately May-June) are followed by dry summers and winters (Table 3). July maximum/minimum temperatures are 98^{o}F and 51^{o}F. Average January temperatures are 29.2^{o}F and 10.9^{o}F. Frost-free season is June – August.

Table 2. Characteristics of experimental field sites near Helena, Montana[1].
UTM 12, (WGS84/NAD83).

Site	Name	Fire Trt.	Insect Trt.	Elevation	Slope/Aspect	Location	
						UTM	Lat/Long
1	German Gulch	B	I	5320	40o/south	445736E 5173310N	46^{o} 42’ 0”N, 111^{o}42’36”W
1	German Gulch	B	-	5280	45o/south	445782E 5173239N	46^{o} 42’ 38”N, 111^{o}42’33”W
2	Kingsbury Gulch	B	I	5100	/west	446137E 5172486N	46^{o} 42’ 14”N, 111^{o}42’17”W
2	Kingsbury Gulch	B	-	5075	37o/west	446082E 5172428N	46^{o} 42’ 12”N, 111^{o}42’19”W
3	Kingsbury Gulch	B	I	5080	/south	446157E 5172449N	46^{o} 42’ 12”N, 111^{o}42’15”W
3	Kingsbury Gulch	B	-	5080	30o/south	446108E 5172352N	46^{o} 42’ 09”N, 111^{o}42’18”W
4	Coxcy Gulch	B	I	5320	/SE	449990E 5171451N	46^{o} 41’ 42”N, 111^{o}39’15”W
4	Coxcy Gulch	B	-	5080	/SE	450185E 5170826N	46^{o} 41’ 21”N, 111^{o}39’05”W
1	York Road	-	I	4060	45o/south	443108E 5174931N	46^{o} 43’ 32”N, 111^{o}44’40”W
1	York Road	-	-	4100	40o/south	443352E 5175200N	46^{o} 43’ 41”N, 111^{o}44’29”W
2	York Road	-	I	4160	/south	443642E 6175423N	46^{o} 43’ 48”N, 111^{o}44’15”W
2	York Road	-	-	4130	/south	443474E 5175301N	46^{o} 43’ 44”N, 111^{o}44’23”W
3	German Gulch	-	I	5290	35o/west	445193E 5173453N	46^{o} 42’ 45”N, 111^{o}43’02”W
3	German Gulch	-	-	4900	30o/west	445076E 5173387N	46^{o} 42’ 42”N, 111^{o}43’07”W
4	York Road	-	I	4100	/SE	443189E 5175048N	46^{o} 43’ 36”N, 111^{o}44’37”W
4	Coxcy Gulch	-	-	5520	/SE	450000E 5171603N	46^{o} 41’ 46”N, 111^{o}39’14”W

[1] All sites are in *Agropyron spicatum/Pinus ponderosa* environmental type.

Table 3. Climate data for the period of September 2001 to September 2003 for Montana weather station (Helena AP ASOS[2]) near study sites. Data was obtained from (Climatological Data Montana, 2000-2003).

		Precipitation		**Temperature**						
Year		Long Term Average	Average	Long Term Average	Average	Ave. Max.	High	Ave. Min.	Low	# Frosts
2000	January	0.63	0.26	19.6	24.9	34.5	52	15.2	-5	31
	February	0.41	0.32	26.4	28.7	40.3	59	17	1	27
	March	0.73	0.26	33.6	38.5	49.4	67	27.5	19	26
	April	0.97	0.73	43.4	47	60.9	75	33	17	15
	May	1.78	0.98	52.5	54.9	66.1	82	43.6	33	0
	June	1.87	1.42	62.1	62.4	76	96	48.8	33	0
	July	1.10	0.43	69.2	69.6	87.6	101	56.6	46	0
	August	1.29	0.73	82	72.1	86.2	99	53	42	0
	September	1.15	0.54	55.4	56.4	70.4	94	42.3	19	5
	October	0.60	2.12	45.1	47.8	59.8	75	35.8	16	13
	November	0.48	0.36	31.6	22.8	32.2	59	13.3	0	30
	December	0.59	0.23	21.2	16.2	25.5	48	6.9	-18	31
2001	January	0.63	0.27	19.6	20.1	29.2	52	10.9	-9	31
	February	0.44	0.17	26.4	17.8	27.3	43	8.2	-4	28
	March	0.73	0.44	33.6	35.2	44.8	58	25.5	6	26
	April	0.97	1.39	43.4	44	55	81	32.9	22	16
	May	1.78	1.23	52.5	59.2	74.5	93	43.8	26	2
	June	1.87	2.11	62.1	64.1	77.4	95	50.7	39	0
	July	1.1	1.94	69.2	72	86.5	98	57.5	51	0
	August	1.29	0.43	82	74.7	92	102	57.3	47	0
	September	1.15	1.38	55.4	64.6	80.2	96	48.9	42	0
	October	0.6	0.54	45.1	48.4	59.3	87	37.4	23	7
	November	0.48	0.13	31.6	39.2	50.6	68	27.8	9	21
	December	0.59	0.28	21.2	24.8	33.9	49	15.7	-4	30
2002	January	0.52	0.04	20.2	29.6	37.9	61	21.1	4	29
	February	0.38	0.29	26.4	30.3	42.5	63	18	-13	26
	March	0.63	0.52	35.1	25.2	35.9	67	14.4	-12	26
	April	0.91	0.61	44.1	43	56	73	30	3	17
	May	1.78	1.86	52.9	53.4	66	90	40.8	24	5
	June	1.82	4.36	61.2	62.8	75.8	93	49.8	36	0
	July	1.34	1.61	67.8	72.4	87.5	105	57.2	45	0
	August	1.29	1.32	66.7	64	78	87	49.9	38	0
	September	--[1]	--	--	--	--	--	--	--	--
	October	0.66	0.16	44.8	40.4	52.8	73	28	-2	20
	November	--	--	--	--	--	--	--	--	--
	December	--	--	--	--	--	--	--	--	--
2003	January	0.52	0.41	20.2	29.4	38.5	57	20.2	1	28
	February	0.38	0.29	26.4	25.3	33.5	46	17	-13	27
	March	0.63	0.74	35.1	34.2	44.8	69	23.5	-7	21
	April	1.91	2.27	44.1	46	57.2	74	34.7	19	11
	May	1.78	1.25	52.9	53.3	65.3	92	41.2	30	7
	June	1.82	1.49	61.2	63.2	76.5	94	49.9	37	0
	July	1.34	0.23	67.8	76.4	92.5	104	60.2	48	0
	August	1.29	1.03	66.7	73.5	89.5	102	57.4	44	0
	September	--	--	--	--	--	--	--	--	--
	October	0.66	0.34	44.8	50.6	64	82	37.2	9	6
	November	0.48	0.2	30.9	28.8	39.1	65	18.4	-1	28
	December	0.46	0.35	21.4	28.3	37.1	58	19.5	-5	31

[1] Dashed line (--) indicates missing data.

[2] Automated Surface Observation System

Treatments

To determine the effect of fire on toadflax and *Mecinus janthinus*, we compared their performance between burned and unburned sites. The wildfire occurred the autumn before our measurements began i.e. the fires of 2000 (BAER 2000). Eight study sites were located in June 2001 (Figure 2). Four sites were in burned areas and four were in unburned areas. Criteria for site selection included presence of toadflax, similarity of native vegetation, and slope aspect. While burned and unburned sites were paired as well as possible, we treat them as independent samples.

To measure the effects of insects on toadflax, treatment plots were inoculated with *Mecinus janthinus*. Treated and untreated plots were 17 x 34 meters and nearly identical with respect to slope, aspect, vegetation, and soil. To ensure *Mecinus* did not spread to the control plots for at least two years, and therefore contaminate them, treatment plots were established at least 200 meters from control plots.

Reference points

For the purpose of inoculation and monitoring, two permanent transects were installed in each plot. The transects were 40 m long, on the contour, parallel, 5-6 meters apart, and staked at each end with iron rebar posts. Sample points (quadrats) were located at two meter intervals along the transects and permanently marked with eight-inch spikes to enable exact remeasurement in successive years (Figure 3). Inconsequential deviance from this pattern, due to a mismeasurement in the field, is documented in the “attached data set”.

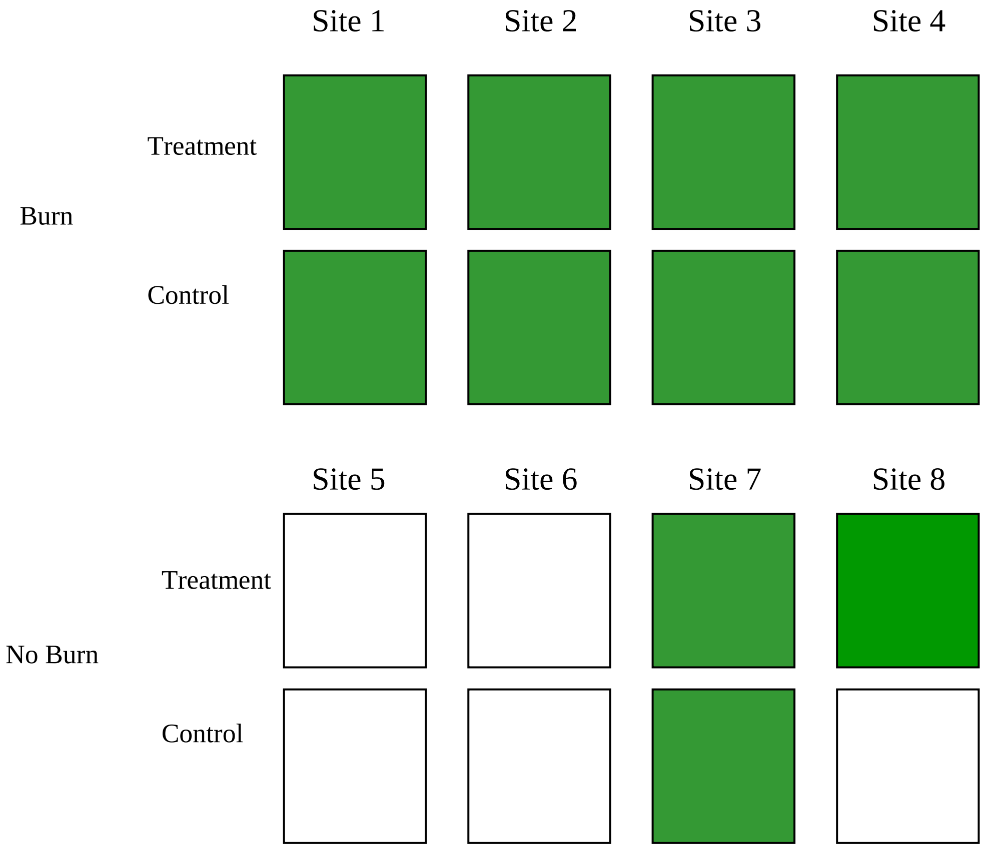

Figure 2. Layout of field experiment. Eight sites (16 paired plots) were located near Helena, Montana. Five plots were accidentally eliminated by a weed control crew. Site 8 treatment plot was then omitted because it lacked a paired control plot.

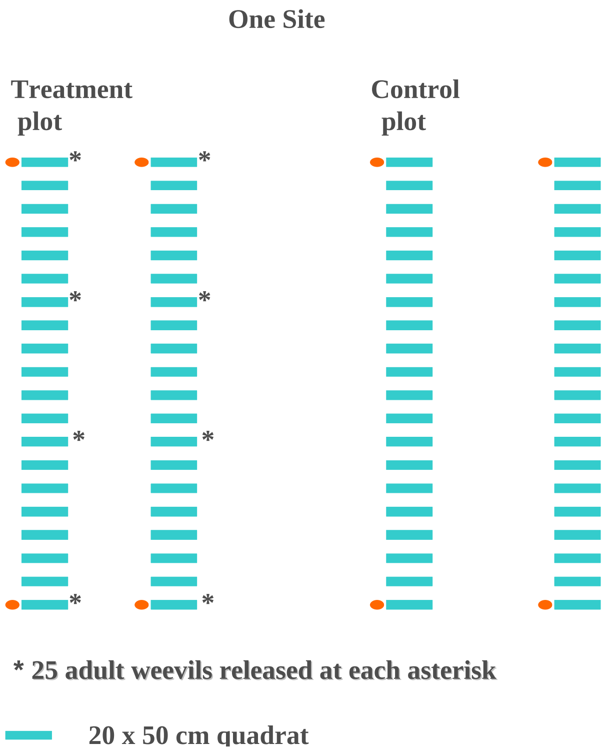

Figure 3. Layout of each site. Forty points along two transects were sampled at each site, eight of which were inoculation points *.

Insects

On June 12 – 15, 2001 each treatment plot received 200 insects. Twenty-five *Mecinus janthinus* were released at four places along each transect i.e. at 0, 14, 28, and 42 meter points (Figure 3**)**. The insects released were collected on 12 June 2001 near Grand Forks, B.C. by Rich Hansen and colleagues of USDA-APHIS-PPQ-CPHST (Rich Hansen personal communication). They were sorted and counted, 25 each, into sixty-four Petri dishes, then transported to the field in coolers and packed with gel ice packs. The weevils were individually placed on toadflax stalks at designated release points.

To measure survival, increase, and spread of *Mecinus*, its numbers were recorded at inoculation (June 12-15, 2001), one year later (July 12-16, 2002), and two years later

(July 1- 5, 2003). In 2002-2003, the previous year's dead toadflax stems were collected from each 20 x 50 cm quadrat on the transects previously described. Previous year presence was recorded by summing the number of emergence holes and dead adults in each dead stem. Emergence holes were confidently identified. Dead adults were tallied by splitting the stems and recording the number present. Over-winter survival rates [emergence holes/(emergence holes + dead adults)] were calculated for comparison between 2001 and 2002.

With population growth, insects diffuse outward from the inoculation points. To describe the spread we plot an exponentially declining line through end of summer insect numbers at points 0, 2, 4, and 6 m from all points in each of the sites one and two years after introduction. We expected to count number present four years after introduction in June 2005.

Population growth of *Mecinus janthinus* can be compared by computing population sizes across years. And compared between years and fire treatments. The initial population size at each inoculation point was twenty-five, or 200 per plot. One year later the population size is the integral, under the graph of number vs. distance and rotated around its axis (Figure 4). Third and fourth year population sizes might be similarly calculated if populations expanding from adjacent inoculation points have not fused. After that, fusion population density will become constant (not exponentially declining) across space.

Insect/fire impact on plants

After the weeds senesced in fall of 2001, plant vigor data was collected. Toadflax was non-destructively sampled to compare its performance both on 'paired' burned/unburned plots and on insect treated/untreated plots. Measurements were made in each 20 x 50 cm quadrat (quadrat = subplot) placed at two meter intervals along the transects. Density was recorded as the number of stems in each quadrat. Height was recorded as the average height across all stems in the quadrat. Branch number was averaged across stems. Seed capsule number was averaged similarly. While the number of seeds per capsule may vary with the level of insect attack, the product of capsule number per plant and the number of stems in a plot is an index of reproductive expenditure under particular conditions.

Three out of four unburned sites were accidentally ruined due to herbicide applied by a USFS weed control crew in Fall 2001, which was discovered 28 June, 2002. The destroyed plots were therefore abandoned. Fire effects on toadflax were appropriately measured on four burned and four unburned sites in 2001, before the spraying of herbicides. However, in 2002 four burned sites were contrasted with the remaining unburned site.

Results and Discussion

Fire favors toadflax

While toadflax is labeled noxious in western Montana, some fear that after fire it will be especially invasive and dominant (INVADERS 2005, Jacobs and Sheley 2003). To determine whether fire gives toadflax a competitive advantage, we examined its performance on ‘paired’ burned and unburned sites, established the spring after Montana’s wildfires in 2000. In the first post-fire season (2001) toadflax performed better on burned than unburned sites (Table 4). That is, on burned sites density, height, branch number, and seed capsules were 31%, 53%, 4%, and 49% higher than those observed on unburned sites. Toadflax performance, i.e. density, height, branch number, and capsules was even greater in the second post-fire season (Table 4), i.e. 165%, 72%, 80%, and 69% higher than those observed on unburned sites, all significant increases (Table 4). While four burned and four unburned sites were compared in 2001, inadvertent poisoning of plants in three of the unburned sites lead to an unbalanced comparison in 2002, i.e. four burned vs. one unburned site. The superior performance of toadflax seen on burned sites (2001 & 2002) was likely because burning improved the competitive position of toadflax by weakening the invaded grassy vegetation more than the deep rooted weed. The generally greater growth of toadflax in the second post-fire year (2002, Table 4) suggests that in the first post-fire year toadflax on burned plots accumulated carbohydrate reserves that further bolstered its competitive advantage in the second year.

Table 4. Effect of fire on toadflax performance, 2001-2002. X, se/N^2

Treatment		Unburned	Burned	% increase	Probability[1]
		First post fire year (2001).			
Density	(#/0.1m^2)	1.18±0.10/347	1.55±0.10/349	31%	0.01
Height	(inches)	11.54±0.99/347	17.61±0.98/349	53%	0.00
Branches	(#/plant)	2.04±0.19/346	2.13±0.18/347	4%	0.73
Capsules	(#/plant)	4.27±0.49/346	6.38±0.49/347	49%	0.00
		Second post fire year (2002).			
Density	(#/0.1m^2)	0.79±0.5/84^2	2.10±0.12/344	165%	0.00
Height	(inches)	7.32±0.27/84	12.59±0.63/344	72%	0.00
Branches	(#/plant)	0.81±0.23/84	1.46±0.11/344	80%	0.01
Capsules	(#/plant)	2.81±1.08/84	4.76±0.53/344	69%	0.11

[1] *Probability of finding this difference by chance.*

[2] N in 2002 was reduced by accidental herbicide spraying from a USFS weed control crew.

Mecinus in the field

Survival. The success of *Mecinus* depends first on its survival in the environment considered, then on its multiplication, dispersal and attack. *Mecinus* survival was observed over two years on our five sites in the *Agropyron spicatum* (*Pinus ponderosa*) environment (4 burned and only 1 unburned - - due to herbiciding of three others). Stem miner attack (density) was recorded in 2002 by counting emergence holes and dead adult weevils in over-wintered stems (winter 2001-2002) from sample plots. Survival rates were measured as the ratio of emergence holes/(emergence holes + dead adults) present in over-wintered stems. Density and survival was similarly recorded for winter 2002-2003.

Over-winter survival rates may vary among years due to climatic influence. Survival rates at inoculation points were 58-83% (x = 68%) in spring of 2002 and 0-73% (x = 60%) in spring of 2003 (Table 5). Despite the early frost, the over-all survival rates in 2001-2002 (73%) and 2002-2003 (66%) did not differ significantly (t = 0.66).

Table 5. Over-winter survival[1] rates of M*ecinus janthinus* at Helena National Forest field sites, 2001-2002 and 2002-2003. Means and standard deviations are calculated across 8 or more 0.1m^2 quadrates at each distance on each site
(*n* = # quadrats)[3].

			Burn										**No burn**	
Year	Distance[2]		Site 1	*n*	Site 2	*n*	Site 3	*n*	Site 4	*n*	x, site 1-4	*SE, n*	Site 3	*n*
2001-2002	0	**mean**	**63.9**	8	**63.2**[a]	1[a]	**70.0**	4	**83.3**	5	**68.9**	*14.2, 18*	**58.5**	7
	2	**mean**	**66.7**	3	**100**[a]	1[a]	*****		- -		**66.7**	*19.5, 4*	- -	
	4	**mean**	*****		**100**[a]	1[a]	**50.0**	1	- -		**50.0**	*26.5, 2*	*****	0
	6	**mean**	-		-		*****		-		*****		-	
2002-2003	0	**mean**	**73.3**	5	*****		**60.0**	1	**45.8**	3	**59.7**	*14.9, 9*	*****	
	2	**mean**	**33.3**	2	**50.0**	2	**66.7**	1	**75.0**	1	**65.0**	*23.9, 6*	**100.0**	2
	4	**mean**	**80.0**	3	**61.5**	3	**100.0**	1	**0****	2	**80.5**	*18.8, 9*	*****	
	6	**mean**	**100.0**	1	**50.0**	1	*****		**0****	1	**61.1**	*21.7, 3*	**33.3**	1

[1] Survival rate = ((emergence holes/emergence holes+ dead adults)(100))
[2] Distance from inoculation point (m).
[3] # quadrats was used in calculation instead of # stems, due to data collection methods.
- Indicates no stems present.
[*] No insects present.
[**] All insects present were dead.
[a] Indicates missing data (stem and dead adult).

Survival might also vary among points at a site (perhaps with temperature/drought, protective snow drifts) or among sites (perhaps with energy - - slope, aspect or elevation - - related snow cover or fire history impacts on litter, ground layer or tree canopy cover). Within site over-wintering survival rate variation was seen during the winter of 2002-2003 (Table 5). We saw no significant variation in survival among our burned sites or between the burned sites and our one unburned site (Table 5). And we saw no significant variation between lower sites (burn #2 and 3) and higher sites (burn #1 and 4, and unburned #3, Table 5).

Increase and dispersal. Insects are expected to multiply at inoculated sites and to disperse outward in a pattern of exponential decline with distance (Krebs 1985). Thus, we hypothesize that on a transect out from a single inoculation point one will at first observe exponentially declining density. In later years a broader shouldered density curve will appear - - due to dispersal from both the inoculation site and secondary sites. In the case of adjacent introduction sites, converging waves of dispersal will eventually meet to produce a uniform density distribution at a practical scale (>100m^2).

In the year of introduction (2001) our insects showed the expected exponentially declining distribution. Population distribution varied little among our four burned sites and from them to our single unburned site (Table 6, Appendix 2. Figure 1). A graph of the dispersal pattern across each of the five sites shows the expected concentration of individuals at the inoculation point, slight dispersal to two-four meters, and no colonists at six meters (Figure 4).

In the following year (2002), waves of dispersal from inoculation points began to fill interpoint space (burn sites 3 & 4) and essentially saturated the area at burn site 1 (Table 6, Figure 5). The fact that the densities observed at inoculation points in year two were lower than those observed at inoculation points the year before (2002) is considered below.

Table 6. Stem borer densities (#/0.1m^2) at increasing distances (0, 2, 4, 6m) from inoculum points. Measures were made by summing emergence holes and dead adults per quadrat in over-wintered stems, spring 2002 and 2003.

		Treatment											
		Burn										**No burn**	
Distance[1]		Site 1	*n*	Site 2	*n*	Site 3	*n*	Site 4	*n*	x, site 1-4	*N*	Site 3	*n*
				insect densities (#/o.1m^2)									
0	**mean**	**13.50**	8	**3.88**	4^a	**3.75**	8	**6.75**	8	**6.97**	28	**13.25**	8
		7.65		*10.56*		*9.02*		*7.03*					
2	**mean**	**0.50**	12	**0.43**	7^a	**0***	14	-		**0.47**	33	-	
		1.17		*1.60*									
4	**mean**	**0***	12	**0.50**	7^a	**0.67**	12	-		**0.59**	31	**0***	12
				1.87		*2.31*							
6	**mean**	-		-		**0***		-				-	
0	**mean**	**1.88**	8	**0***	8	**0.50**	8	**2.70**	8	**1.27**	32	**0***	
		1.89				*1.58*		*4.03*					
2	**mean**	**0.25**	12	**0.29**	14	**0.21**	14	**0.33**	12	**0.27**	52	**0.33**	12
		0.62		*0.73*		*0.80*		*1.15*					
4	**mean**	**0.42**	12	**0.93**	14	**0.08**	12	**0.33****	12	**0.44**	50	**0***	12
		0.90		*2.67*		*0.29*		*0.89*					
6	**mean**	**0.42**	12	**0.50**	4	**0***		**0.1****	10	**0.26**	26	**0.25**	
		1.44		*1.00*				*0.32*					

- Indicates no stems present.
* No insects present.
** All insects present were dead.

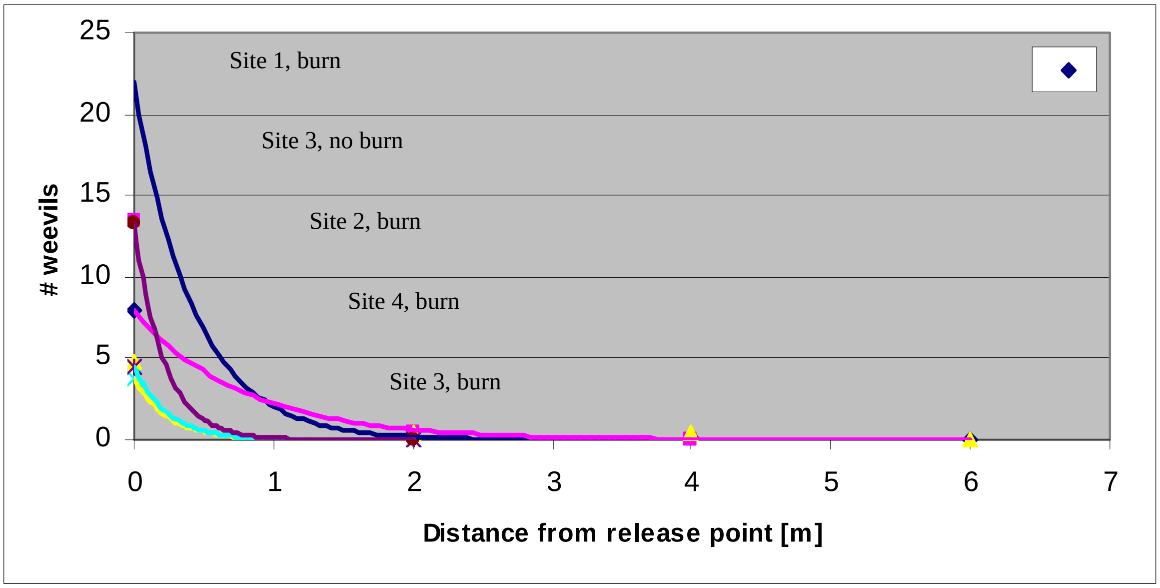

Figure 4. Weevil distribution 1 year post-introduction. (See Appendix B, Figure 1 for individual site distribution curves).

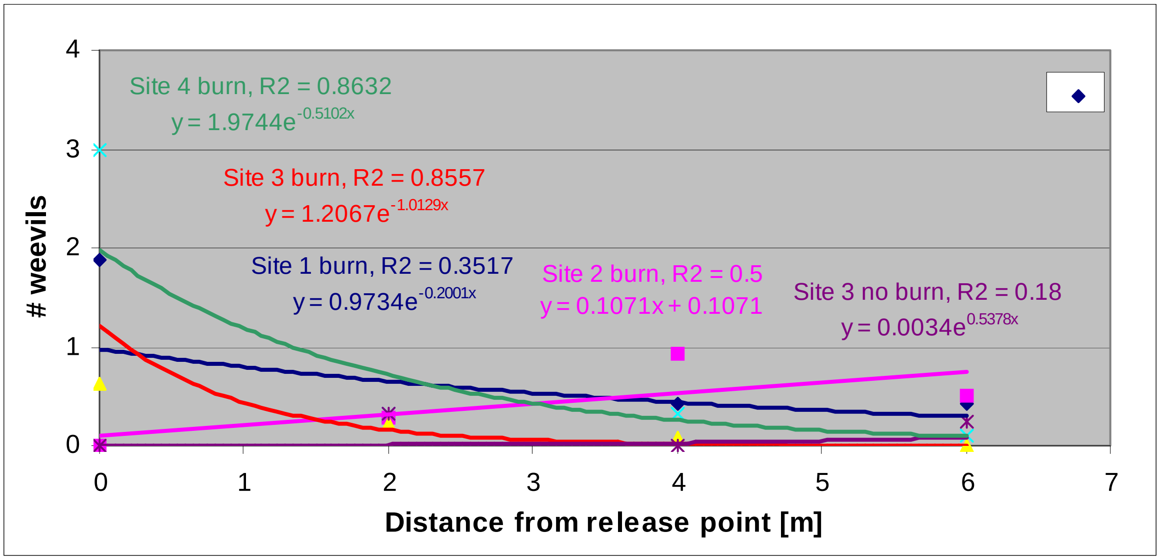

Figure 5. Weevil distribution 2 years post-introduction.

Mecinus densities in our plots were calculated. 1) In the first summer (2001) density at the inoculation point was measured directly by counting emergence holes plus dead adult weevils in each 0.1m^2 inoculation quadrat. The average across the eight inoculation points at each site is reported in Table 7. 2) First summer total-plot density was determined by calculating *Mecinus* numbers within six meters of each inoculation point, summing across the eight introduction points in each plot, and dividing by the plot area (17 x 34 m) (Table 7). The number of insects resulting from a single inoculation was calculated by plotting density against distance from the point, integrating under the curve, and rotating the radial measurement around the axis to account for dispersal in other directions and integrating under the resultant 'cone' (Figure 6). 3) Second summer density was calculated similarly at burned sites 1, 3, and 4. Where insect numbers no longer declined exponentially, burned site 2 and unburned site 3, we treated the distribution as uniform (Table 7, Figure 5). The latter estimate may be high - - to the extent that there may be unpopulated areas between the points. 4) We hypothesize that, if measured, fourth and fifth summer densities will be calculated as uniform distributions.

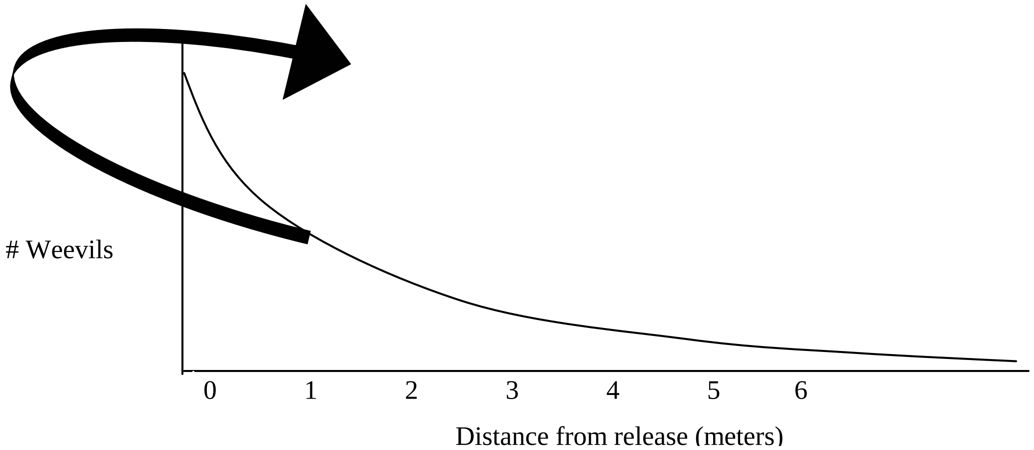

Figure 6. Diagram of calculation of *Mecinus janthinus* density by triangle/cone integration. Number of insects at increasing distance from inoculation point is plotted. Total number of insects resulting from one inoculation point is thus found by integrating under the number of insects vs. distance curve and rotating this surface around the axis and integrating under the resultant cone.

Weevil densities in the summer of introduction (2001, measured 2002) were 3.75-13.50/0.1m^2 at the introduction points (Table 6) and 5-18/m^2 in the 17 x 54 m plots (Table 7). Densities declined to 0-17/m^2 on the plots in 2002 (measured 2003) (Table 7). Three treatment plots were still filling in (2002, measured 2003) and two were more-or-less uniformly populated in the following summer (Table 7, 2002, measured 2003). Even uniformly filled sites may well have been less than saturated with only resource rich micro-sites filled. Samples in the summers of 2004 and 2005 would more likely estimate true carrying capacity, assuming that the toadflax resource won't have and survival of the *Mecinus* reproductive stock will be high enough to provide a strong inoculum.

Table 7. Estimates of *Mecinus janthinus* density. Comparison of hand fit formula with Excel exponential formula generated by Excel package. (See Appendix 2, Table 1).

		Regression equation				linear	circular		
		a	b	c	d	integral		#/plot	$\#/m^2$
	Site			[m]	[m]	N	N		
2001	**all sites**	6.90	1.38	0	4	5	125	1002	1.73
Excel-exp[1]	**1B**	**9.35**	**1.74**	**0**	**4**	**5**	**135**	**1081**	1.87
Hand fit[2]	*1B*	*12.78*	*1.49*	*0*	*4*	*9*	*215*	*1723*	2.98
Excel-exp	**2B**	**7.88**	**1.26**	**0**	**4**	**6**	**156**	**1246**	2.16
Hand fit	*2B*	*4.45*	*1.28*	*0*	*4*	*3*	*87*	*697*	1.21
Excel-exp	**3B**	**3.75**	**4.11**	**0**	**4**	**1**	**23**	**183**	0.32
Hand fit	*3B*	*3.96*	*1.55*	*0*	*4*	*3*	*64*	*512*	0.89
Excel-exp	**4B**	**4.50**	**4.21**	**0**	**4**	**1**	**27**	**215**	0.37
Hand fit	*4B*	*4.48*	*1.54*	*0*	*4*	*3*	*73*	*583*	1.01
Excel-exp	**3NB**	**13.25**	**4.75**	**0**	**4**	**3**	**70**	**561**	0.97
Hand fit	*3NB*	*13.56*	*1.63*	*0*	*4*	*8*	*208*	*1666*	2.88
2002									
Excel-exp	**1B**	**0.97**	**0.20**	**0**	**6**	**3**	**128**	**1025**	1.77
Excel-exp	**3B**	**1.21**	**1.01**	**0**	**6**	**1**	**45**	**358**	0.62
Excel-exp	**4B**	**1.97**	**0.51**	**0**	**6**	**4**	**139**	**1112**	1.92
Excel-exp	**3NB**	**0.00**	**0.54**	**0**	**6**	**0**	**0**	**2**	0.00
	2B[3]								

[1] Excel-exp = equation of the exponential line fit by Excel
[2] Hand fit = equation derived from the hand fit line.
[3] 2nd year 2B = due to high variance and lack of trend, a slopeless line at the average value was used. Mean # weevils/0.1m^2= 0.57, # weevils/m^2 = 5.7
[4] insects = $(a)(e^{-bx})$

<u>Field impact of fire on *Mecinus*.</u> Fire might affect *Mecinus* populations by killing insects, reducing vegetation cover, or by increasing/decreasing resource (toadflax) availability. Since we introduced the insects the summer after the fire we have no test of direct fire effects on *Mecinus*. Our unbalanced sample (four burned vs. one unburned plot) prevents rigorously contrasting insect establishment or over-wintering on burned with unburned sites. The lack of differences of survival rates on burned vs. unburned plots (63-83% vs. 58% in 2001-2002 and 54-76% vs. 67% in 2002-2003, Table 5) don’t

indicate either vegetation effects (due to shelter of complex vegetation on unburned sites) or forage effects (due to more vigorous growth of toadflax on burned than on unburned sites, Table 8).

Field impact of *Mecinus* on toadflax between site comparisons. First summer impact of *Mecinus* on toadflax in our treatment plots cannot have been significant because *Mecinus* occupied less than 1% of the area ((0.1m^2 x 8 inoculation points)/(17 x34 m)). Thus for 2001 we expect no significant difference in toadflax performance between insect treated/not treated plots across our eight sites - - and if we found a difference we would attribute it to vegetation/environmental differences among the plots. If insects do not contaminate control plots, comparison of toadflax performance on exposed and *Mecinus*-free plots (the four burned and one unburned plots) after *Mecinus* distribution becomes uniform (2003, 2005 and 2006) might show an impact on toadflax at the field scale.

Field impact of *Mecinus* on toadflax within site comparisons. Because within plot *Mecinus* densities differed in 2001 and 2002, plant performance can be compared across densities in environmentally identical plots at our four burned and one unburned sites. This could be done by ANOVA of low M*ecinus* density (2-6m) vs. high *Mecinus* density (0m) quadrats across 4-5 sites, by ANOVA across varying density level, or by regression of plant performance across density levels. Because *Mecinus* densities are essentially +/- we have applied the first method here.

Table 8. Response of toadflax to stem borer attack ((mean # emergence holes + dead adults)/quadrat)). Plant performance at the inoculation point (0) is compared with performance at 2-6m. The full data set is shown in Appendix 2.

			Burn									**No burn**								
Year	Distance		Site 1	*n*	Site 2	*n*	Site 3	*n*	Site 4	*n*	x, site 1-4	Site 1	*n*	Site 2	*n*	Site 3	*n*	Site 4	*n*	x, site 1-4
			Stem borer attack (mean # emerged + dead adults/quadrat)																	
2002	**0**	**mean**	**13.50**	*8*	**3.88**	*4*	**3.75**	*8*	**6.75**	*8*	**6.97**	-		-		**13.25**	8	-		
		stdev	*7.65*		*10.56*		*9.02*		*7.03*											
	2-6m	**mean**	**0.16**	*24*	**0.39**	*14*	**0.24**	*26*	**0***		**0.27**	-		-		*****		-		
		stdev	*0.69*		*1.58*		*1.39*									*0.00*				
2003	**0**	**mean**	**1.88**	*8*	**0.00**	*8*	**0.50**	*8*	**2.70**	*8*	**1.27**	-		-		*****		-		
		stdev	*1.89*				*1.58*		*4.03*											
	2-6m	**mean**	**0.35**	*36*	**0.58**	*32*	**0.12**	*26*	**0.26**	*34*	**0.33**	-		-		**0.19**	36	-		
		stdev	*1.01*		*1.82*		*0.55*		*0.85*							*0.62*				
			Stem density (#/0.1m2)																	
2001	0	**mean**	**1.75**	*8*	**2.00**	*8*	**1.88**	*8*	**4.13**	*8*	**2.44**	**2.63**	8	**0.88**	8	**1.25**	8	**1.63**	8	**1.59**
		stdev	*1.58*		*2.33*		*1.89*		*3.52*			*2.62*		*1.36*		*1.39*		*0.74*		
	2-6m	**mean**	**1.81**	*36*	**0.82**	*32*	**1.03**	*32*	**1.72**	*34*	**1.34**	**2.72**	36	**1.08**	36	**0.58**	36	**1.36**	36	**1.44**
		stdev	*1.97*		*1.37*		*1.68*		*1.95*			*2.96*		*1.95*		*1.00*		*1.35*		
2002	0	**mean**	**2.50**	*8*	**2.88**	*8*	**1.44**	*8*	**4.33**	*8*	**2.79**	-		-		**1.25**		-		
		stdev	*1.69*		*2.59*		*1.88*		*3.67*											
	2-6m	**mean**	**1.81**	*36*	**2.01**	*32*	**0.94**	*32*	**2.31**	*34*	**1.77**	-		-		**0.81**		-		
		stdev	*2.01*		*2.69*		*1.54*		*2.65*							*1.13*				
			Stem height (in)																	
2001	0	**mean**	**38.32**	*8*	**13.37**	*8*	**13.82**	*8*	**31.71**	*8*	**24.30**	**18.42**	8	**6.88**	8	**27.68**	8	**15.28**	8	**17.06**
		stdev	*26.22*		*12.21*		*12.07*		*38.28*			*12.22*		*9.77*		*23.18*		*7.31*		
	2-6m	**mean**	**41.32**	*36*	**6.53**	*32*	**9.78**	*32*	**10.45**	*34*	**17.02**	**15.09**	36	**9.84**	36	**18.91**	36	**13.72**	36	**14.39**
		stdev	*28.49*		*10.35*		*13.19*		*10.14*			*12.00*		*12.41*		*29.59*		*10.74*		
2002	0	**mean**	**19.32**	*8*	**13.21**	*8*	**14.97**	*8*	**12.86**	*8*	**15.09**	-		-		**10.96**	8	-		
		stdev	*8.65*		*9.73*		*15.47*		*11.38*							*7.18*				
	2-6m	**mean**	**14.03**	*36*	**12.53**	*32*	**10.48**	*32*	**11.15**	*34*	**12.05**	-		-		**7.24**	36	-		
		stdev	*11.44*		*10.22*		*14.38*		*10.96*							*8.92*				
			Branches per stem																	
2001	0	**mean**	**2.93**	*8*	**1.55**	*8*	**3.01**	*8*	**7.44**	*8*	**3.73**	**5.86**	8	**2.31**	8	**1.81**	8	**2.63**	8	**3.15**
		stdev	*2.66*		*1.59*		*2.79*		*2.99*			*4.79*		*2.71*		*2.12*		*2.00*		
	2-6m	**mean**	**2.42**	*36*	**0.72**	*32*	**1.64**	*32*	**2.74**	*34*	**1.88**	**2.39**	36	**2.38**	36	**1.16**	36	**2.21**	36	**2.04**
		stdev	*2.60*		*1.49*		*2.88*		*4.15*			*2.74*		*3.34*		*2.05*		*2.85*		
2002	0	**mean**	**1.33**	*8*	**0.14**	*8*	**2.79**	*8*	**3.07**	*8*	**1.83**	-		-		**1.19**	8	-		
		stdev	1.39		0.27		2.84		4.13							1.77				
	2-6m	**mean**	**1.51**	*36*	**0.80**	*32*	**1.08**	*32*	**2.21**	*34*	**1.40**	-		-		**0.90**	36	-		
		stdev	*1.96*		*1.68*		*1.67*		*2.70*							*1.81*				
			Seed capsules per stem																	
2001	0	**mean**	**8.46**	*8*	**7.56**	*8*	**7.26**	*8*	**18.63**	*8*	**10.48**	**6.45**	8	**4.59**	8	**7.22**	8	**4.56**	8	**5.71**
		stdev	*8.04*		*7.99*		*10.20*		*13.71*			*7.24*		*6.32*		*11.16*		*3.31*		
	2-6m	**mean**	**8.62**	*36*	**3.41**	*32*	**5.29**	*32*	**8.30**	*34*	**6.40**	**5.58**	36	**5.85**	36	**5.18**	36	**5.32**	36	**5.48**
		stdev	*10.89*		*7.81*		*11.90*		*12.93*			*6.56*		*9.75*		*10.72*		*6.24*		
2002	0	**mean**	**9.94**	*8*	**3.61**	*8*	**11.38**	*8*	**9.74**	*8*	**8.67**	-		-		**4.96**	8	-		
		stdev	*10.78*		*7.17*		*23.34*		*16.90*							*9.68*				
	2-6m	**mean**	**6.17**	*36*	**2.11**	*32*	**6.59**	*32*	**4.31**	*34*	**4.79**	-		-		**3.89**	36	-		
		stdev	*8.42*		*2.93*		*14.23*		*9.40*							*10.95*				

Mecinus 'treatments'.

In the year of introduction *Mecinus* density was much higher at release points than in adjacent points at 2, 4, or 6 m (Table 8). Inoculation point density averaged 3.75-13.5 insects/0.1m^2 on burned sites and 13.25 on the unburned site (Table 8). The average density at 2-6m from the introduction points was 0.27/0.1m^2, 0.38 times as many as the average density at the introduction points. At inoculation sites, densities were lower in the following year (2002, measured in 2003), averaging 1.27 per 0.1 m^2 on burned sites, and 0.00/0.1m^2 on unburned sites. Average *Mecinus* density on burned and unburned sites was 0.30/0.1 m^2. Since plant densities at inoculation points did not decline (Table 8) the drop in densities at inoculation points was not due to resource destruction (see below); it may have been due to "predation, climate, or plant condition". The density increase at distance was due to dispersal.

Tillering response.

Insect attack near inoculation points apparently stimulated compensatory tillering of toadflax on burned sites. All the end of the first post-burn introduction summer (2001) toadflax stems on burned plots average 2.44/0.1m^2 (82%) at inoculation points vs. 1.34 on nearby (2, 4, and 6m) insect-free quadrats (Table 8, $p = 0.003$). Compensatory tillering was much smaller (10%) on unburned sites, with 1.59/0.1m^2 at release points on burned sites vs. 1.44/0.1 m^2 on unburned sites. We speculate that, in contrast to toadflax on burned sites, toadflax plants on unburned sites were too stressed by native grass competition to muster the energy/material resources for strong compensatory growth.

The difference was maintained into the second post-burn, first post-inoculation year (2002). On burned sites, inoculation point densities were 158% ($2.79/0.1m^2$) of those on neighboring (2, 4, 6 m) points (x = 1.77%, Table 8, p = 0.034). On the single surviving unburned site inoculation point density was 154% ($1.25/0.1m^2$) of that on neighboring points ($0.81/0.1m^2$).

Individual responses.

Responses of other measures of toadflax vigor - - plant height, branching, and capsule number paralleled the tillering response. Due to normal allometric relationships they also paralleled each other.

Average plant heights in the first post-burn, post-inoculation summer (2001), on burned sites (reduced competition) were 24cm (40% greater) at inoculation points vs. 17cm on insect-free (2, 4, 6 m) sites (Table 8, p = 0.172). In the more competitive unburned vegetation, toadflax heights at inoculation points were 17cm (21% greater) vs. 14 cm at sites without insects (Table 8, p = 0.441). In the second year post-fire, post-inoculation we might expect the difference to diminish due to increased competition from recovering native vegetation and spread of insects into the insect-free (2, 4, 6 m) zone. In 2002, toadflax heights on burned plots average 15 cm at inoculation points vs. 12 cm on *Mecinus* low-density points. On the unburned site, plants at inoculation points were 11 cm vs. 7 cm at a distance (Table 8). Plant heights cannot be compared directly between plots because 2002 was drier than in 2001.

Branching supports resource acquisition (leaves and photosynthesis) and seed production (flowers and reproductive capsules/stem). In the first post-burn inoculation summer (2001), branch numbers per plant at inoculation points were 98% (3.73/0.1m^2) greater than those at adjacent insect-free (2, 4, 6 m) points (1.88/0.1m^2, Table 8, p = 0.003). On unburned sites, the branching response at inoculation points - - relative to adjacent points - - was almost significant (p = 0.086), but less (55%), presumably due to native grass competition (Table 8). In the second post-burn, post-inoculation year branching at inoculation points was still 31% of that at adjacent points. And on the surviving unburned site (#3) branching at inoculation points was still compensating - - similar to that seen on the burned site (33%).

Toadflax capacity to long-distance disperse is proportional to the numbers of seed produced - - and may thus be proportional to the number of capsules produced. In the first post-burn inoculation summer (2001), ‘competitively released’ toadflax plants (in burned plots) produced 64% (10.5/0.1m^2, Table 8) as many capsules per plot at inoculation points as at insect-free points (6.4/0.1m^2, Table 8, p = 0.058). While the increase in capsule production was 39% on unburned site 3 in 2001, it was 28% in 2002. Consistent with the model of reduced compensatory growth due to increasing post-burn competition from the surrounding vegetation.

CHAPTER 3

GARDEN EXPERIMENT

Introduction

Our field experiment showed that *Mecinus* established, survived two years, and at low densities (e.g. 3 to 13/0.1m^2, Table 8), induces compensatory growth in toadflax, i.e. increased density, height, number of branches, and greater number of seed capsules.

Since *Mecinus* densities of 1 to 20/m^2 (Table 7) have been observed and higher densities can be imagined, we sought to measure the impact of *Mecinus janthinus* at densities higher than were observed in the field. A garden experiment was completed in which toadflax responses (total, stem, leaf, and flower biomass) were compared among plants exposed to increasing numbers of *Mecinus* per plant, i.e. 0, 2, 4, 8, 16, and 32.

Methods

Our field experiment informs us about the impact of a short exposure of *Mecinus* at low densities on toadflax. Our garden experiment was intended to measure the short-term impact of *Mecinus* at higher densities. Without the years of observation originally planned, neither experiment records the effect of the chronic low-density exposure likely to occur in the field.

Toadflax plants were dug at our Coxcy Gulch field site (Table 2) just before bud break 19 May 2002 (Table 9). Due to relatively sandy soil the root systems remained astonishingly intact. They were transported to Bozeman, soaked in insecticide, fungicide and bleach, then potted less than 24 hours after digging (9 inch, ---liter pots) and acclimated under low stress greenhouse condition (19 May thru 8 June 2002). Before out-planting the plants were sorted, by approximate aboveground size, into ten homogenous groups (blocks).

Table 9. Calendar of events in the toadflax/*Mecinus* garden experiment.

Collect plants	May 20, 2002
Pot plants	May 20, 2002
Pot adapt plants	May 20 - June 8, 2002
Out-plant plants	June 8, 2002
Bag plants	June 8, 2002
Inoculate plants	June 15, 2002
Harvest plants	September 28-30, 2002
Dry plants	Sept. 30, 2002 -Jan. 3, 2003
Weigh plants	January 3 - 30, 2003

Two garden plots (10 x 10 ft.) at the USFS greenhouse on the MSU-Bozeman campus were cultivated and laid out for our experiment. The layout of each garden included five rows (blocks) of six sites (treatments) with rows separated by 55.45 cm and plants separated by 47 cm. A block of plants was planted, still in their perforated-bottom pots, into each row 8 June 2002. In the planting, large and small plant blocks were alternated. Plants were allowed to establish for almost three weeks before introducing *Mecinus* treatments.

Individual plants were caged to contain the insects they were being exposed to. The cages were nylon mesh bags (dimension) suspended over three heavy gage wire stakes. The mesh was white, fine, and a bit too heavy – it reduced sun and probably raised humidity. The cage's lower margin was buried and its top could be opened.

The cage and insect treatment ran from 15 June to 30 September 2002. The insects were collected near Grand Forks, British Columbia on 11 June 2002 by the B.C. Ministry of Forests, transported to the US Forestry Sciences Lab at MSU – Bozeman, and stored in a refrigerator for one day before treatment. The insects were counted into sixty Petri dishes (10 reps x 6 treatments) for dispersal. The treatments (0, 2, 4, 8, 16, 32 insects per caged plant) were applied, at random, to plants in each row (block). Late in the summer, some cages still contained adult weevils of the original inoculum.

The gardens were drip-line irrigated and cultivated June-September while the plants grew. The gardens were weed-contained rather than weed-free.

The plants were harvested in late September, before a heavy freeze, to allow for maximum plant growth and to allow time for maximum growth differences expected due to treatment effects, i.e. different numbers of second generation stem boring weevils (Table 10).

Stem-borer establishment in treated plants was assessed by splitting the stems in, late fall and recording numbers of adult weevils in their chambers.

Plant response to *Mecinus* treatments was assessed by measurements of biomass. Harvested plants were dried at 120^{o}F in the MSU Bozeman Plant Growth Center drying room. Each harvested plants was separated into stems, leaves, and flowering parts and each aggregated component was weighed. Because rain splattered soil was present on some leaves and flowers these organs were ashed and the ash weight was subtracted from initial dry weights to provide dependable ash-free weights.

Results and discussion

Stem-borer establishment.

Stem-borer establishment generally increased with the number of adults applied (Table 10). With no inoculation there was no establishment. With an inoculation of two insects per plant, establishment was slight (40%, Table 10). With inoculations of four or more establishment was 90% or more. The number of larvae establishing increased ‘linearly’ with the size of the inoculum up through sixteen per plant (Table 10, Figure). And large plants (L1-5), listed first in Table 10, supported more larvae than smaller ones (L6-10).

Stem-borer impact. At summer’s end growth was documented as relative size - - % of the largest individual within each block - - and is subject to variance due to observation of aboveground parts only. Final plant size was measured as total aboveground, stem, leaf, and floral biomass. And expressed in three ways. 1) % of the cases in which the treatment yielded the largest plants – expected to be high at low inoculation rates. 2) % of the cases in which the treatment yielded the smallest plants - - expected to be high at high inoculation rates. 3) Mean relative yield, that is averaged, at an insect treatment, across blocks at each treatment level (# insects).

Plant size was expected to diminish with exposure to (attack by) increasing numbers of weevils. Due to allometric relations, we expected the results of all four measures to parallel each other. Thus, Table 11 summarizes all plant responses to the density series simultaneously.

Table 10. Numbers of insects established in toadflax stems in each block as a result of *Mecinus* treatment (0-32 stem-borer innoculum). Plants in a block (L1-L10) were matched by aboveground appearance; plant size declines from block L1-L10.

		Values as actual counts per plant					
Block	Rank	0 bugs	2 bugs	4 bugs	8 bugs	16 bugs	32 bugs
1A	L1	0	25	67	14	173	206
2A	L6	0	0	0	11	0	32
3A	L2	0	0	27	96	178	136
4A	L10	0	0	11	20	24	44
5A	L3	0	0	12	56	92	95
1B hypo[1]	**L9**	**0**	**1**	**9**	**0**	**39**	**43**
1B record[1]	L9	0	43	39	0	9	1
2B	L4	0	1	10	41	98	149
3B	L8	0	0	2	6	0	46
4B	L5	0	0	78	76	117	31
5B	L7	0	31	3	83	114	66
	mean	0	5.80	21.90	36.64	83.50	84.80
	st dev	0	16.45	27.89	35.29	68.49	64.63

		Relative values, percent of the blocks largest value					
Block	Rank	0 bugs	2 bugs	4 bugs	8 bugs	16 bugs	32 bugs
1A	L1	0	12	33	7	84	100
3A	L2	0	0	15	54	100	76
5A	L3	0	0	13	59	97	100
2B	L4	0	1	7	28	66	100
4B	L5	0	0	67	65	100	26
2A	L6	0	0	0	34	0	100
5B	L7	0	27	3	73	100	58
3B	L8	0	0	4	13	0	100
1B hypo[1]	**L9**	**0**	**2**	**21**	**0**	**91**	**100**
1B record[1]	L9	0	100	91	0	21	2
4A	L10	0	0	25	45	55	100
	mean	0	14.00	26.00	38.00	62.00	76.00
	stdev	0	33.00	31.00	24.00	42.00	38.00

[1] Block 1B appears to be misrecorded. Recorded values appear as 1B record. Hypothetical values appear as 1B hypo. 1B record was used in calculating the summary statistics.

Table 11. Toadflax biomass compared among six *Mecinus* inoculation density treatments (0-32 insects). (n always = 10) See tables 12-15.

Exposure (insects/plant)	0	2	4	8	16	32
Probability % of largest plant in block[1]						
Aboveground mass	20	**40**	**40**	-	-	-
Stem mass	10	**30**	**40**	20	10	-
Leaf mass	10	**60**	10	0	10	10
Flower mass	**30**	**30**	**30**	0	10	0
Probability % of smallest plant in block[1]						
Aboveground mass	10	10	10	-	**40**	**40**
Stem mass	10	20	10	-	20	**40**
Leaf mass	-	10	**-**	-	**30**	**60**
Flower mass	-	-	30	20	**40**	**70**
mean percent of the maximum in block[1]						
Aboveground mass	**76**	**76**	**76**	70	60	51
Stem mass	72	**75**	**75**	74	62	57
Leaf mass	55	**79**	58	52	47	46
Flower mass	6**0**	**55**	**50**	33	33	20

[1] Percentages sum to slightly more than 100% when there are tie values.

Plants with two insects were largest (or tied for largest) for aboveground biomass, leaf mass, and flower mass. Plants exposed to four insects were largest for total aboveground biomass, stem, and flowers. Plants exposed to 2-4 insects were more likely to be larger than those exposed to no insects, thus showing again toadflax's compensatory response to a low-density *Mecinus* attack (<8 weevils/plant).

While plants exposed to 0-8 insects were occasionally the smallest in their blocks, plants with sixteen insects were smallest in 20-40% of the cases and plants exposed to thirty-two insects were smallest in 40-70% of cases. It appears, then, that toadflax has a limited capacity to compensate for *Mecinus* attack: short term stimulation appears when there are fewer than eight 'attackers' per plant and inhibition occurs when there are more than eight ‘attackers’ per plant.

The effect of density on toadflax’s average relative size provides a quantitative estimate of the short-term impact of *Mecinus* on the weed. Plants with two insects averaged 75-79% - - depending on the character observed - -of the largest. Plants with zero or four insects were near ties (Table 11). Total aboveground production of plants exposed to sixteen and thirty-two insects was 60 and 51%, that is, 80% and 68% as great as at the low impact densities (0-4 insects per plant).

Flower and leaf mass seem to be more sensitive to stem borer attack than stem mass or total aboveground biomass. This reduction is especially apparent in the mean biomass and smallest plant data.

To evaluate the reduction in vegetative (and floral) growth occurring with harsher insect treatments/insect infection we tested the significance of variation in ‘mean percent of the maximum’ across the treatments with ANOVA. Total biomass, i.e. vegetative growth, fell with increasing attack rate ($p = 0.06$, Table 12, Figure 7), i.e. with the 32 insect treatment reducing growth more than the 2-4 insect treatment. The trend is parallel, but less significant, for stem (36%, Table 13, Figure 7, $p = 0.36$) and leaf (50%, Table 14, Figure 7, $p = 0.5$) biomasses. The marginal significance of vegetative effects may have been due to excessive irrigation or to variance introduced in management of the experiment. Regarding possible excess irrigation, several workers believe that stem borer damage to the vascular system has a smaller impact when water is plentiful - - and a greater impact in sites/seasons when water is scarce (refs). Regarding variance due to management, watering might have been more even, weeds might have been less present, and suspicious data recorded in one block might have been double checked.

While both vegetative and floral growth were reduced by heavy attack rates, the reduction in flowering was stronger. Flower weights trended down with very significant reduction by 16-32 insects (Table 15, Figure 7, $p = 0.008$). The flowering response may be especially sensitive because flowers are borne high on stems (with a high potential for interruption of water delivery by stem borers) and flowering occurs later in the summer (when good delivery is important because water availability is least).

Table 12. Comparison of toadflax individual weights (total biomass) when subjected to six *Mecinus* attack rates (0-32). Plants in a block (L1-L10) were matched by aboveground appearance; plant size declines from L1 to L10.

Values as actual counts

Block	Rank	0 bugs	2 bugs	4 bugs	8 bugs	16 bugs	32 bugs
1A	L1	47.00	45.33	46.57	34.65	30.98	34.03
2A	L6	4.92	12.18	2.61	4.41	0.72	0.75
3A	L2	28.15	33.91	22.09	28.18	26.41	19.01
4A	L10	7.05	5.69	9.91	3.04	2.72	4.78
5A	L3	10.30	27.93	12.70	20.17	16.91	17.16
1B	L9	5.06	4.60	8.02	6.06	4.58	3.49
2B	L4	39.20	34.95	55.69	41.22	50.32	16.35
3B	L8	13.59	2.30	14.28	9.50	8.27	5.39
4B	L5	23.28	16.15	17.56	21.59	15.86	17.27
5B	L7	8.25	8.46	4.88	7.79	7.56	6.73
	mean	18.68	19.15	19.43	17.66	16.43	12.50

Relative values, percent of the blocks largest value

Block	Rank	0 bugs	2 bugs	4 bugs	8 bugs	16 bugs	32 bugs
1A	L1	1.00	0.96	0.99	0.74	0.66	0.72
3A	L2	0.83	1.00	0.65	0.83	0.78	0.56
5A	L3	0.37	1.00	0.45	0.72	0.61	0.61
2B	L4	0.70	0.63	1.00	0.74	0.90	0.29
4B	L5	1.00	0.69	0.75	0.93	0.68	0.74
2A	L6	0.40	1.00	0.21	0.36	0.06	0.06
5B	L7	0.98	1.00	0.58	0.92	0.89	0.80
3B	L8	0.95	0.16	1.00	0.67	0.58	0.38
1B	L9	0.63	0.57	1.00	0.76	0.57	0.44
4A	L10	0.71	0.57	1.00	0.31	0.27	0.48
	mean	0.76	0.76	0.76	0.70	0.60	0.51
	stdev	0.24	0.28	0.28	0.21	0.26	0.23

Table 13. Comparison of toadflax stem weights when subjected to six *Mecinus* attack rates (0-32). Plants in a block (L1-L10) were matched by aboveground appearance; plant size declines from L1 to L10.

Values as actual counts

Block	Rank	0 weevils	2 weevils	4 weevils	8 weevils	16 weevils	32 weevils
1A	L1	18.30	26.20	28.14	20.11	17.68	21.02
2A	L6	3.38	4.94	1.85	2.67	0.43	0.52
3A	L2	18.43	21.30	13.55	15.84	15.77	11.87
4A	L10	2.97	3.81	5.18	2.40	1.88	3.60
5A	L3	5.30	13.37	7.37	13.38	9.75	12.88
1B	L9	2.82	3.10	4.42	2.90	2.59	2.37
2B	L4	23.08	16.32	22.48	23.70	27.41	10.14
3B	L8	7.01	1.26	9.77	5.58	5.38	3.44
4B	L5	12.44	7.86	11.69	15.10	9.90	10.30
5B	L7	6.06	5.18	2.30	5.01	5.23	4.25
	mean	9.98	10.33	10.68	10.67	9.60	8.04

Relative values, percent of the blocks largest value

Block	Rank	0 weevils	2 weevils	4 weevils	8 weevils	16 weevils	32 weevils
1A	L1	0.65	0.93	1.00	0.71	0.63	0.75
2A	L6	0.68	1.00	0.37	0.54	0.09	0.11
3A	L2	0.87	1.00	0.64	0.74	0.74	0.56
4A	L10	0.57	0.74	1.00	0.46	0.36	0.69
5A	L3	0.40	1.00	0.55	1.00	0.73	0.96
1B	L9	0.64	0.70	1.00	0.66	0.59	0.54
2B	L4	0.84	0.60	0.82	0.86	1.00	0.37
3B	L8	0.72	0.13	1.00	0.57	0.55	0.35
4B	L5	0.82	0.52	0.77	1.00	0.66	0.68
5B	L7	1.00	0.85	0.38	0.83	0.86	0.70
	mean	0.72	0.75	0.75	0.74	0.62	0.57
	st dev	0.17	0.28	0.26	0.19	0.26	0.24

Table 14. Comparison of toadflax leaf weights when subjected to six *Mecinus* attack rates (0-32). Plants in a block (L1-L10) were matched by aboveground appearance; plant size declines from L1 to L10.

		Values as actual counts					
Block	Rank	0 bugs	2 bugs	4 bugs	8 bugs	16 bugs	32 bugs
1A	L1	15.61	12.99	15.10	9.56	8.09	12.01
2A	L6	1.25	4.45	0.76	1.74	0.29	0.23
3A	L2	7.92	11.26	7.80	10.24	7.65	6.13
4A	L10	1.80	1.10	1.88	0.64	0.71	1.18
5A	L3	2.75	8.94	3.30	5.39	5.08	3.74
1B	L9	1.50	1.15	2.05	2.81	1.99	1.12
2B	L4	9.17	10.08	17.63	11.36	18.69	4.74
3B	L8	4.51	0.91	2.86	3.64	2.89	1.95
4B	L5	4.72	5.78	4.77	4.63	4.54	6.69
5B	L7	1.98	2.03	2.44	1.67	1.55	2.38
	mean	5.12	5.87	5.86	5.17	5.15	4.02

		Relative values, percent of the blocks largest value					
Block	Rank	0 bugs	2 bugs	4 bugs	8 bugs	16 bugs	32 bugs
1A	L1	1.00	0.83	0.97	0.61	0.52	0.77
3A	L2	0.70	1.00	0.69	0.91	0.68	0.54
5A	L3	0.31	1.00	0.37	0.60	0.57	0.42
2B	L4	0.49	0.54	0.94	0.61	1.00	0.25
4B	L5	0.71	0.86	0.71	0.69	0.68	1.00
2A	L6	0.28	1.00	0.17	0.39	0.07	0.05
5B	L7	0.81	0.83	1.00	0.68	0.64	0.98
3B	L8	1.00	0.20	0.63	0.81	0.64	0.43
1B	L9	0.53	0.41	0.73	1.00	0.71	0.40
4A	L10	0.96	0.59	1.00	0.34	0.38	0.63
	mean	0.68	0.73	0.72	0.66	0.59	0.55
	st dev	0.27	0.28	0.28	0.21	0.24	0.30

Table 15. Comparison of toadflax flower weights when subjected to six *Mecinus* attack rates (0-32). Plants in a block (L1-L10) were matched by aboveground appearance; plant size declines from L1 to L10.

Values as actual counts

Block	Rank	0 bugs	2 bugs	4 bugs	8 bugs	16 bugs	32 bugs
1A	L1	12.60	6.14	3.33	4.98	5.21	1.00
2A	L6	0.29	2.79	0.00	0.00	0.00	0.00
3A	L2	1.80	1.35	0.74	2.10	2.99	1.01
4A	L10	2.28	0.78	2.85	0.00	0.13	0.00
5A	L3	2.25	5.62	2.03	1.40	2.08	0.54
1B	L9	0.74	0.35	1.55	0.35	0.00	0.00
2B	L4	6.95	8.55	15.58	6.16	4.22	1.47
3B	L8	2.07	0.13	1.65	0.28	0.00	0.00
4B	L5	6.12	2.51	1.10	1.86	1.42	0.28
5B	L7	0.21	1.25	0.14	1.11	0.78	0.10
	mean	3.53	2.95	2.90	1.82	1.68	0.44

Relative values, percent of the blocks largest value

Block	Rank	0 bugs	2 bugs	4 bugs	8 bugs	16 bugs	32 bugs
1A	L1	1.00	0.49	0.26	0.40	0.41	0.08
3A	L2	0.60	0.45	0.25	0.70	1.00	0.34
5A	L3	0.40	1.00	0.36	0.25	0.37	0.10
2B	L4	0.45	0.55	1.00	0.40	0.27	0.09
4B	L5	1.00	0.41	0.18	0.30	0.23	0.05
2A	L6	0.10	1.00	0.00	0.00	0.00	0.00
5B	L7	0.17	1.00	0.11	0.89	0.62	0.08
3B	L8	1.00	0.06	0.80	0.14	0.00	0.00
1B	L9	0.48	0.23	1.00	0.23	0.00	0.00
4A	L10	0.80	0.27	1.00	0.00	0.05	0.00
	mean	0.60	0.55	0.50	0.33	0.30	0.07
	st dev	0.34	0.34	0.41	0.29	0.33	0.10

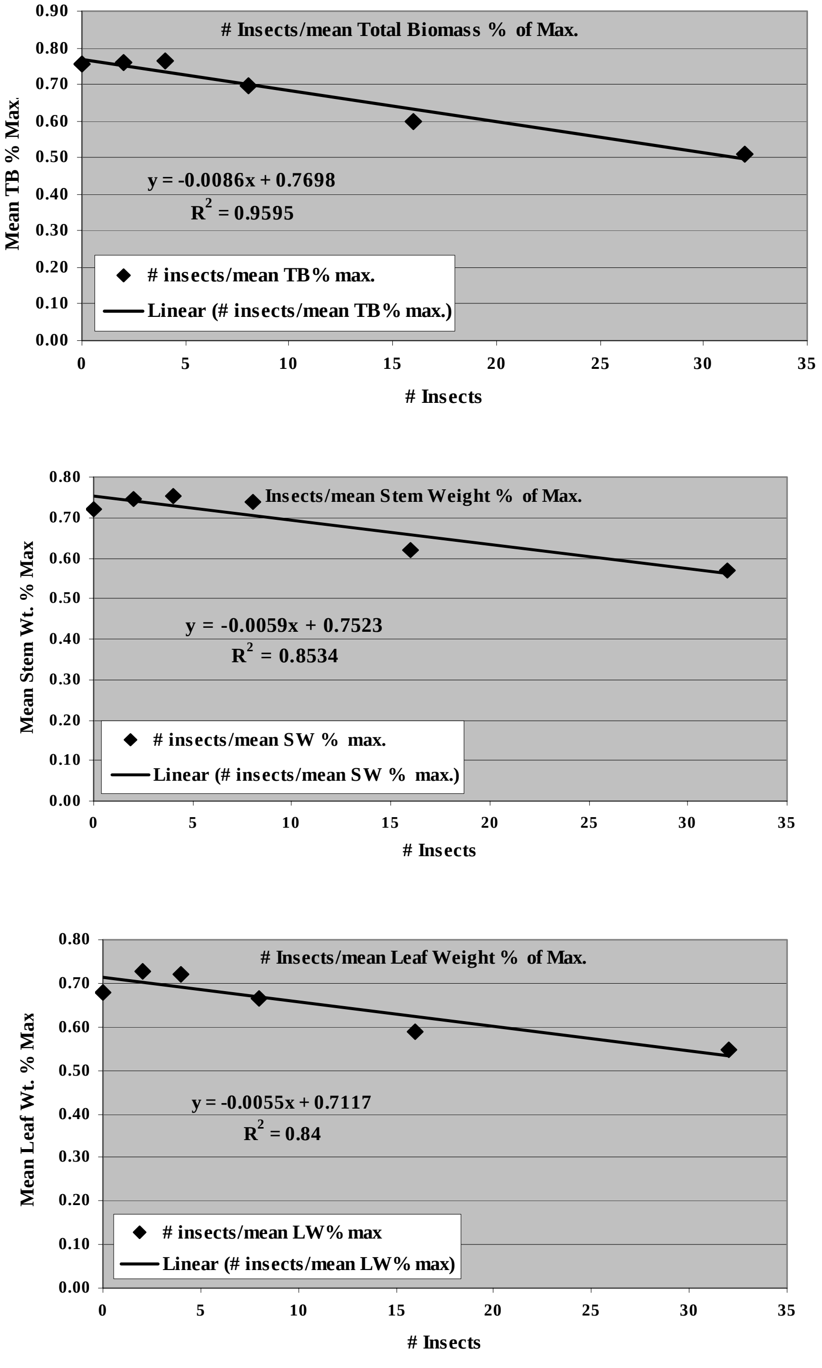

Figure 7. Plant biomass response to *Mecinus* treatments. Plant biomass (total, stem, leaf) falls with increasing insect numbers. At low densities biomass may increase with an insignificant attack rate. Stem-borer numbers may determine biomass or may be determined by biomass.

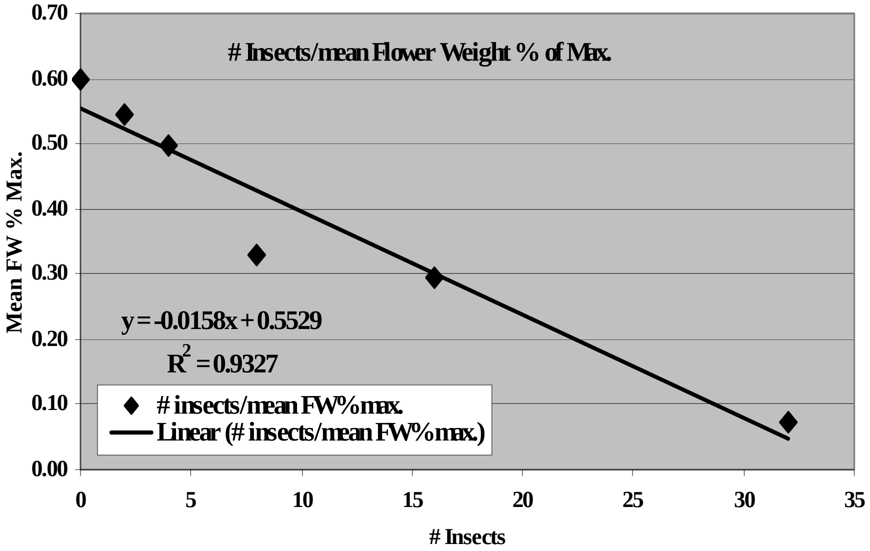

Figure 8. Flower biomass response to *Mecinus* treatments. Flower biomass declines strongly with increasing insect numbers. The decline in flower numbers is likely due to reduction of carbohydrate/water resources to the flowers.

CHAPTER 4

CONCLUSION

Toadflax is a noxious weed of Montana. It establishes in the foothills zone of western Montana especially in the *Agropyron spicatum* (Mueggler 1980) and *Pinus ponderosa*/ *Agropyron spicatum* (Pfister 1977) environmental types.

On our eight field sites, in this environmental zone, toadflax grew better on burned than unburned sites, probably because it was less impacted by fire than the grassy vegetation it was invading, probably because fire gave this storage roots plant a competitive advantage over the shallow/diffuse rooted grasses.

Mecinus janthinus, a stem-boring insect reputed to control toadflax, was introduced on half of each field site. We saw it survive for two years, increase in the first year, and spread (2-6 m/yr). Rates of survival and spread may have been related to elevation, snow cover, or burn intensity.

Comparison of intermingled invaded and insect-free quadrats shows a stimulation of plant performance (stem density, height, branching, and capsule production) by *Mecinus*. Since others have reported control of toadflax by *Mecinus*, we speculate that the insect attack is damaging, that plants show compensatory growth, and that, as ‘compensatory growth’ exhausts their root reserves, the plants will eventually be controlled.

The compensatory growth observed in the field was induced by attack rates of 3-4.5 insects per stem. In a garden experiment we exposed caged plants to insects at densities ranging from 0-32 *Mecinus* per plant (mpp). Stem-borer establishment was proportional to inoculum size. At low attack densities (0-4 mpp) plants usually produced as much biomass or more than plants that were not exposed. At high rates (16-32 mpp) vegetative growth declined. Flower production fell linearly with increasing exposure/ attack. Flower production may be more sensitive than vegetation production both because all of flowering production was initiated after insect establishment (some vegetative growth occurred before inoculation) and because flowers are borne high on stems, where stem borers will have maximal impact on transport of resources to them.

In the garden experiment we also observed that larger plants were more heavily infected than smaller plants, perhaps because they supported multiple individuals or because the stems of the smaller plants could not support complete larval development (Jeanneret and Schroeder 1992). In this case the effect was probably not due to the discretion of the egg-layer (because mothers caged with plants could not choose among larger and smaller plants) and the weevil tends to be indiscriminate about stem size when ovipositing (Jeaneret and Schroeder 1992), though mothers might conceivably lay eggs in proportion to stem size to prevent competition among their offspring. In any case, this might select against the most aggressive plants either in ecological or evolutionary time.

APPENDICES

APPENDIX A

EFFECT OF DISTURBANCE ON COMPETITION BETWEEN *AGROPYRONSPICATUM* GRASSLAND AND *LINARIA DALMATICA*

APPENDIX A

Effect of Disturbance on Competition Between *Agropyron spicatum* Grassland and *Linaria dalmatica*

T. Weaver and A. Anthony

Our primary task was to observe the survival, spread, and impact of *Mecinus janthinus* on *Linaria dalmatica*; two experiments dealt directly with this question. The following (third) experiment was used to observe the effects of other disturbances on the competitive balance between toadflax and *Agropyron spicatum* grassland vegetation.

The study site lay in an *Agropyron spicatum/Pinus ponderosa* environmental type invaded by clonal toadflax. The site was located on the toe of a south-facing slope in the foothills of the Big Belt Mountains east of Helena on York Road, approximately 1.5 miles east of the York Bar.

Four treatments were selected to simulate diverse disturbance types. They were undisturbed, moderate one-time grazing, burning, and harrowing. Grazing was simulated with an early summer harvest of all herbage in a 1.5 x 1.5 m plot and sampled in the central 1 m2 of that plot. Burning was simulated by ‘flame throwing’ a 1.5 x 1.5 plot surrounded by a portable galvanized iron barrier and sampling vegetation in the internal 1 m2. Harrowing was simulated by vigorously raking a 1.5 x 1.5 plot with a hand cultivator and sampled in the central 1 m^2. The unsampled border partially compensates for edge effect.

To compare the effects of these treatments on sites variously occupied by *Linaria*, we applied them to sites with three densities on radii of established toadflax clones. One stratum investigated was at the high density center of a toadflax clone. The second was at clone edge and always contained 1-3 shoots on the quadrat's clone side; the objective was to determine whether disturbance favors toadflax invasion of native *Agropyron* vegetation. The third stratum was toadflax-free vegetation two meters out from the slightly invaded quadrat; its objective was to determine whether disturbance favors establishment from seed-based long distance dispersal.

Basic plant response to the treatments was recorded before treatment and should have been recorded annually or semi-annually for the 2-4 more years we expected the project to continue. Base vegetation characterization included cover of grasses and forbs and the number and height of toadflax stems in each plot (i.e., 4 treatments x 3 toadflax infection levels x 12 reps). We expected to analyze the data, by response, with straightforward ANOVAs.

Field installation of this experiment involved the location of a large clone, choosing a segment that was edaphically homogeneous and isolated from tree roots or shade, and installing the four treatments on four parallel radii. Twelve reps were installed. Pre-sampling was finished on November 4, 2001. Fire treatments were conducted, with the help of Helena foresters, on November 6, 2001. The experiment was abruptly ended when the plots were herbicided by an apologetic USFS weed control crew.

APPENDIX B

ESTIMATES OF *MECINUS* DENSITY

APPENDIX B

Table 1. Estimates of *Mecinus* density[1] at five field sites. Number of insects in plot was calculated by finding insects present within six meters of each inoculation point and multiplying by eight for the 8 points in each plot.

Year	**Site[2]**	**Formula[3]**	**R^2**	**Under curve[4]**	**Under Rotated curve[5]**
2002					
	1 burn	$y = 12.78e^{-1.49x}$	0.97	9	215
	2 burn	$y = 4.45e^{-1.28x}$	0.94	3	87
	3 burn	$y = 3.96e^{-1.55x}$	0.9	3	64
	4 burn	$y = 4.48e^{-1.54x}$	0.88	3	73
	3 non-burn	$y = 13.56e^{-1.63x}$	0.99	8	208
2003					
	1 burn	$y = 0.97e^{-0.20x}$	0.35	3	128
	2 burn	$y = 0.11x+0.11$	0.5	3	84
	3 burn	$y = 1.21e^{-1.01x}$	0.86	1	45
	4 burn	$y = 1.97e^{-0.51x}$	0.86	4	139
	3 non-burn	$y = 0.003e^{-0.54x}$	0.18	0	0

[1] *Mecinus* density = emergence holes + dead adults/quadrat.

[2] Sites = site number and treatment.

[3] Formula for “hand-fit” curve of number of insects vs. distance from inoculation points with its R^2.

[4] Area under the “hand fit” curve.

[5] Area under the conical formed by rotating fit curve around the axis.

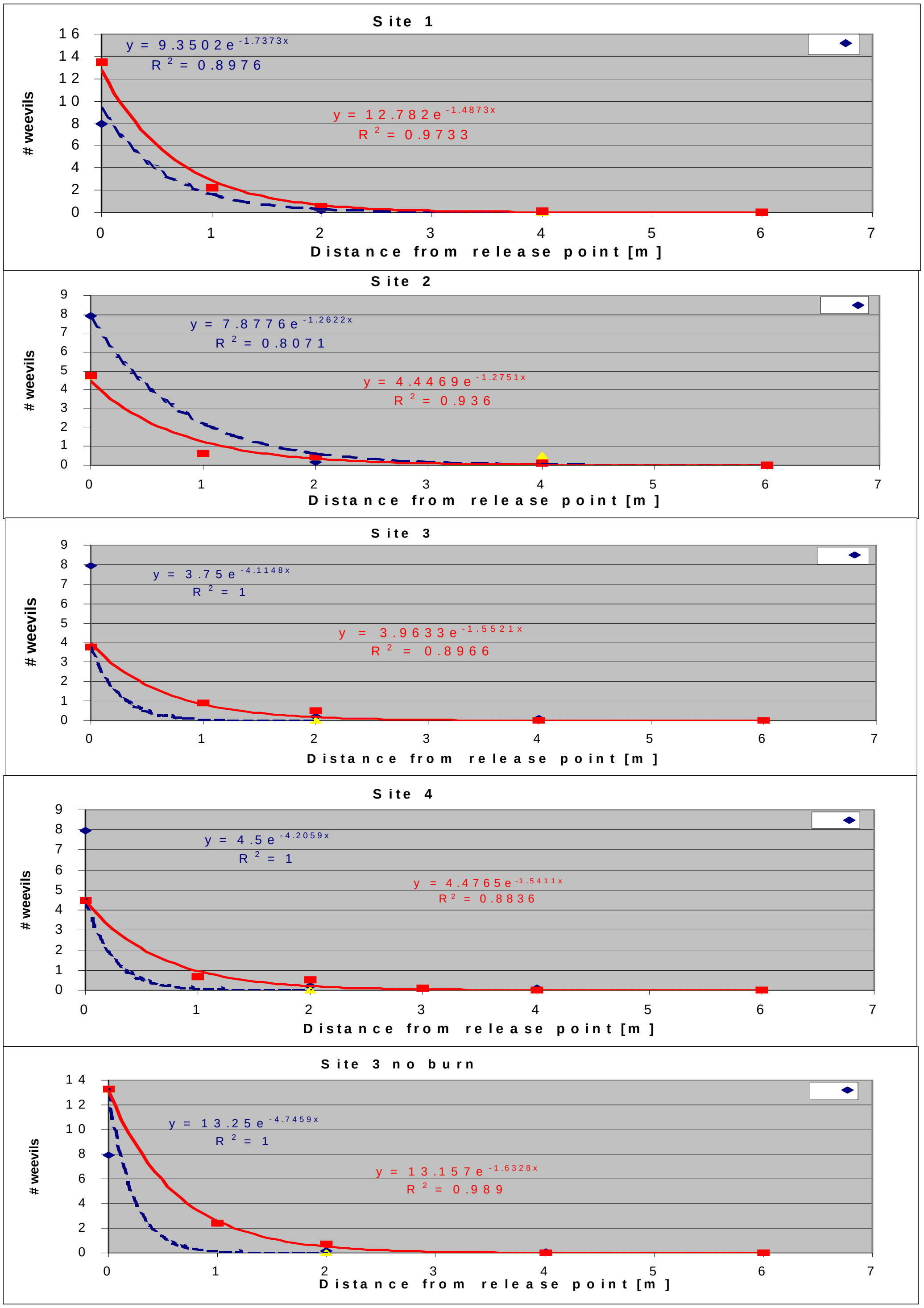

Figure 1. Autumn 2001 *Mecinus* density at 0, 2, 4, and 6 meters from inoculation points. Hand fit (solid line), Excel exponential fit (dashed line).

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