Effects of stress inducing factors on musk thistle (Carduus nutans L.) including--grass competition, Rhinocyllus conicus Froel., terminal flower loss, and insecticides
by Daniel Robert Corr

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology
Montana State University

Abstract:

Musk thistle (Carduus nutans L.) is a common colonizer of overgrazed pastures within the Gallatin Valley despite the success of chemical and biological control measures. Research was undertaken to evaluate the thistle's response to relieved grazing and other stress inducing factors in 1985 and 1986.

Four individual sites within the Gallatin Valley were chosen because they had been continually overgrazed and had high levels of musk thistle infestation. Areas of approximately 1000 m2 were fenced to exclude grazing at each site. Individual plants were tagged and monitored both inside and outside these enclosures. Thistle damage by Rhinocyllus conicus Froel. increased as a result of relieved grazing. The types of seed heads attacked by the weevil was dependant upon thistle growth as affected by rainfall and temperature. During drier years (1985) thistles responded to increased plant competition by concentrating energy reserves within terminal and secondary seed heads. When rainfall was more plentiful (1986) stressed thistles produced more but smaller tertiary seed heads.

The major effect of relieved grazing on musk thistle was to reduce seedling numbers and eliminate microsites needed to promote rosette establishment.. Large musk thistles dropped more seeds to their base and rosettes preferred to establish around small-canopied adults.

A substantial number of tagged, field grown thistles lost their terminal seed heads during the summer of 1985. These thistles had significantly lower growth and reproduction especially under conditions of relieved grazing. Thistles grown in the greenhouse which lost their terminal flowers after full bloom had an increase in lateral branch production.

The insecticide, aldicarb, was applied to individual field grown thistles in an attempt to exclude weevils and. isolate the effects of plant competition. To assess the effects of insecticides on thistle growth and reproduction, thistle rosettes were collected in the field, potted, and placed in the greenhouse. Thistles were placed within blocks and divided into the following treatments: 1) control, 2) low aldicarb, 3) high aldicarb; 4) malathion, 5) low aldicarb plus malathion. Thistle growth was monitored and thistles were harvested and separated to determine vegetative and reproductive biomass.

Aldicarb application at recommended dosages produced no significant effects. Synergistic effects caused by the combination of aldicarb and malathion were significant, enhancing the growth and reproduction of musk thistle.

EFFECTS OF STRESS INDUCING FACTORS ON MUSK THISTLE (*CARDUUS NUTANS* L.) INCLUDING: GRASS COMPETITION, *RHINOCYLLUS CONICUS* FROEL., TERMINAL FLOWER LOSS, AND INSECTICIDES

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

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CHAPTER 1

LITERATURE REVIEW

Introduction

Carduus nutans L., commonly called musk thistle, is a spiny, unpalatable weed which has become widely established on western ranges. The thistle is either a winter annual or biennial and is found in overgrazed pastures, disturbed areas, and all types of land except deserts, dense forests, and newly cultivated lands (Rees, 1982). It is a prolific seed producer and can spread into both native ranges and irrigated pastures (Hull and Evans, 1973). A vigorous competitor, it reduces yields of other pasture species by competing for light, water, and nutrients (Boldt, 1979).

Musk thistle, like most weedy species of the genera Carduus, Cirsium, and Silybum, probably originated in southern Europe since so many endemic species are found there (Kasmi, 1964). It becomes economically important when introduced into new areas of similar climate that lack its original compliment of natural enemies (Schroeder, 1980).

This plant was introduced into the United States at least 100 years ago, but was not reported as a weed until the early 1940's (McCarty, 1978). Its earliest recorded appearance was in the state of Pennsylvania (Stuckey and Forsyth, 1971). At least 40 of the adjacent 48 states have recorded its presence, and 12% of these states rate their infestations as economically important (Dunn, 1976; Boldt and Kok, 1982). Harris (1984) observed that musk thistle densities of

150,000/ha (15/m^2) were sufficient to totally eliminate cattle grazing within a pasture.

A few endophagous insects, native to North America, are associated with musk thistle (e.g. _Papaipema nebris_ Guenee, _Platyptilia carduidactyla_ Riley, and _Homoeosoma ellectellum_ Hulst). However, these lepidopteran insects have been rarely sampled and are therefore considered transient species which are of little help in controlling the thistle (Morihara and Balsbaugh, 1976).

The growth and phenology of musk thistle is strongly influenced by environmental conditions. Thistles transplanted into pastures which had been denuded by herbicides had enhanced growth rates (Edmonds and Popay, 1983). North American thistles demonstrate a wide range of phenotypic plasticity having winter annual as well as spring and autumn biennial life cycles (Lee and Hamrick, 1983). Early autumn germination and establishment is necessary for winter annual behavior while late autumn or spring germination causes biennial cycling. In New Zealand, where annual cycling is common for musk thistle (Popay, et al., 1979), good rosette establishment is the key to winter annual cycling (Popay and Thompson, 1979). This type of life cycle was most prevalent when the thistle experienced low levels of competition in sparse vegetation (Popay and Thompson, 1980).

Methods of Musk Thistle Control

The use of the herbicide (2,4-dichlorophenoxy) acetic acid alkanolamine was the traditional chemical method of controlling musk thistle (Roeth, 1980). This herbicide was found to have its greatest effect when applied during the spring to pre-bolting rosettes (Roeth, 1980). Rotation of this herbicide with 3,6-dichloropicolinic acid was reported to be the most effective method for long term chemical control but the natural reoccupation of treated sites by perennial grasses was extremely slow (Reece, 1983). Applications of ammonium nitrate fertilizer at these same sites was found to increase thistles more than perennial grasses (Reece, 1983). Due to high application costs and the inconsistent affects of herbicides, biological control of this weed has been initiated.

Rhinocyllus conicus, a seed head inhabiting weevil and one of a number of phytophagous species attacking the flower heads of Carduus nutans in Europe, was reported to have excellent potential as a biological control agent (Zwolfer, 1980). This weevil has adapted, as a result of competition with other European insects, toward oviposition on a broad range of Carduus populations. This "compensation strategy" has helped the species spread over large bodies of thistle-infested land in Europe and North America as well (Zwolfer, 1980).

This weevil was released in California in 1969 as a biological control agent on milk thistle, Silybum marianum L. (Hawkes, et al., 1972). It overwintered and fed on thistle foliage for 2 to 3 weeks in the spring before oviposition on the lower surface of seed head bracts. Larvae burrowed into the seed head and damaged the receptacle of the flower. Only one generation per summer was observed and was reportedly due to early senescence of the thistle (Hawkes, et al., 1972).

In the Gallatin Valley of Montana, releases of R. conicus occurred gradually between 1969-73. In 1974 Rees reported that the weevil had established successfully over a broad range. Overcrowding within seed heads was reported and larvae feeding within the top of the thistle's stem resulted in abortion of terminal heads. Reduction in musk thistle seed production and seedling densities was reported by Rees in 1977. Populations are now often at saturation levels on some sites (Rees, 1980).

The weevil was released in Nebraska in 1972 where larval densities of 30 or more per seed head prevented seed development (McCarty, et al., 1981). Despite high weevil densities, a period of 7 to 10 years was required for the weevil to significantly reduce musk thistle populations (McCarty, et al., 1981).

Early establishment of _R. conicus_ on musk thistle varied according to climate and weevil mortality rates. In Virginia, the first weevils introduced, suffered high mortality due to egg masses being damaged by wind and rain (Surles and Kok, 1976). Just six years later, the weevil had established well enough that high larval mortality and reduced adult size due to overcrowded conditions within flower heads was reported (Surles, et al., 1981). Weevil crowding caused complete abortion of thistle heads at high larval densities with subsequent death of the larvae (Dowd and Kok, 1981).

Releases of _R. conicus_ in Canada in 1975 were very successful causing damage to 95% of thistles at release sites within three years following release. Eighty percent of the weevils eggs were found on the terminal head. A false, second weevil generation was described but this was due to the release of laboratory mated weevils in late August (Laing and Heels, 1978).

Problems Associated With Musk Thistle Control

Considerable hybridization occurs between species and subspecies in the Carduus nutans group and therefore their exact identification is difficult (Kazmi, 1964). Since the weevil R. conicus accepts all taxa within the group researchers have used C. nutans in a broad sense to represent all taxa in the group (McCarty, 1983). Differences between two species within the Carduus genus in terms of thistle growth and weevil attack were found to be insignificant in studies conducted in Montana (Rees, 1986).

The relatively broad host range of R. conicus and its ability to attack native thistles has caused some concern among researchers (Turner, et al., 1987). There seems to be a possibility that the seed head weevil may damage populations of native thistles where musk thistle densities are low (Zwolfer and Preiss, 1983). Turner et al. (1987) recorded emergence of adult R. conicus from 12 species of native, non-target Cirsium thistles in California. Rees (1977) has also reported the utilization of native thistles (Cirsium arvense (L.) Scop., C. vulgare (Savi) Tenore, and C. undulatum (Nutt.) Spreng.) by R. conicus, however damage to the non-target thistles was found to be minimal. The lack of significant weevil damage to native thistles was reported to be primarily due to a lack of synchrony between thistle bud production and high spring weevil emergence (Rees, 1979). Under different environmental conditions the results have been different as French strains of this weevil, have been found to show a preference for Cirsium vulgare over Carduus nutans in Europe (Zwolfer and Preiss, 1983).

McCarty and Lamp (1982) reported that the plant persisted on disturbed sites due to residual seed production by unattacked lateral heads.

The continued persistence of musk thistle has prompted the introduction of another thistle feeding weevil, <u>Trichosirocalus horridus</u> (Panz.). This weevil was imported to the U.S. from Italy in 1974 and has established in Virginia (Kok and Trumble, 1979). This beetle emerges earlier in the season than <u>R</u>. <u>conicus</u>, feeds on the rosette stage of the plant, and disrupts apical dominance. <u>T</u>. <u>horridus</u> will hopefully complement the effects of <u>R</u>. <u>conicus</u>, but establishment has been slow.

The success of <u>R</u>. <u>conicus</u> as a biological control agent led to efforts to integrate herbicide applications with weevil attack. At recommended doses, applications of 2,4-D to adult female weevils showed no significant increase in mortality (Trumble and Kok, 1980). However, damage to adult musk thistle plants from 2,4-D applications during the spring caused near total mortality of larva within developing heads (Rees, 1977). Rees recommended that 2,4-D be applied during the fall after weevil oviposition and development has been completed.

<u>Carduus</u> <u>nutans</u> may retard natural succession of native grassland species (Higgins and Baker, 1982). Musk thistle is unpalatable to most herbivores and thus it remains on disturbed sites for an extended period of time (McCambridge, et al., 1982). The thistle has a tendency to remain on overgrazed sites despite successful chemical and biological efforts to control it.

CHAPTER 2

EFFECTS OF RELIEVED GRAZING AND *RHINOCYLLUS CONICUS* FROEL. ON MUSK THISTLE

Introduction

Nonconventional management strategies for controlling musk thistle have focused on the importance of fostering good stands of competing grasses to stress the thistle and prevent seed set. Rotational grazing and fencing of drought stricken pastures has been recommended to help hasten the decline of thistle populations (Koller, 1979; Hartridge, 1979). Popay and Thompson (1980) reported that increased plant competition in pastures resulted in reduced seed germination and high mortality of mature thistles in New Zealand. Rapid reductions in thistle populations on ungrazed weevil release sites in Kansas (Horber, 1980) have demonstrated the success of integrating weevil releases and grazing management.

Given adequate moisture, weevils tend to develop best in thistles growing in fertile soil, but can also develop in plants growing in poor soil (Dowd and Kok, 1983). A four year study of nutrient poor, disturbed sites in Canada revealed that a reduction in seed production caused by *R. conicus* in combination with reduced soil disturbance eliminated musk thistle on these sites (Harris, 1984). Elimination of grazing reduced, by 50%, the time necessary for thistle control using the weevil alone (Harris, 1984). Tall fescue (*Festuca arundinacea* Schreb.) in combination with *R. conicus* caused a reduction in thistle growth and seed production on cultivated plots as compared to the effects of the weevil alone (Kok, et al., 1986).

Rees (1979) found that reductions in musk thistle populations within the Gallatin Valley were steady over the first four years following initial weevil releases and that populations of *R. conicus* had extended beyond the valley. Despite well established populations of *R. conicus* in the Gallatin valley and other areas, isolated infestations of the thistle have persisted on disturbed or overgrazed lands.

The mating period of the weevil has been reported to fluctuate. A 28 day mating period in 1976 was followed by a 16 day mating period in 1977 (Rees, 1979). Since musk thistle phenology varies with varying environmental conditions (Lee and Hamrick, 1983; Smith, et al., 1984) and *R. conicus* prefers the bud stage of musk thistle for oviposition (Surles and Kok, 1976) the relief of grazing may cause variation in the synchrony between weevil and thistle.

The purpose of this study was to determine the effects of *R. conicus* and relieved grazing on the dynamics of musk thistle in uncultivated, natural pasture in foothill grasslands of Montana.

Methods and Materials

Study sites

Four grazed pastures having substantial musk thistle infestations were chosen for this study. All sites were in the Gallatin Valley of Montana. In the summer of 1985, an ca. 1000 m^2 area was fenced off to remove grazing at each site. Three sites were fenced in mid-June of 1985. Site no. 1, the "Belgrade" site, was located near Belgrade, MT.

(NE1/16 of NE1/8 of NW1/4 of Section 7, R4E T1S) at an elevation of 4400 ft. Site no. 2, the "Amsterdam" site, was located near Amsterdam, MT (NW1/16 of NW1/8 of SE1/4 of Section 33, R3E T1S), elevation 4600 ft.. Site no. 3, the "Bozeman" site, was located near Bozeman, MT (SE1/16 of NW1/8 of NW1/4 of Section 5, R6E T2S), elevation 4760 ft.. This site was further divided according to slope into a wetter "swale" area and a drier "ridge" area. Site no. 4, the "Four Corners" site, was located near Four Corners, MT (NE1/16 of SE1/8 of NE1/4 of Section 14, R4E T2S) at an elevation of 4720 ft. and was not fenced until late August of 1985.

Initial plant coverage

Twenty 2 dm x 5 dm frames placed along two randomly chosen transects (both within and outside the fenced areas) were used to determine the initial plant composition, plant coverage, and frequency in late July of 1985.

Standing crop

In the fall of 1985, samples were clipped from six rectangular 1/2 m^2 frames placed along random transects both within and outside the fenced areas at all sites. All plant material within these frames was clipped, separated into plant type categories, bagged, dried for 10 days at 35° C, and weighed. This procedure was repeated with 15 frames per transect on three of the five sites in the fall of 1986.

1985 thistle growth and weevil effects

In late June of 1985, four randomly chosen, 25 m transect lines were run at both the Belgrade and Amsterdam sites. Two of these transects were within the fenced area and two were outside. The Bozeman site had four subsites: ridge enclosed, ridge open, swale enclosed, swale open. Each was sampled via quadrats placed along two 25 m transects. Samples to assess thistle growth and weevil effects were not taken at the Four Corners site.

Twenty adult musk thistle plants along each transect were flagged at approximately 1 m intervals. Alternate thistles along these transects were treated with the systemic insecticide aldicarb at a rate of 10 Kg/A or 0.233 gm/plant to eliminate weevil damage. These sites were visited at weekly intervals throughout the summer to monitor aspects of thistle growth.

Treated and untreated plants were clipped at the base and plant parts were separated into three categories: 1) terminal seed head, 2) lateral seed heads, 3) vegetative stems and lateral branches. These were bagged, dried for 10 days at 35° C and weighed. Seed heads were later dismantled and the number of cells produced by weevil pupation as well as the number of mature seeds remaining were determined.

1986 thistle growth and weevil effects

Transects established in 1985 were revisited in early May of 1986. In addition, a fifth set of transect lines were established at the Four Corners site. Twenty musk thistle rosettes were flagged at 1 m intervals along all transects. Upon bolting and appearance of the terminal bud, aldicarb was again applied to alternate plants along all transects. The sites were visited weekly to monitor both the growth of tagged thistles and the general rate of weevil development within random untagged thistles.

Harvest of seed heads began in early August at all sites. When weevil damaged seed heads were determined to contain fully developed adults and prior to weevil emergence they were harvested, separated into three categories: 1) terminal head; 2) secondary lateral heads; 3) tertiary lateral heads, and bagged. When undamaged seed heads were determined to be fully mature and prior to seed release they were harvested and separated as to categories above.

In late August of 1986, all plants at each site were clipped at the base and plant parts were separated into the following categories: 1) remaining tertiary seed heads and 2) vegetative stems and laterals. These were bagged and, along with previously collected seed heads, dried for 10 days at 35°C and weighed. Seed heads were later dismantled and the number of adult weevils and mature seeds determined.

Statistical analysis

Multifactor analysis of variance was used to determine differences among treatments at a significance level of 0.05. Additional mean comparisons were obtained by using a Tukey's Studentized Range test, also at a significance level of 0.05. Significant interactions between treatments were further analyzed by comparing graphs produced from individual treatment combination means (Neter, et al., 1985).

Results and Discussion

Initial coverage

Grasses provided the highest percent coverage at all sites. The perennial grass, Poa pratensis L., was dominant at four of five plots while the annual, Bromus tectorum L., dominated the Belgrade site (Table 1). The presence of B. tectorum indicated that the Belgrade site had a history of overgrazing (McCambridge, et al., 1982).

The Belgrade site and the Bozeman ridge site had the lowest initial total grass coverage (Table 1). Prior to fencing, both sites had greater grass coverage in the ungrazed areas than in the grazed areas (Belgrade site, $P < 0.05$; Bozeman site, $P < 0.01$). There was also lower Carduus nutans coverage in these ungrazed areas ($P < 0.05$, Table 1). Since high grass coverage tends to inhibit musk thistle infestations (Edmonds and Popay, 1983), it appeared that the grazed areas on these two sites may have been preferentially used by cattle prior to fencing. This should be taken into consideration when interpreting standing crop comparisons below.

The other three sites showed no initial difference in grass coverage between grazed and ungrazed areas. There were, however, significant but inconsistent differences in initial musk thistle coverage ($P < 0.05$, Table 1).

At the Amsterdam site the ungrazed area had lower total coverage due to litter than did the grazed area as well as the lowest thistle coverage. Musk thistle seeds have been shown to retain germinability for extended periods if covered by litter (Popay and Thompson, 1979; Burnside, et al., 1981). Hamrick and Lee (1987) found increased germination of musk thistle seeds due to reduced evaporation from low levels of litter.

Unlike the other three sites, the ungrazed areas of the Bozeman swale site and the Four Corners site had higher initial musk thistle coverage than grazed areas ($P < 0.05$, Table 1). Ungrazed areas on these sites had a significantly higher total forb coverage also ($P < 0.05$, Table 1). The ungrazed Four Corners site had 5.9% total forb coverage with 5.8% C. nutans while the ungrazed Bozeman swale site had 19.5% total forb coverage with only 3% being C. nutans (Table 1). The fenced area at the Four Corners site was located next to a commonly used feeding and watering area. Therefore, greater disturbance in this area accounted for its greater C. nutans coverage. In contrast, the ungrazed portion of the Bozeman swale site appeared to favor all forb species, a component of which was musk thistle.

The initial differences in coverage at these sites can be used to explain other results obtained during this study.

1985 standing crop

Comparisons based on standing crop data for the summer of 1985 were restricted to three of the five sites studied. The Four Corners site was eliminated due to late fencing which prevented any grazing comparisons at this site. The Belgrade site had extensive damage to musk thistle and other forb species due to ground squirrel feeding activity. These sites were also eliminated from thistle growth and weevil effect studies done during the summer of 1985.

Table 1. 1985 vegetation composition in grazed and ungrazed musk thistle sites in Montana. Centered dots indicate the species did not occur at that site. See Appendix for scientific and common names corresponding to plant species codes.

	Belgrade		Four Corners		Amsterdam	
	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
	Mean % Cover ± SD (% Frequency)					
Total Grass	28.1a	50.5b	63.3b	64.4b	57.3b	58.1b
Agrsmi	4.9 ± 4.3 (87)	1.4 ± 1.8 (60)	• • •	• • •	10.5 ± 6.2 (100)	23.1 ± 7.0 (100)
Broine	• • •	• • •	24.7 ± 6.7 (100)	23.3 ± 7.4 (100)	• • •	• • •
Brotec	22.9 ±11.6 (100)	29.2 ±10.4 (100)	• • •	• • •	• • •	• • •
Carste	0.1 ± 0.4 (3)	0.4 ± 0.7 (27)	• • •	• • •	• • •	• • •
Carpra	• • •	• • •	• • •	• • •	0.7 ± 2.8 (8)	0.0 ± 0.0 (0)
Dacglo	• • •	• • •	• • •	• • •	• • •	• • •
Koecri	0.1 ± 0.4 (7)	0.0 ± 0.1 (3)	• • •	• • •	• • •	• • •
Stivir	• • •	• • •	• • •	• • •	0.2 ± 0.6 (10)	0.0 ± 0.2 (3)
Poapra	0.2 ± 4.4 (100)	19.5 ±13.4 (97)	39.6 ± 9.5 (100)	41.1 ± 9.3 (100)	45.9 ±14.2 (100)	35.0 ± 9.3 (100)
Bare Ground	10.1 ± 8.7 (73)	9.5 ±11.1 (43)	24.6 ± 9.8 (100)	16.9 ± 7.8 (98)	7.9 ± 7.0 (80)	14.6 ± 9.2 (88)
Litter	20.1 ± 9.7a (100)	23.1 ± 7.8a (100)	10.9 ± 5.2a (100)	15.6 ± 8.6a (100)	30.4 ±11.6b (100)	17.8 ± 8.5a (100)
Cryptogams	30.1 ± 9.1 (100)	17.9 ±10.9 (100)	9.8 ± 6.8 (90)	10.7 ± 9.3 (83)	2.0 ± 4.0 (35)	9.3 ± 8.5 (85)

Table 1 (cont'd).

	Bozeman Ridge				Bozeman Swale			
	Grazed		Ungrazed		Grazed		Ungrazed	
	Mean % cover ± SD (% Frequency)							
Total Grass	18.4a		40.6b		55.5b		41.8b	
Agrsmi	2.1 ± 3.1	(58)	2.1 ± 4.4	(35)	0.1 ± 0.2	(5)	5.5 ± 7.2	(70)
Broine	1.5 ± 3.5	(15)	0.0 ± 0.0	(0)	. .	.	. .	.
Brotec	. .	.	. .	.	. .	.	. .	.
Carste	. .	.	. .	.	. .	.	. .	.
Carpra	. .	.	. .	.	. .	.	. .	.
Dacglo	0.0 ± 0.0	(0)	0.2 ± 0.8	(5)	1.0 ± 2.8	(13)	3.2 ± 5.7	(30)
Koecri	. .	.	. .	.	. .	.	. .	.
Stivir	0.1 ± 0.3	(3)	2.2 ± 4.8	(25)	0.0 ± 0.0	(0)	0.6 ± 2.3	(8)
Poapra	4.7 ± 9.2	(98)	36.1 ± 9.0	(100)	54.4 ±15.4	(100)	32.5 ±10.6	(100)
Bare ground	24.6 ±12.0	(100)	7.8 ± 9.4	(100)	19.8 ± 9.3	(93)	28.8 ±11.0	(100)
Litter	19.7 ±10.6a	(100)	0.6 ±10.7b	(97)	23.4 ±11.4a	(100)	15.1 ± 7.4a	(100)
Cryptogams	25.0 ±12.6	(98)	0.6 ±11.4	(64)	0.4 ± 1.8	(8)	1.2 ± 2.1	(35)

Table 1 (cont'd).

	Belgrade				Four Corners				Amsterdam			
	Grazed		Ungrazed		Grazed		Ungrazed		Grazed		Ungrazed	
	Mean % Cover ± SD (% Frequency)											
Total Forb	8.5b		10.2b		1.7a		5.9b		7.9b		11.3b	
Carnut	1.7 ± 3.5b	(33)	0.8 ± 2.1a	(33)	1.0 ± 3.0a	(13)	5.8 ± 5.2b	(75)	5.4 ± 8.9b	(55)	4.1 ± 6.0a	(45)
Achmil	5.1 ± 5.1	(73)	4.8 ± 6.2	(73)	. .	.	. .	.	0.2 ± 0.8	(5)	5.0 ± 7.2	(55)
Alyaly	1.4 ± 1.5	(80)	4.5 ± 2.9	(93)	. .	.	. .	.	. .	.	. .	.
Andsep	0.0 ± 0.0	(0)	0.0 ± 0.1	(10)	. .	.	. .	.	. .	.	. .	.
Artlud	. .	.	. .	.	. .	.	. .	.	. .	.	. .	.
Astpan	. .	.	. .	.	. .	.	. .	.	. .	.	. .	.
Chrvil	. .	.	. .	.	. .	.	. .	.	. .	.	. .	.
Cirarv	. .	.	. .	.	0.0 ± 0.2	(3)	0.0 ± 0.0	(0)	2.0 ± 8.8	(8)	0.0 ± 0.0	(0)
Cirvul	. .	.	. .	.	0.3 ± 1.6	(3)	0.0 ± 0.2	(3)	. .	.	. .	.
Cynoff	. .	.	. .	.	. .	.	. .	.	. .	.	. .	.
Erocic	. .	.	. .	.	. .	.	. .	.	. .	.	. .	.
Grisqu	. .	.	. .	.	. .	.	. .	.	0.0 ± 0.0	(0)	1.1 ± 4.2	(5)
Lepcam	. .	.	. .	.	. .	.	. .	.	. .	.	. .	.
Medlup	. .	.	. .	.	0.0 ± 0.0	(0)	0.1 ± 0.2	(5)	. .	.	. .	.
Meloff	. .	.	. .	.	. .	.	. .	.	0.2 ± 1.3	(3)	0.0 ± 0.0	(0)
Phllon	. .	.	. .	.	. .	.	. .	.	. .	.	. .	.
Silvul	. .	.	. .	.	. .	.	. .	.	. .	.	. .	.
Solmis	. .	.	. .	.	.03 ± 0.2	(3)	0.0 ± 0.0	(0)	0.0 ± 0.0	(0)	0.9 ± 3.6	(13)
Taroff	0.3 ± 0.7	(20)	0.1 ± 0.3	(13)	0.3 ± 0.7	(20)	0.0 ± 0.2	(3)	0.0 ± 0.0	(0)	0.2 ± 0.6	(10)
Tradub	. .	.	. .	.	. .	.	. .	.	0.1 ± 0.5	(3)	0.0 ± 0.0	(0)
Equi spp.	. .	.	. .	.	. .	.	. .	.	0.1 ± 0.5	(8)	0.4 ± 1.8	(5)

Table 1 (cont'd).

	Bozeman Ridge				Bozeman Swale			
	Grazed		Ungrazed		Grazed		Ungrazed	
	Mean % cover ± SD (% Frequency)							
Total Forb	17.6b		17.4b		5.5a		19.5b	
Carnut	3.1 ± 6.8b	(38)	1.6 ± 2.1a	(10)	1.5 ± 3.8a	(33)	3.0 ± 4.9b	(40)
Achmil	0.6 ± 2.5	(8)	5.3 ±10.4	(40)	0.4 ± 1.6	(13)	4.8 ± 7.2	(50)
Alyaly	0.1 ± 0.3	(13)	.03 ± 0.2	(3)	0.0 ± 0.0	(0)	0.3 ± 1.6	(10)
Andsep	. .	.	. .	.	. .	.	. .	.
Artlud	3.1 ± 8.5	(18)	0.5 ± 2.0	(5)	. .	.	. .	.
Astpan	0.1 ± 0.8	(3)	2.8 ± 6.0	(35)	. .	.	. .	.
Cirarv	. .	.	. .	.	0.4 ± 1.1	(15)	0.0 ± 0.0	(0)
Cirvul	. .	.	. .	.	. .	.	. .	.
Chrvil	0.0 ± 0.0	(0)	0.4 ± 2.4	(3)	. .	.	. .	.
Cynoff	0.1 ± 0.5	(0)	1.3 ± 4.6	(13)	1.4 ± 4.4	(13)	2.2 ± 5.1	(40)
Erocic	2.8 ± 4.0	(8)	1.3 ± 4.0	(23)	0.1 ± 0.5	(5)	0.0 ± 0.0	(0)
Grisqu	1.7 ± 3.3	(45)	0.0 ± 0.0	(0)	0.5 ± 3.1	(3)	0.0 ± 0.0	(0)
Lepcam	0.9 ± 4.0	(40)	1.0 ± 2.8	(40)	0.1 ± 0.3	(3)	0.5 ± 2.4	(15)
Medlup	0.1 ± 0.5	(13)	0.0 ± 0.0	(0)	. .	.	. .	.
Meloff	. .	.	. .	.	. .	.	. .	.
Phllon	0.0 ± 0.0	(0)	0.3 ± 1.1	(5)	. .	.	. .	.
Silvul	0.0 ± 0.0	(0)	1.3 ± 5.5	(5)	. .	.	. .	.
Solmis	2.5 ± 4.6	(40)	1.1 ± 3.8	(10)	0.2 ± 0.9	(8)	4.2 ± 7.2	(35)
Taroff	2.1 ± 4.5	(30)	1.4 ± 3.0	(28)	0.9 ± 1.8	(30)	3.6 ± 4.6	(53)
Tradub	0.4 ± 1.4	(8)	0.1 ± 0.3	(5)	0.0 ± 0.0	(0)	0.8 ± 2.9	(8)
Equi spp.	0.0 ± 0.0	(0)	1.3 ± 4.8	(8)	. .	.	. .	.

Table 2. The effect of relieved grazing on standing crop, 1985; comparison between sites across all treatments, and between grazed and ungrazed across all sites and treatments.

Standing crop variable	Site			Grazing	
	Amsterdam	Boz. Ridge	Boz. Swale	Present	Absent
	gm/m^2				
Total[ab]	72.5 ± 5.7a	85.4 ±10.7ab	94.4 ±12.1a	58.9 ± 3.3a	109.3 ± 7.1b
Total forbs	3.5 ± 1.4a	28.2 ± 5.2b	10.1 ± 5.6a	7.6 ± 3.0a	20.4 ± 5.0b
Annual forbs	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Perennial forbs	3.5 ± 1.4a	28.2 ± 5.2b	10.1 ± 5.6a	7.6 ± 3.0a	20.4 ± 5.0b
Total grasses	69.0 ± 4.6a	57.2 ± 7.2a	84.2 ± 8.6b	51.3 ± 4.0a	89.0 ± 4.5b
Annual grasses	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Perennial grasses[b]	69.0 ± 4.6a	57.2 ± 7.2a	84.2 ± 8.6b	51.3 ± 4.0a	89.0 ± 4.5b
Carduus nutans	10.8 ± 5.6	19.5 ± 6.9	6.6 ± 3.4	15.1 ± 5.6	9.5 ± 3.2
Total annuals	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Total perennials[b]	72.5 ± 5.7a	85.4 ±10.7ab	94.4 ±12.1b	58.9 ± 3.3a	109.3 ± 7.1b

[a] Values within a row without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

[b] Significant interactive treatment effects.

Significant differences between grazed and ungrazed areas within the three sites analyzed were found for all plant types sampled ($P < 0.05$, Table 2). Grazed areas had a reduced total standing crop after a single year of grazing pressure, but significant interactions between site and grazing treatments were also obtained. Analysis of these interactions for total standing crop and perennial grasses revealed that 86% of the reduction in standing crop was due to the two Bozeman sites. This meant that the Amsterdam site experienced relatively low grazing pressure during the summer of 1985. In fact, the majority of cattle grazing at this site occurred during late August and early September.

Note that 33% of the standing crop at the Bozeman ridge site was composed of forbs (excluding _C. nutans_), while the Bozeman swale and Amsterdam sites had 10.7% and 4.8% forb content, respectively. The Bozeman ridge site also had the highest musk thistle component (Table 2), which again indicates that this site had experienced unusually high grazing pressure prior to fencing. Prolonged grazing restricts natural succession in grasslands from broadleaf or weedy vegetation to natural perennial grass vegetation (Feldman, et al., 1968). High forb standing crop at this site might also indicate that the sloped character of the ridge and resulting lower moisture content (from increased runoff) caused a reduction in grass coverage and favored more deep rooted forb species. Moisture content has been demonstrated to be the primary limiting factor to grass production on natural grasslands (Hartridge, 1979).

1986 standing crop

The same five study sites were again used for standing crop comparisons during the summer of 1986. However, extensive predator damage to musk thistle plants, which had been tagged for thistle growth and weevil effect studies, eliminated the use of two sites (Amsterdam and Bozeman ridge). A higher total standing crop than in 1985 was obtained due to increased precipitation in spring and summer of 1986 (Table 3 & 4). As observed in 1985, a significant difference in total standing crop between grazed and ungrazed areas was demonstrated indicating the effects of grazing pressure ($P < 0.05$, Table 4). These differences were much more pronounced the second year of relieved grazing. In 1985 a 50.4 gm/m^2 difference in total standing crop between grazed and ungrazed areas was observed (Table 2). This increased to a 188.6 gm/m^2 difference in 1986 (Table 4).

Interactions between site and grazing treatments with respect to total standing crop helped reveal differences in grazing pressure among sites. The Bozeman swale site accounted for 80-90% of the grazing differences while the Belgrade and Four Corners sites accounted for 13-15% and 5-7% of this difference, respectively. The site/grazing interaction in perennial forb standing crop is explained by the initially high coverage of perennial forbs on the ungrazed Bozeman swale site (Table 1). The Belgrade site was the only site to produce a substantial standing crop of annual species thus explaining the interactive effects obtained. This reenforces the results of the initial coverage study and indicates long term grazing pressure at this site.

Table 3. Spring and summer precipitation (normal and departures from normal), Bozeman, Montana, 1984-86.[a]

	Average Precipitation and Departures (mm)						
	Mar	Apr	May	Jun	Jul	Aug	Total
Average	69	79	110	117	48	59	482
1984	+24	- 9	-21	- 1	- 7	+52	+ 38
1985	+16	-17	-35	-82	- 9	+21	-106
1986	-17	+22	+33	-14	+73	- 7	+ 90

[a] National Oceanic and Atmospheric Administration, Climatological Data Annual Summary, Montana. 1984, 87(13); 1985, 88(13); 1986, 89(3-8).

After one summer of relieved grazing (1985) differences in musk thistle standing crop among grazing treatments were not significant and the slightly higher C. nutans standing crop observed on ungrazed areas ($5.6\ gm/m^2$, Table 2) might have been due to initial coverage rather than relieved grazing. However, grazed areas had $17.0\ gm/m^2$ more musk thistle standing crop than ungrazed areas after the second summer of relieved grazing (Table 4). This increase in musk thistle standing crop in grazed areas, although not significant, may become so in time. Results of studies designed to assess seedling numbers and rosette establishment (Chapter 3) indicated that young thistles established less frequently under relieved grazing.

Table 4. The effect of relieved grazing on standing crop, 1986; comparison between sites across all treatments, and between grazed and ungrazed areas across all sites and treatments.

Standing crop variable	Site: Belgrade	Site: Four Corners	Site: Boz. Swale	Grazing: Present	Grazing: Absent
	gm/m^2				
Total[ab]	120.9 ±10.4a	200.4 ± 6.9b	251.0 ±39.0c	87.4 ±12.0a	276.0 ±20.6b
Total forbs[b]	31.6 ± 3.1b	2.4 ± 1.2a	34.6 ± 7.8b	9.9 ± 2.1a	35.5 ± 5.4b
Annual forbs[b]	10.1 ± 1.8b	0.0 ± 0.0a	1.8 ± 0.9a	1.9 ± 0.6a	6.0 ± 1.4b
Perennial forbs[b]	21.5 ± 2.4b	2.4 ± 1.2a	32.8 ± 7.6b	8.0 ± 1.7a	29.9 ± 5.2b
Total grasses[b]	89.3 ± 9.1a	198.0 ± 6.6b	216.4 ±34.0b	95.7 ±11.3a	240.2 ±18.5b
Annual grasses[b]	35.8 ± 4.9b	0.0 ± 0.0a	0.0 ± 0.0a	8.3 ± 2.3a	15.6 ± 4.2b
Perennial grasses[b]	53.5 ± 6.6a	198.0 ± 6.6b	216.4 ±34.0b	87.4 ±12.0a	224.6 ±20.8b
Carduus nutans	17.9 ± 8.9a	11.7 ± 4.0a	59.9 ±11.9b	38.3 ± 9.2	21.3 ± 6.0
Total annuals[b]	45.9 ± 6.3b	0.0 ± 0.0a	1.8 ± 0.9b	10.2 ± 2.8a	21.6 ± 5.3b
Total perennials[b]	75.0 ± 6.9a	200.4 ± 6.9b	149.0 ±38.6c	95.3 ±11.2a	254.4 ±23.0b

[a] Values within a row without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

[b] Significant interactive treatment effects.

1985 thistle growth and weevil effects

Growth and weevil effects were complicated in 1985 because 69% of the tagged thistles lost terminal flower heads due to feeding damage by ground squirrels and other unknown predators (Amsterdam site - 86%, Bozeman ridge - 78%, Bozeman swale - 73%). Heads from damaged thistles were either totally absent or those which remained at the base of the thistle were green and had been torn open by the predator. There was no significant difference in terminal loss between grazed and ungrazed areas on these sites (61% - grazed, 73% - ungrazed, $P > 0.05$).

Only 41% of the remaining terminal flower heads experienced weevil damage and only 14% of all lateral seed heads were attacked by _R. conicus_. This is a relatively low figure when compared with the levels of attack (98% and 62%, respectively) reported for the Gallatin Valley in 1976 by Rees. The dry spring may have affected the synchrony between plant and weevil development which is strongly influenced by temperature (Smith, et al., 1984).

Thistle growth. No difference in initial rosette area per thistle was detected. This is important as initial rosette area has been shown to be the best predictor of thistle growth success (Smith, et al., 1984; Lee and Hamrick, 1983).

Thistles on the Bozeman ridge site did produce a significantly lower number of seed heads ($P < 0.05$, Table 5) and had a significantly lower total mass per plant ($P < 0.05$) than the Amsterdam and Bozeman swale sites (5.6 g/plant vs. 14.8 g/plant and 16.3 g/plant respectively). This was most likely due to the slope's lower soil moisture content.

Interactions between site and grazing treatments were evident on most thistle growth measurements. Thistles grown on ungrazed areas produced a greater mass/seed head at two of the three sites (Table 5). The only site in which this trend was not demonstrated was the Amsterdam site which had less grazing pressure (Table 2). Total plant mass was unaffected by grazing treatments ($P > 0.05$) therefore, thistles appeared to respond to plant competition stress by concentrating nutrients into a few reproductive areas.

The level of grazing and terminal loss also affected musk thistle growth. The effect of terminal loss on growth and reproduction of musk thistle is discussed in Chapter 4.

Weevil effects. A 70% rate of damage to terminal heads on ungrazed areas compared to a 0% rate of terminal damage on grazed areas affected the number of *R. conicus* adults, as measured by counting total pupation chambers per plant and per terminal seed head. Ungrazed areas had a significantly higher number of terminal pupation chambers (Table 5). Rees (1977) noted that cattle grazing disturbed weevil mating and oviposition. This may have caused the increase in flower damage seen for ungrazed sites.

There was a greater number of damaged lateral heads and more pupal cells per lateral head on plants grown in ungrazed areas at two of the three sites ($P < 0.05$, Table 5). The Bozeman ridge site, which had the highest initial forb coverage (Tables 1 & 2), had more damage and adult weevil production in the ungrazed area. Sixty seven percent of the lateral cells counted came from heads produced on the ungrazed area of the Bozeman swale site. This area had high forb coverage (Table 1) and

Table 5. The effect of relieved grazing on musk thistle and weevil damage to musk thistle, 1985; variables compared across all treatments are: sites, grazing, insecticide use, and terminal flower condition.

	Site			Grazing	
Variable	**Amsterdam**	**Boz. Ridge**	**Boz. Swale**	**Present**	**Absent**
	Mean ± SD				
Rosette area (cm^2)	350.8 ±32.6	294.0 ±34.2	530.0 ±60.4	442.2 ±33.5	355.8 ±37.9
Total seed heads[a]	8.0 ± 0.6b	2.1 ± 0.2a	9.2 ± 1.3b	7.1 ± 0.6	5.8 ± 0.8
Seed head mass (gr)[b]	3.7 ± 0.4b	0.6 ± 0.1a	5.0 ± 1.1b	3.2 ± 0.4	3.2 ± 0.7
Mass/seed head[b]	0.4 ± 0.0b	0.3 ± 0.0a	0.4 ± 0.0b	0.4 ± 0.0a	0.4 ± 0.0b
Total lateral heads damaged[b]	0.7 ± 0.2ab	0.2 ± 0.1a	1.8 ± 0.5b	0.4 ± 0.2a	1.2 ± 0.3b
Pupal cells in terminal head	1.4 ± 0.7	5.1 ± 3.5	8.0 ± 1.8	0.0 ± 0.0a	7.9 ± 1.8b
Pupal cells in lateral heads[b]	2.2 ± 0.7ab	0.8 ± 0.4a	7.9 ± 2.5b	1.2 ± 0.6a	5.5 ± 1.5b
Cells/damaged head	2.9 ± 0.7	1.4 ± 0.6	3.5 ± 0.6	1.7 ± 0.3	3.6 ± 0.6
Total no. seeds[b]	167.8 ±23.1b	17.9 ±10.6a	145.3 ±35.3b	121.7 ±20.8	115.8 ±22.4

[a] Values within a row without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

[b] Significant interactive treatment effects.

Table 5 (cont'd).

Variable	Insecticide		Terminal Flower	
	Present	Absent	Present	Absent
	Mean ± SD			
Rosette area (cm^2)[a]	389.9 ±33.1	395.3 ±40.2	520.6 ±70.4	351.1 ±25.2
Total seed heads[b]	6.9 ± 0.9	5.8 ± 0.4	9.9 ± 1.8b	5.2 ± 0.4a
Seed head mass[b] (gm)	3.2 ± 0.5	3.3 ± 0.7	6.6 ± 1.4b	2.1 ± 0.2a
Mass/seed head[b]	0.4 ± 0.0	0.4 ± 0.0	0.6 ± 0.0b	0.4 ± 0.0a
Total tertiary heads damaged[b]	0.9 ± 0.3	0.9 ± 0.2	2.3 ± 0.7	0.4 ± 0.1
Pupal cells in terminal head	4.4 ± 1.8	4.9 ± 1.6	4.7 ± 1.2	0.0 ± 0.0
Pupal cells in lateral heads[b]	3.3 ± 1.2	4.0 ± 1.3	10.7 ± 3.2b	1.3 ± 0.4a
Cells/damaged head	2.8 ± 0.6	3.1 ± 0.6	3.9 ± 0.7	2.4 ± 0.5
Total seeds	113.7 ±18.6	122.8 ±24.7	199.9 ±46.9	91.7 ±13.2

[a] Values within a row without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

[b] Significant interactive treatment effects.

a much higher standing crop when compared with the grazed area at this site (Table 2). The combination of relieved grazing and diverse coverage appeared to enhanceweevil damage to lateral flowerheads thus producing more adult weevils. This was only true if the terminal flower was not lost to predators.

Plants in grazed areas had higher damage to lateral flower heads as well as higher numbers of pupal cells within these heads if their terminals were lost. The opposite was true for thistles grown under relieved grazing. Companion studies (Chapter 4) done to determine the effects of terminal loss on musk thistle growth determined that thistles stressed by both plant competition and terminal loss were unable to compensate by producing lateral seed heads. Therefore, the reduced availability of lateral seed heads on these plants resulted in a lower level of attack by *R. conicus* (i.e., fewer pupal cells were produced in the lateral flower heads).

Weevil success, as measured by the number of cells/damaged lateral flower head, was not significantly different between grazed and ungrazed areas. This was apparently due to the predominance of interacting factors.

Insecticide treatments had no significant effect on thistle growth or weevil damage and success.

1986 thistle growth and weevil effects

In 1986 only 14% of the tagged thistles lost their terminals, eliminating the importance of this factor. Insecticide treatments had no significant effect on thistle growth or weevil damage and success. The effects of aldicarb on thistle growth are described in Chapter 5.

A dramatic increase in both thistle growth and weevil activity was noticed during the summer of 1986 (Table 6). The percent of terminal seed heads damaged by R. conicus increased to 86%. Lateral seed head damage also increased to 90% for secondary lateral heads and 49% for tertiary lateral heads. This increase was most likely due to increased moisture (Table 3) and lower temperatures causing increased synchrony between weevil emergence and the number of seed heads available for attack. Smith, et. al. (1984) found that lower temperatures retarded weevil emergence and enhanced musk thistle lateral seed head production.

Differences among treatment sites during the summer of 1986 were complicated by an initial sampling bias. Initial rosette area per plant at the Belgrade site was significantly lower than other sites ($P < 0.05$, Table 6). Thistle growth and weevil effects for this site are consequently less pronounced than those observed for the other two sites (Table 6).

Thistle growth. Thistles on ungrazed areas at all sites produced the same number of secondary seed heads as those grown in grazed areas ($P > 0.05$, Table 6) but, the mass of these heads was significantly reduced ($P < 0.05$, Table 6).

There appeared to be no difference in terminal flower mass between grazing treatments (Table 6). This was due however, to an interactive effect caused by an increase in terminal mass on thistles grown in the ungrazed area of the Four Corners site. The other two sites showed a decrease in terminal mass with increased plant competition. The lack of grazing pressure at the Four Corners site complicated the results and probably prevented the appearance of a main treatment affect.

Relieved grazing also caused thistles at 2 of the 3 sites to produce more total seed heads primarily due to an increased number of tertiary heads (Table 6). However, this increase in the total number of seed heads per plant was not accompanied by an increase in total seed head mass. Therefore, a reduction in the mass per lateral head occurred in thistles grown on ungrazed areas at the heavily grazed, Belgrade and Bozeman sites ($P < 0.05$, Table 6). No difference in total plant biomass was detected among treatments. Therefore, this increase in tertiary seed head number and subsequent reduction in terminal and secondary seed head mass was probably due to a reduced allocation of nutrients to terminal and secondary heads in response to plant competition. This response was the opposite of that seen during the drier summer of 1985.

Weevil effects. Thistles grown under relieved grazing had a greater number of tertiary heads damaged by R. conicus ($P < 0.05$, Table 6). Increases in tertiary head damage to thistles grown on ungrazed areas was due to the presence of a greater numbers of tertiary heads per plant in these areas. However, thistles at the heavily grazed Belgrade site did not have increased weevil damage to tertiary heads. These thistles were initially smaller and had fewer lateral seed heads (Table 6). The smaller thistles on the ungrazed area of the Belgrade site may have been less attractive for oviposition, regardless of their having more tertiary heads. Grazing treatments did not effect the total number of R. conicus adults produced on musk thistle plants (Table 6). However, the distribution of adults among seed heads within thistles on ungrazed sites was effected. Thistles grown under relieved grazing produced fewer adults in terminal ($P < 0.05$, Table 6) and secondary flower heads and more adults within tertiary seed heads when compared to thistles in grazed areas (Table 6). In thistles stressed by plant competition, the reallocation of nutrients away from terminal and secondary flowers may have caused weevil numbers to follow this same gradient.

R. conicus developmental success as measured by the number of adults per damaged lateral was not affected by grazing treatments.

Total seed production

The combined effects of plant competition and weevil attack did not reduce the total seed production of musk thistle during either year of this project (Tables 5 & 6). Since the thistle is primarily a biennial under conditions of plant competition (Lee and Hamrick, 1983), most of the plants used for this study had established under less rigorous plant competition during previous years. A longer period of relieved grazing may be necessary to show significant reductions in seed production.

Table 6. The effect of relieved grazing on musk thistle and weevil damage to musk thistle, 1986; comparison between sites across all treatments, and between grazed and ungrazed across all sites and treatments.

Variable	Site			Grazing	
	Belgrade	Four Corners	Boz. Swale	Present	Absent
	Mean ± SD				
Rosette area^{ab} (cm^2)	597.7 ±42.1a	1111.0 ±102.9b	1571.0 ±109.0b	980.1 ± 61.3	1198.0 ± 98.6
Total no. seed heads^{b}	6.7 ± 0.1a	14.7 ± 1.3b	18.2 ± 2.1b	10.4 ± 0.8a	15.9 ± 1.6b
Secnd. lateral heads	2.3 ± 0.1a	2.8 ± 0.1b	2.8 ± 0.1b	2.6 ± 0.1	2.6 ± 0.1
Ter. lateral heads^{b}	4.5 ± 0.5a	11.9 ± 1.3b	16.3 ± 2.3b	8.1 ± 0.7a	13.4 ± 1.7b
Total seed head biomass^{b}	9.0 ± 0.8a	26.3 ± 2.5b	31.8 ± 3.0b	19.9 ± 1.5	24.7 ± 2.5
Terminal biomass^{b}	1.2 ± 0.1a	2.3 ± 0.1b	2.2 ± 0.2b	2.0 ± 0.1	1.9 ± 0.1
2nd lateral biomass	4.0 ± 0.3a	6.4 ± 0.3b	6.9 ± 0.4b	6.4 ± 0.3b	5.2 ± 0.2a
Ter. lateral biomass	4.2 ± 0.6a	17.7 ± 2.3b	23.5 ± 3.2b	12.1 ± 1.3	18.0 ± 2.6
Biomass/lateral head^{b}	1.3 ± 0.1a	1.7 ± 0.0b	2.1 ± 0.1b	1.9 ± 0.1b	1.5 ± 0.1a
Total no. heads damaged	4.3 ± 0.4a	10.4 ± 1.1b	10.0 ± 1.3b	6.6 ± 0.5	9.8 ± 1.1
Secnd. heads damaged	1.9 ± 0.1a	2.6 ± 0.1b	2.7 ± 0.1b	2.4 ± 0.1	2.4 ± 0.1
Ter. heads damaged^{b}	2.4 ± 0.3a	7.7 ± 1.0b	8.4 ± 1.5b	4.4 ± 0.5a	7.9 ± 1.2b
Adults/damaged lat.	5.9 ± 0.5a	7.5 ± 0.4a	11.3 ± 0.8b	8.7 ± 0.5	7.9 ± 0.5
Total no. adult weevils	36.7 ± 4.0a	98.9 ± 9.3b	111.9 ± 12.8b	71.3 ± 5.4	93.5 ± 10.2
Term. head adults	10.6 ± 1.4a	17.2 ± 1.1b	13.3 ± 1.3ab	16.7 ± 1.0b	11.6 ± 1.0a
Secnd. head adults	20.4 ± 2.5a	37.3 ± 2.8b	45.2 ± 2.9b	36.0 ± 2.5	32.4 ± 2.4
Tert. head adults	9.3 ± 1.8	45.5 ± 7.9	58.9 ± 7.4	23.7 ± 4.1	51.8 ± 10.9
Total no. seeds	255.8 ±32.9a	849.0 ± 96.7b	902.3 ±140.7b	605.7 ± 60.7	731.4 ±104.7
Term. head seeds	16.1 ± 7.6	11.5 ± 3.7	11.2 ± 4.8	11.7 ± 3.6	13.7 ± 4.8
Secnd. head seeds	144.1 ±24.4	108.1 ± 14.2	130.3 ± 21.0	147.5 ± 17.5	107.0 ± 15.1
Ter. head seeds	108.2 ±16.3a	740.2 ± 99.3b	800.9 ±155.1b	483.0 ± 60.9	619.4 ±104.7

[a] Values within a row without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

[b] Significant interactive treatment effects.

Summary

Relieved grazing increased total standing crop significantly and a trend toward reduced musk thistle standing crop in areas of increased grass competition was detected.

Growth patterns of musk thistle stressed by grass competition were considerably different for the years of 1985 and 1986. At times of overall water stress (1985) thistles reduced seed head production concentrating more reserves into fewer heads. The opposite effect was true during the wetter summer of 1986. The plasticity of musk thistle under different environmental conditions has been noted (Lee and Hamrick, 1983) and will be discussed in later chapters.

During the dry summer of 1985, relieved grazing enhanced weevil damage on both the terminal and lateral flower heads of musk thistle. Higher numbers of tertiary flower heads produced on thistles stressed by plant competition had greater _R_. _conicus_ damage during the wetter summer of 1986.

Relieved grazing caused an increase in adult _R_. _conicus_ numbers within seed heads during 1985 but there was no difference in adult production between grazing treatments in 1986. Production of adult weevils within thistles experiencing increased plant competition during the wetter summer of 1986 appeared to be controlled by reallocation of nutrients away from terminal and secondary flowers. This caused an increase in weevils within tertiary seed heads of thistles on ungrazed sites and a corresponding decrease in adults developing within terminal flowers.

Thistles which lost their terminal flower heads under relieved grazing had significantly lower weevil damage and produced fewer adult weevils due to a lack of lateral seed heads.

Relieved grazing during dry years appears to be an important long range strategy for musk thistle control which would increase grass competition and enhance weevil attack. The long range effects of relieved grazing during wetter years may be to increase weevil populations by increasing the availability of oviposition sites.

CHAPTER 3

ASSESSMENT OF MUSK THISTLE SEEDLING/ROSETTE DENSITY AND DISTRIBUTION ON GRAZED AND UNGRAZED GRASSLANDS

Introduction

Musk thistle does not reproduce vegetatively and is therefore dependant upon seeds for distribution and establishment. Stratification of the seed is necessary in order to stimulate natural germination (Medd and Lovett, 1978a). Short days (8 hr) and cold nights with temperatures between -25° and -10° C produce maximum germination (Young, et al., 1978). In Montana, with its cold winters, stratification is assured while variations in moisture and light affect germination at different microsites. The young seedling stage is apparently the point of highest mortality for the thistle (Popay and Thompson, 1980) and vernalization of rosettes is necessary for spring bolting (Medd and Lovett, 1978b).

A potential for allelopathy has been demonstrated in laboratory experiments where root and foliar phenolics caused reduced germination in dicots and radical growth reductions in monocots (Woodward and Glenn, 1983).

Smith and Kok (1984) found the thistle to have a limited seed dispersal capability, concluding that the majority of the seeds are deposited within 50 meters of their release point. It seems plausible that low dispersal coupled with the microsite requirements for germination, establishment, and growth may determine the patchy spatial dispersion patterns commonly associated with musk thistle infestations.

The degree of clumping may be different for seedlings, established rosettes, and bolting plants and may vary with microsite differences.

"In the field individuals are almost always found not to be randomly distributed but show contagious distribution" (Greig-Smith, 1983a). The notion that seed dispersed plants will have a random distribution may be due to the use of an incorrect quadrat size when measuring dispersion. Very small quadrats have a high tendency for vacancy even in random systems, therefore they are preferred if the species pattern is not known. If the species is clumped and density of individual patches is low, however, a large number of samples may be necessary to detect them, making their clumped nature easy to miss (Greig-Smith, 1983a).

For randomly distributed populations only the number of quadrats examined is important, independent of their size. A coefficient of dispersion or variance/mean ratio close to or equal to one indicates a random spatial dispersion pattern. This variance/mean ratio can be tested for significance with a Chi-square test (Kershaw, 1974).

A coefficient of dispersion ratio greater than one will indicate a contagious distribution for a population only if the correct size and number of quadrats are used. As quadrat size approaches the patch size in a clumped population the variance will rise sharply and fewer quadrats will be necessary to indicate a contagious distribution (Greig-Smith, 1983b).

A sudden increase in variance as the quadrat size approaches the patch size can then be used to detect the patch size of a species. When densities of many different species are determined within a particular community and an ANOVA is used to compare differences among species, a plot of mean squares versus quadrat size can be used to detect patch sizes for each species (Greig-Smith, 1983b). For a single species, Morisita's index can be used (Morisita, 1962):

$$I_\delta = n\Sigma(X^2)-\Sigma(X)/(\Sigma X)^2-\Sigma X$$

where n is the number of samples taken and X is the number of plants within each sample. This index can be determined for each quadrat size used. If q is the size of the beginning quadrat and $I_\delta 1$ is its index then 2q can be used for the next quadrat size and $I_\delta 2$ as its index. A plot of $I_\delta 1/I_\delta 2$ for each successive pair of quadrat sizes will show a sharp spike ($I_\delta 1:I_\delta 2 > 1$) when the patch size is reached (Elliott, 1979). By using the correct quadrat size, fewer samples will be needed to detect the patch size of the species (Greig-Smith, 1983b).

If musk thistle microsite requirements are an important determinant of spatial dispersion patterns, then a difference in the amount of clumping of individuals may be detected between different environmental conditions. To detect this difference an index of clumping can be determined (Greig-Smith, 1983b):

$$w = -1/2 \ln (V_1 h_2/V_2 h_1)$$

where V_1 and V_2 are the variances and h_1 and h_2 are the means associated with the clumping of individuals from the two different environments. If w lies outside the range ±2.5/n-1, where n equals the number of quadrats used, then a significant difference in clumping exists between environmental conditions (Greig-Smith, 1983b).

The purpose of this study was to determine the densities and degree of aggregation of musk thistle seedlings and over-wintering rosettes in grazed and ungrazed grasslands. The influence of microsite differences and quadrat size are considered with respect to estimating these parameters.

Methods and Materials

Study site

The study site used in 1985 and 1986 was located 1 Km NE of Bozeman, Gallatin Co., MT. in SE1/16 of NW1/8 of NW1/4 of Section 5, R6E, T2S at an elevation of 4760 ft. The site contained both dry ridge and wetter swale areas. One ridge and swale area was fenced in late spring, 1985 to prevent cattle grazing. A similar area was left open to grazing. The wet swale areas at this site tended to have higher thistle densities and were dominated by perennial grass cover making them ideal for this study. This site was also unique in that it contained no other thistle species whose seedlings could be mistaken for those of musk thistle.

Density and distribution

Two transects were randomly placed within the grazed and ungrazed areas of the site and twenty 1/2 m^2 frames (centered on adult plants) were established along each transect in late spring of 1985. Pins were placed at the corners of these frames to provide a reference for later mapping of musk thistle seedlings and rosettes. The height, rosette size, and canopy size of adult thistles in these quadrats were measured throughout the summer.

In spring of 1986 the transects, both within and outside the fenced area, were revisited. Every seedling and rosette within each frame was mapped as to its size and location. Densities of rosettes and seedlings could then be determined for each frame. It was also possible to project different quadrat sizes over the mapped area by using a grid system (Kershaw, 1960). Counts of plants within each successive-sized quadrat could then be used to estimate the best size for determining seedling and rosette patch size. The following quadrat sizes were used for these projections: 1/16 m^2, 1/8 m^2, 1/4 m^2, and 1/2 m^2. Pielou (1969) has questioned the statistical validity of this method for determination of patch size but she has concluded that its use has been of considerable value in studies of this type.

In order to compare random versus plant-centered seedling/rosette densities and distributions, two additional transects were added during spring of 1986, one was randomly positioned inside the fenced area and the other outside. Twenty 1/2 m^2 frames were placed at meter intervals along each of these transects and seedling and rosette counts were taken.

Statistical methods

Multifactor ANOVA was used to assess density differences due to grazing and plant sampling treatments found in the spring of 1986.

For the determination of patch size, Morisita's index was used (Morisita, 1962). The "I_δ" values for each quadrat size were compared and plotted to determine the ratio of highest value, which indicated the patch size. Using this patch size the variance/mean ratio or coefficient of dispersion was calculated for grazed and ungrazed areas and tested for significance using a Chi-square test (Kershaw, 1974).

Clumping under grazed and ungrazed treatments as well as plant-centered and random quadrat treatments were compared using an index of clumping, w (Greig-Smith, 1983b).

Linear regression analysis was used to compare adult plant characteristics such as rosette size, plant height, and canopy size to rosette and seedling densities within plant-centered frames.

Results and Discussion

Thistle densities

Both seedling and rosette densities were significantly lower in the ungrazed plot than in the grazed plot after a single season of relieved grazing ($P < 0.01$, 1986, Table 7). Reduced musk thistle seed germination and high rosette mortality as a result of plant competition has been previously demonstrated (Popay and Thompson, 1979). A rapid decline in thistle densities has also been documented by Horber (1980) on ungrazed sites in Kansas. Grazing probably contributes to thistle establishment by providing germination sites and reducing competition between thistles and the surrounding vegetation. The animals' direct removal of plant material as well as trampling of competing vegetation accounts for the reduced competition.

Seedling counts obtained from plant-centered quadrats were similar to those obtained from random quadrats (Table 7). The fact that similar seedling densities were found in randomly-spaced quadrats

Table 7. Seedling and rosette densities under different grazing and sampling methods, Bozeman, Montana 1986 (n = 20 for each category).

Category	Seedlings[a]	Rosettes
Treatment	(no./m^2 ± SE)	
Grazed	31.84 ±15.91b	5.00 ± 2.62b
Ungrazed	9.85 ± 8.00a	1.50 ± 1.25a
Sampling method		
Plant-centered	22.10 ±15.60a	4.35 ± 3.11b
Random	19.60 ± 9.74a	2.15 ± 1.89a

[a] Values within a column under each category without a letter in common were significantly different ($P < 0.01$).

suggests that musk thistle has 1) a distribution of seed which though random at a small scale is more uniform at a larger scale and 2) an effective ability to colonize new microsites within an area. In contrast, significantly higher rosette densities were found within plant-centered quadrats ($P < 0.01$). Plant centered quadrats may be wetter than random quadrats due to snow trapping (Harris, 1984), site configuration, or soil condition. The use of this excess moisture for establishment may explain the greater rosette densities obtained near these established plants.

Patch size

The observation of clumping was maximized with 1/4 m^2 quadrats for musk thistle seedlings and rosettes. A patch size of 1/4 m^2 was most obvious in grazed areas (Figure 1). The fact that seedling and rosette patch sizes were similar is not surprising when one considers that a surviving seedling will produce a rosette in the same position that it germinates.

Coefficient of dispersion for grazing treatments

Examination of the coefficient of dispersion with respect to grazing treatments (Table 8) showed that seedlings demonstrated a significant degree of clumping in both grazing regimes ($P < 0.01$), while rosettes did not. Significant clumping of seedlings suggested that certain microsites were preferred for germination within grazed and ungrazed areas. A lower degree of clumping among rosettes than seedlings could arise in two ways. A less aggregated spacing might be expected if a quadrat which contained few if any seedlings had rosettes which established in earlier years. A more likely explanation however, is that intraspecific competition during rosette establishment within certain quadrats resulted in death of many seedlings in each clump and therefore a less aggregated distribution within specific quadrats. Differences in rosette distribution estimated using different sampling methods are discussed below.

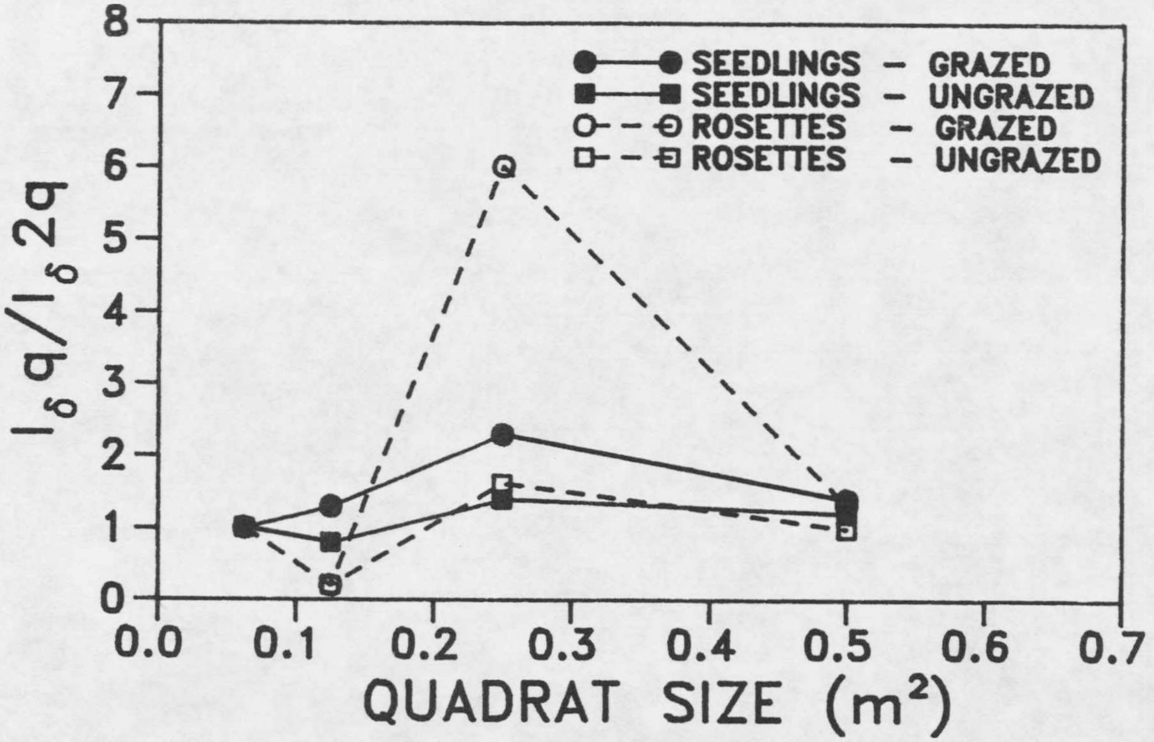

Figure 1. Ratio's of Morisita's index for seedlings and rosette musk thistles around adult thistle plants under varying conditions of grazing.

Table 8. Coefficient of dispersion for seedlings and rosettes of musk thistle plants under different grazing treatments and sampling methods. Asterix (*) indicates significant clumping.

	Seedlings[c]	Rosettes
Treatment[a]		
Grazed	7.95*	1.37
Ungrazed	6.50*	1.04
Sampling method[b]		
Plant-centered	11.02*	2.23*
Random	4.84*	1.67*

[a] Plant-centered 1/4 m^2 quadrats, n = 20 (optimal size for clump detection).

[b] 1/2 m^2 quadrats, n = 40.

Coefficient of dispersion for sampling method

Both seedlings and rosettes were found to be significantly clumped in random and plant-centered quadrats (Table 8). However, Plant-centered quadrats which were used to detect the spacial dispersion pattern on grazed and ungrazed plots did not show clumping of rosettes (Table 8). This difference could indicate that the 1/4 m^2 quadrat size was not the true patch size for rosettes on ungrazed plots (Figure 1). Therefore the use of a reduced number of quadrats (n = 20) while making grazing comparisons, would require a larger coefficient of dispersion to show significance. Note that the coefficient of dispersion was greater for both seedling and rosette thistles under previous year adult plants. Musk thistle microsite requirements appeared to be selective, favoring seedling and rosette establishment sites proximate to certain previous-year adults. This difference will be addressed below using an index of clumping.

Index of clumping between grazing treatments

No difference in clumping was found for seedlings occurring in the two different grazing regimes (Table 9). In other studies over ninety-five percent of fully developed musk thistle seeds were found to germinate regardless of the date of bloom (McCarty and Lamp, 1982) and ninety percent germination within a single year of sowing has been demonstrated (Roberts and Chancellor, 1979). This suggests that perhaps germination is not the most critical phase in thistle phenology and that seeds within a clump are able to germinate regardless of competing vegetation. The fact that seedlings had a significant coefficient of dispersion under both grazing conditions indicates that contagiousness was more likely due to seed distribution rather than specific germination requirements as influenced by plant competition.

When the index of clumping under the two conditions of grazing was determined for rosettes, they were found to be slightly more aggregated in the grazed site after a single year (Table 9, 1986). Despite the fact that rosettes were found to be randomly distributed as measured by the coefficient of dispersion (Table 8), a higher degree of clumping of rosettes in the disturbed, grazed area indicated that more seedlings established in specific microsites found there.

Index of clumping between sampling methods

The use of the clumping index (w) on seedlings employing different sampling methods showed significantly greater clumping under adult plants (Table 9, 1986). This indicated that either more seeds fell directly to the base of some mature plants or that germination was enhanced at the base of some adults.

Seedling densities within plant-centered quadrats were significantly correlated with the initial rosette size of the adult thistle they germinated under ($r = 0.44$, d.f. = 39, $P = 0.02$). When the analysis was conducted using data from relieved grazing conditions alone this relationship was even more pronounced ($r = 0.56$, d.f. = 19, $P = 0.01$). This supports the hypothesis of Lee and Hamrick (1983), that rosette size is the best predictor of reproductive success in musk thistle. Observations by Rees (1982) have shown that only two percent of the seeds are tightly attached to the pappus, thus the majority fall to the base of the plant. Larger plants appear to drop more seeds to their base increasing the density of seedlings at those microsites. This may be enhanced under conditions of grazing due to trampling and feeding around the periphery of these same plants. High moisture content under larger adult plants due to winter snow accumulation mentioned above (Harris, 1984) and the fact that high moisture enhances thistle germination (Medd and Lovett, 1978a), may also account for some increased seedling numbers under larger adult plants.

Table 9. Index of clumping (w) for seedlings and rosettes of musk thistle under different grazing treatments and sampling methods. Asterisk (*) indicates a significant difference in clumping between treatments.

	Seedlings	Rosettes
Grazing[a]	-0.1009	-0.1356*
Sampling Method[b]	-0.4110*	-0.1450*

[a] Plant-centered 1/4 m^2 quadrats, n = 20 (optimal size for clump detection)

[b] 1/2 m^2 quadrats, n = 40

When an index of clumping was used to compare plant-centered versus random rosette distribution a significant difference was noted (Table 9). This further supports the suggestion that microsites occur around some adult plants which enhance establishment.

Regression analysis showed a negative relationship between rosette densities and adult plant canopy size under grazing pressure (r = -0.57, d.f. = 19, P = 0.09). Light is a very important factor for young seedling development as between 20-30% full sunlight is needed for maximum growth (Medd and Lovett, 1978a). Since the rosettes sampled established during the previous growing season under these adult plants, light availability appeared to be an important factor influencing this establishment. It is important to note that although rosette densities tended to be greater under all adults, rosette establishment was better under smaller canopied adults (as inferred from the regression analysis).

Summary

This study demonstrated the importance of grazing pressure and microsite conditions on musk thistle seedling/rosette survival, establishment, density, and spatial dispersion.

Relieved grazing reduced seedling and rosette densities by reducing the number of sites available for thistle establishment.

Seedlings occurred most commonly under large previously established adult plants regardless of grazing treatment. The preference for these microsites was probably due to increased moisture content and higher seed dispersal under these larger plants.

Rosettes were clumped under small canopied adults primarily on grazed plots.

CHAPTER 4

EFFECTS OF TERMINAL FLOWER LOSS ON GROWTH AND REPRODUCTION OF MUSK THISTLE

Introduction

Terminal flower heads of musk thistle are the first to flower and tend to produce the best quality seeds (McCarty, 1981). Approximately 1000 seeds/head can be produced if they are allowed to mature on the plant. Lateral heads continue to be produced for up to four weeks after terminal heads bloom, but seed production declines to only 12 seeds/head for the lower most flowers (McCarty, 1981).

R. conicus, an introduced seed head weevil, attacks musk thistle by laying many eggs on flower head bracts. Hatching larvae feed continually within the receptacle of a flower until they reach the pupal stage and clipping of the flower prior to pupation causes near total weevil mortality (Rees, 1980). Weevils may induce the production of callus material primarily during the white pappus (preopening) stage of the terminal head. This material can be used as additional food by other larvae and its production further consumes plant resources (Shorthouse and Lalonde, 1984). Severe weevil attack can also cause total abortion of terminal heads (Kok and Surles, 1975; Rees, 1979).

Native insect predators may affect insects introduced for biological control of weed species and thus the target weed itself. In the case of spotted knapweed, Centaurea maculosa Lamarck, mortality of the seed head flies Urophora affinis Frauenfeld and U. quadrifasciata Meigen has occurred as a result of small rodent and avian predation (J.

Story pers. comm.).

Similarly *R. conicus* growth was inhibited by cropping of musk thistle seed heads by an unknown predator at our musk thistle research sites. It is conceivable that the predator(s) may be harvesting the thistle heads to obtain a rich protein source offered by the seed head weevil, *R. conicus* (Chapter 2).

The purpose of this aspect of the study was to determine the response of musk thistle to terminal flower loss, such as that which might be induced by high population levels of *R. conicus* or by a predator of *R. conicus* predator. The effects were tested at various growth stages and under varying environmental conditions. This information was used in a companion study to assess the relative impacts of the seed head weevil and plant competition on the population dynamics of musk thistle.

Methods and Materials

Field experiment

An overgrazed pasture approximately 25 miles west of Bozeman, Montana was fenced to relieve cattle grazing in early summer of 1985. The site was located in NW1/16 of NW1/8 of SE1/4 of section 33, R3E T1S at an elevation 4600 feet. Later in the summer, eighty plants at this site were tagged to observe the effects of relieved grazing. Forty of these were within the enclosure and forty were outside. Upon tagging of these plants it was noticed that a substantial number of plants (55 of 80 ; 30 inside and 25 outside) had lost their terminal flower due to cropping by an unknown predator. An additional six plants lost their terminals later in the season leaving only 19 plants (8 inside and 11 outside) with terminal flowers. Both plants with heads and headless plants were monitored for growth throughout the summer and harvested in late August.

Greenhouse experiment

Thirty-six musk thistle rosettes were collected in mid October, 1985 from a single site 8 mi. W of Bozeman, Montana, Gallatin Co. (NE1/16 of SE1/8 of NE1/4 of section 14, R4E T2S) at an elevation of 4720 feet. The rosettes were transplanted into six inch round pots containing sterile soil mix of equal volumes of silt loam, sand, and peat. Prior to bolting of shoots, 36 pots were objectively selected for uniformity of plant size and then randomly divided into 9 blocks. To determine effects of the timing of terminal flower loss, one of the following four treatments was assigned to one of 4 pots in each block: 1) control, 2) terminal removed at bud stage, 3) terminal removed at preopening, white pappus stage and, 4) terminal removed at full bloom, purple pappus stage. The plants were then placed on a greenhouse bench in a randomized complete block design. Pots within blocks were systematically rotated weekly to reduce bench location and edge effects. All plants were watered with a standard nutrient solution three times weekly. A photoperiod of 16 hrs. light and 8 hours dark was maintained with wide spectrum fluorescent lighting. Minimum day and night temperatures were maintained at 23° and 18° C, respectively. Insecticidal soap was periodically applied to all plants to control white fly populations.

After two months of rosette growth, no bolting was evident so bolting was initiated by application of gibberellic acid (GA_3). A stock solution of 30 mg of GA_3 dissolved in 0.1 ml of dimethyl sulfoxide (DMSO) and diluted to 100 ml with distilled water was prepared. Four one ml doses of this stock solution per plant over a 45 day period (total dose 1.2 mg GA_3 per plant) were required to initiate bolting.

Artificial pollination of flowers was required because of the lack of insect pollinators in the greenhouse. Flowers were randomly cross-pollinated by transferring pollen between flowers on different plants with an artists paintbrush. Plants were harvested in May of 1986.

Thirty three percent of the plants were eliminated from the analysis. Four plants died early from unknown causes, three plants reached a height of approximately 25 cm and grew no further, and five plants produced no terminal flower for unknown reasons. These losses reduced the degrees of freedom and prevented the use of blocks.

Field and greenhouse analysis

Plant material from the field and greenhouse was separated into vegetative (main stem and lateral branches) and reproductive (terminal and lateral flower heads) categories and placed in separate bags, and dried in an oven for one week. Quantity and biomass of vegetative and reproductive plant parts were then determined. A two-way ANOVA was used to compare environmental treatments (i.e. greenhouse, grazed and ungrazed pasture) and terminal removal (i.e. terminal loss or no terminal loss) treatments. Interaction effects demonstrated from the initial analysis were subsequently explained using single factor ANOVA.

Field analysis

A similar two-way ANOVA was run using only pasture grown thistles and early or late terminal loss. Again, the resulting interaction effects were explained using single factor ANOVA.

Greenhouse analysis

Single factor ANOVA was used to compare only greenhouse plants experiencing terminal removal at different stages.

Results and Discussion

Field and greenhouse comparisons

No significant difference in total thistle biomass was detected among greenhouse, grazed field and ungrazed field conditions ($P > 0.05$, Table 10). It was concluded, therefore, that any biomass allocation differences among the environmental treatments were environmentally induced.

Thistles grown under relieved grazing had a significantly lower reproductive biomass (flowers and seeds) than those grown under grazed conditions. Field grown thistles produced fewer seeds and consequently had a lower seed biomass than those grown in the greenhouse ($P < 0.05$, Table 10). Reduced reproductive biomass under increasing environmental stress was probably due to the low number of lateral seed heads on plants grown under high plant competition ($P < 0.05$, Table 10).

Thistles grown under grazing produced 50% more vegetative laterals than greenhouse grown plants (Table 10). This increase in vegetative lateral growth was apparently at the expense of seed production (Table 10). Further analysis of vegetative lateral production is made below.

Greenhouse and field grown thistles which lost their terminals had fewer seed heads per vegetative lateral than intact plants ($P < 0.05$, Table 10). However, terminal loss caused no effect on total seed numbers or biomass ($P > 0.05$). Surles and Kok (1978) also found no reduction in total seed production in greenhouse grown thistles whose terminals were removed. Thistles appeared to compensate for terminal loss by decreasing the number of seed heads per lateral branch and increasing the number of seeds within these heads.

A significant interaction between environment and terminal loss was obtained when comparing treatments with respect to biomass per seed ($P < 0.05$, Table 10). Plants grown in ungrazed pastures which had not lost their terminals produced a higher biomass per seed than those grown under grazing (Table 11). If the terminals were lost however, the effect of grazing on seed weight was not significant. It appeared that thistles which experienced increased grass competition (due to a lack of grazing) tended to produce especially heavy seeds in their terminal flowers. Heavy seeds would be advantageous for thistles establishing under competition.

McCarty (1982) found that musk thistle directs a substantial amount of energy toward terminal flower production. We determined that thistles experiencing increased plant competition directed even more energy toward terminal flowers by producing heavier seeds . This could be significant for bio-control efforts since _R_. _conicus_ tends to do its greatest damage to terminal flower heads (Laing and Heels, 1978). The combination of relieved grazing and weevil attack may reduce the reproductive capacity of the thistle significantly.

Table 10. Vegetative and reproductive growth of musk thistle plants under varying environmental condition and terminal flower condition.

	Total biomass (gm)	Vegetative biomass (gm)	Reproductive biomass (gm)	Number of vegetative laterals	Number of lateral seed heads
Growth Environment					
Greenhouse	14.5 ± 1.1a	10.2 ± 0.6	4.3 ± 0.5ab	3.6 ± 0.4a	6.7 ± 0.9ab
Grazing	19.6 ± 2.9a	13.8 ± 2.0	5.1 ± 0.8a	5.4 ± 0.4b	9.0 ± 1.0a
Ungrazed	10.6 ± 1.6a	8.2 ± 1.3	2.3 ± 0.4b	4.1 ± 0.3ab	4.9 ± 0.6b
Terminal flower					
Present	17.7 ± 2.2	12.5 ± 1.7	4.9 ± 0.7	3.8 ± 0.3	7.9 ± 1.2
Absent	13.8 ± 1.5	10.2 ± 1.1	3.5 ± 0.4	4.7 ± 0.2	6.5 ± 0.6

	Number of seed heads per lateral[a]	Seed biomass (gm)	Total number of seeds	Biomass per seed[b] (mg)
Growth Environment				
Greenhouse	3.3 ± 0.2a	0.9 ± 0.1a	447.9 ± 65.2a	2.1 ± 0.07
Grazing	1.8 ± 0.2b	0.5 ± 0.1b	245.4 ± 38.3b	2.0 ± 0.10
Ungrazed	1.2 ± 0.1b	0.2 ± 0.0b	102.4 ± 23.5b	2.2 ± 0.10
Terminal flower				
Present	2.5 ± 0.4a	0.5 ± 0.1	244.3 ± 52.7	2.2 ± 0.18
Absent	1.7 ± 0.1b	0.5 ± 0.1	234.8 ± 30.3	2.1 ± 0.07

[a] Values within a column within category followed by different letters were significantly different ($P < 0.05$, Tukey's studentized range test.

[b] Significant interaction between grazing and time of terminal loss ($P < 0.05$).

Table 11. Interaction between environment and loss of terminal flower as expressed by per seed biomass.

Terminal flower	Greenhouse	Grazed Pasture	Ungrazed Pasture	P-value[b]
	Plant growth environment			
	mg/seed			
Present[a]	2.2 ± 0.13ab	1.7 ± 0.20a	2.7 ± 0.39b	0.04
Absent	2.0 ± 0.01	2.1 ± 0.01	2.0 ± 0.14	0.91
P-value[b]	0.17	0.09	0.06	

[a] Values within a row without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

[b] P-values from single factor ANOVA.

Field comparisons

When greenhouse grown thistles were eliminated from the analysis significant differences in musk thistle reproductive output between grazing treatments were noticed. Thistles grown in the ungrazed area had significantly lower reproductive and seed biomass, reduced seed numbers, ($P < 0.05$, Table 12) and higher biomass per seed ($P < 0.05$, Table 12). This affect did not interact with the time of terminal loss. It appeared that the plants grown under competition concentrated nutrients into a few seeds rather than producing many seeds.

Table 12. The effect of environment and time of terminal flower loss on musk thistle growth in the field, 1985.

	Total biomass (gm)	Vegetative biomass (gm)	Reproductive biomass[a] (gm)	Number of vegetative[b] laterals	Number of lateral seed heads
Environment					
Grazing	19.6 ± 2.9	13.8 ± 2.0	5.1 ± 0.8a	5.4 ± 0.4	9.0 ± 1.0a
No grazing	10.6 ± 1.6	8.2 ± 1.3	2.3 ± 0.4b	4.1 ± 0.3	4.9 ± 0.6b
Terminal loss					
No loss	19.0 ± 2.9	13.5 ± 2.2	5.0 ± 1.0	3.9 ± 0.4	8.4 ± 1.5
Early loss	13.7 ± 2.1	10.2 ± 1.6	3.2 ± 0.6	4.9 ± 0.3	6.5 ± 0.8
Late loss	11.5 ± 1.9	8.5 ± 1.5	3.3 ± 0.9	6.0 ± 1.0	6.6 ± 1.4

Category	Number of seed heads per lateral	Seed biomass (gm)	Total Number of Seeds	Biomass per seed (mg)
Environment				
Grazing	1.8 ± 0.2	0.5 ± 0.1a	245.4 ± 38.3a	2.0 ± .1a
No grazing	1.2 ± 0.1	0.2 ± 0.0b	102.4 ± 23.5b	2.2 ± .1b
Terminal loss				
No loss	2.3 ± 0.4a	0.3 ± 0.1	179.4 ± 49.1	2.2 ± .2
Early loss	1.2 ± 0.1ab	0.3 ± 0.1	160.3 ± 27.6	2.1 ± .1
Late loss	1.0 ± 0.1b	0.6 ± 0.3	259.5 ±108.3	2.2 ± .2

[a] Values within a column within category followed by different letters were significantly different ($P < 0.05$, Tukey's studentized range test.

[b] Significant interaction between grazing and time of terminal loss ($P < 0.05$).

Presumably, by increasing endosperm reserves, thistles have adapted to insure a more vigorous seedling which can compete more successfully with surrounding vegetation upon germination. Dowd and Kok (1983) also found that thistles grown under nutrient and moisture stress produced normal seed, and that R. conicus within these plants were therefore significantly smaller. Thistles were apparently able to reallocate enough nutrients under stress to both fill seeds and mature weevils, at least under moderate levels of weevil infestation.

As seen during the first analysis, terminal loss tended to reduce the number of seed heads per lateral branch (Table 12) without affecting total seed numbers or weight. This was especially true for those plants which lost terminals late in the growing season. This suggests either that there was insufficient time to produce these late blooming flowers or that the plant responded to terminal loss in the field by concentrating nutrients within fewer heads as described before. The second hypothesis is supported by analysis of greenhouse results alone.

A significant interaction between environment and time of terminal loss was obtained by comparing the number of vegetative lateral branches per plant ($P < 0.05$, Table 12). Plants in grazed pastures, which had lost their terminals, produced an unexpectedly large number of lateral branches ($P < 0.05$, Table 13) and the later the terminal loss occurred the greater the increase in lateral stem numbers (Table 13). Increased lateral growth in response to terminal loss was also seen in greenhouse grown plants and will be discussed below. However, thistles which grew in ungrazed areas did not bloom laterally in

Table 13. The interaction between grazing and time of terminal loss on the number of vegetative lateral branches produced by field grown musk thistle plants, 1985.

	Plant growth environment		
	Grazed Pasture	Ungrazed Pasture	P-value[b]
No terminal loss	4.1 ± 0.5a	3.6 ± 0.7a	0.516
Early terminal loss	5.6 ± 0.5b	4.3 ± 0.0a	0.023
Late terminal loss	7.5 ± 0.7c	3.0 ± 0.0a	0.003
P-value[b]	0.024	0.328	

[a] Values within a column or row without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

[b] P-value from single factor ANOVA.

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response to terminal loss. This demonstrated again the thistles' inability to adapt to a combination of terminal loss and added environmental stress caused by increased grass competition.

Greenhouse experiment

Greenhouse thistles, having ample moisture and nutrients, showed a remarkable ability to recover from the loss of their terminal flower. Few significant differences in yield or allocation among plants that lost their terminals or with terminals intact were detected (Table 14).

Their was a tendency for plants suffering late terminal loss to have reduced reproductive capacity, however. In a similar study, McCarty (1982) found that greenhouse grown thistles whose terminals were removed soon after full bloom produced only 26 seeds/plant as compared to 3580 seeds/plant for those with no seed head removal.

Plants which lost their terminals in the bud stage tended to produce significantly more reproductive biomass than plants losing terminals during full bloom primarily due to increased seed production (Table 14). There was only one reversal in this trend and that was in terms of vegetative lateral stem production. Plants losing their terminals after full bloom tended to produce even more laterals than plants which lost their terminals during the bud stage (Table 14). The increase in lateral stems due to late terminal loss is similar to field grown thistles under relieved grazing. Production of laterals appears to be a "last resort" effort by the plant to compensate for terminal loss under good growing conditions.

Unlike field grown thistles, greenhouse plants which lost their terminals did not differ in the number of seed heads / lateral branch. Apparently the increased availability of nutrients and moisture decreased this response to terminal loss and adds support to the idea that thistles losing terminals under field conditions respond by concentrating nutrients into fewer flower heads.

Table 14. The effect of the time of terminal flower loss on musk thistle growth in the greenhouse, 1986.

Terminal flower phenology upon removal	Total biomass (gm)	Vegetative biomass (gm)	Reproductive biomass (gm)	Number of vegetative laterals	Number of lateral seed heads
Not removed	14.1 ± 1.1	9.6 ± 0.6	4.4 ± 0.60ab	3.6 ± 0.6	6.1 ± 0.7
Bud	17.8 ± 3.0	11.5 ± 1.8	6.3 ± 1.31a	4.3 ± 1.0	10.0 ± 3.2
White pappus	13.9 ± 1.8	9.9 ± 1.2	4.0 ± 0.73ab	2.8 ± 0.3	5.6 ± 0.7
Purple pappus	12.2 ± 2.1	9.6 ± 1.5	2.6 ± 0.69b	3.6 ± 1.1	5.0 ± 1.1

Terminal flower phenology upon removal	Number of Seed heads per lateral	Seed biomass[a] (gm)	Total Number of Seeds	Biomass per seed (mg)
Not removed	3.0 ± 0.5	1.0 ± 0.3ab	428.3 ±126.1ab	2.2 ± 0.1
Bud	2.8 ± 0.5	1.6 ± 0.3a	712.8 ±139.1a	2.1 ± 0.1
White pappus	3.7 ± 0.4	0.8 ± 0.2ab	415.7 ± 99.4ab	2.1 ± 0.1
Purple pappus	3.5 ± 0.6	0.5 ± 0.2b	234.7 ± 98.7b	1.1 ± 0.1

[a] Values within a column without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

Summary

Since R. conicus attacks primarily terminal seed heads and abortion of these heads often occurs during times of heavy weevil infestation, the weevil may initiate thistle compensatory growth responses (Cartwright and Kok, 1985). Thistles whose terminals were aborted, and whose nutrient supply was adequate (i.e. low grass competition) would benefit by producing many secondary vegetative lateral branches with fewer lateral flower heads to which the weevil could not respond under normal univolting conditions (Chapter 2). On the other hand increased grass competition, caused by relieved grazing, reduces the thistles ability to reallocate nutrients toward secondary growth. The combination of increased grass competition and R. conicus damage would thus reduce seed production and lessen the time necessary to control musk thistle on overgrazed sites.

CHAPTER 5

EFFECTS OF INSECTICIDES ON GROWTH AND REPRODUCTION OF MUSK THISTLE

Introduction

The effect of insecticides on photosynthesis and growth in higher plants has been little studied, especially in comparison to the effects of herbicides on plants. Ferre (1979) has suggested, however that insecticides should be screened for their influences on plant photosynthesis and reproduction. Legal application limits for insecticides shown to have phytotoxic effects have been suggested by Toscano, et al. (1982a, 1982b).

Studies have shown that the major effect of herbicides on plant photosynthesis is inhibition of plastoquinone activity within the thylakoid (Murthy, 1983). Carbamates and organophosphate insecticides, carbaryl and monocrotophos, for example were found to be similar to herbicides affecting electron transport within the thylakoid membrane of pecans (Wood and Payne, 1984).

Organophosphates may affect other metabolic pathways as well. Terbufos has increased yields of grasses within forest biomes (Kelly and Klostermeyer, 1985). Monocrotophos and dicrotophos have caused toxic glucoside storage in beans (Garner and Menzer, 1986) while malathion inhibits protein synthesis in _Vigna_ _sinensis_ L. seeds by reducing incorporation of amino acids into cellular membranes (Chakraborti, et al., 1982). Malathion also inhibits membrane hydrolytic enzymes but, when combined with gibberellic acid (GA_3)

treatments, this inhibition is reduced (Chakraborti, et al., 1983). Malathion also affects cellular membranes by causing increased permeability to K^+ and Ca^{++} (Antunes-Madeira and Antunes-Madeira, 1979) and decreases stem elongation in alfalfa when used in a 1:1 combination with methoxychlor (Fick, 1977).

Aldicarb, a carbamate, when applied to chrysanthemums, increases their rate of development and the number of flowers produced per plant (Baun and Peterson, 1981). The carbamate carbaryl increases photosynthesis in apples (Ayers and Barden, 1975), but is phytotoxic to oats and cucumbers (Nash and Harris, 1973).

Insecticides have been used as a tool in biological control studies to exclude insect natural enemies of weeds and enable the comparison of weed population dynamics with and without natural enemies (Andres, pers. comm.). However, the direct effects of insecticides on the growth and reproduction of the target weeds have not been previously considered in biological control studies. The purpose of this study was to assess the effects of aldicarb and malathion alone and in combination, on the growth and reproduction of musk thistle. This information could then be used to determine whether the insecticides are validly used to compare musk thistle dynamics in the presence or absence of an insect (i.e. *Rhinocyllus conicus*).

Methods and Materials

Experimental design

One-hundred musk thistle rosettes were collected in mid-October, 1985 from a site 1Km NE of Bozeman, Gallatin Co., Montana (NE1/16 of

SE1/8 of NE1/4 of section 14, R4E T2S) at an altitude of 4720 ft. Rosettes were transplanted into six inch round pots containing a sterile soil mix with equal volumes of silt loam, sand, and peat. Prior to bolting, 55 pots were selected for uniformity of plant size and randomly divided into 11 blocks. One of the following five treatments was then assigned to each pot of each block: 1) control, 2) low aldicarb, 3) high aldicarb, 4) malathion, and 5) low aldicarb plus malathion. The plants were then placed on a greenhouse bench in a randomized complete block design. Pots within blocks were rotated weekly to eliminate the effects of bench location. The 45 remaining pots of musk thistle were placed around the perimeter of the experiment to minimize edge effects.

All plants were watered with a standard nutrient solution three times per week. A photoperiod of 16 hrs. light and 8 hrs. dark was maintained with wide spectrum fluorescent lighting. Minimum day and night temperatures were maintained at 23° and 18° C, respectively. Insecticidal soap was applied to all plants periodically to control white fly populations.

Bolting and pollination

After two months of rosette growth, no bolting was evident. Bolting was therefore induced by application of gibberellic acid (GA_3). A stock solution of 30 mg of GA_3 dissolved in 0.1 ml of dimethyl sulfoxide (DMSO) and diluted to 100 ml with distilled water was prepared. Four one ml doses of this stock solution per plant over a 45 day period (total dose 1.2 mg GA_3 per plant) were used to initiate bolting.

The flowers were artificially pollinated because of the lack of insect pollinators in the greenhouse. The flowers were randomly cross-pollinated by transferring pollen between flowers on different plants with an artists paintbrush.

Treatment application

Insecticide treatments were first applied in mid- February, 1986, 21 days after bolting was initiated and prior to emergence of the terminal flower bud. A single application of granular aldicarb [2-methyl-2-(methylthio) propionaldehyde-O-(methylcarbamoyl)oxime] was applied at a rate of 10 kg ai/A (0.23 gm/plant) for the low aldicarb treatment, and at 10x this recommended rate for the high aldicarb treatment (100 kg/A or 2.33 gm/plant). Malathion (0,0-dimethyl phosphorodithioate of diethyl mercaptosuccinate) was applied weekly at a rate of 16 oz ai/A (0.02 ml/plant) by hand spraying. To prevent contamination of non-malathion-treated plants, pots receiving malathion treatments were removed from the experiment bench to an insecticide application area, treated as prescribed, and returned to the bench after 2 hours.

Analyses

Rosette size prior to treatment assignment and application of GA_3 was recorded and an analysis of variance (ANOVA) performed to test for uniformity of plant size. Prior to the first treatment application, the height of each plant was recorded and an ANOVA was performed to demonstrate uniformity across treatments and blocks. All subsequent height measurements were recorded as changes in height from the pretreatment height. Plant heights were measured weekly until the plants were harvested for biomass analysis.

Four months after the initial treatment each plant was harvested at ground level and the individual plant parts were separated into the following categories: 1) terminal flowers, 2) lateral flowers, 3) main shoot, and 4) vegetative lateral shoots. Plant parts from individual plants were then placed in separate paper bags, oven dried for ten days at 35° C, and weighed. All flower heads were dismantled and the seeds counted and weighed. Yields of all plant parts, including seed number and biomass, were compared across treatments with ANOVA and Tukey's Studentized Range test (Neter, et. al., 1985).

Results and Discussion

Growth responses

Musk thistle rosettes had a mean (±SEM) area of 1145 cm^2 ± 19.38 when transplanted; no significant differences in initial rosette area were found among the treatments ($P = 0.80$). The mean height of these plants after bolting and just prior to treatment application was 44.47 cm ± 2.88 and did not differ among treatments ($P = 0.21$).

Growth responses of musk thistle to the five different treatments are shown in Table 15 and Figure 2. Neither the low aldicarb nor the low aldicarb-plus-malathion treatment affected the height growth of musk thistle ($P > 0.05$, df = 16). In contrast, both malathion and high aldicarb significantly reduced height growth ($P < 0.01$, df = 16). The pattern of growth reduction was different for the malathion and high aldicarb treatments. Growth of high aldicarb-treated plants was

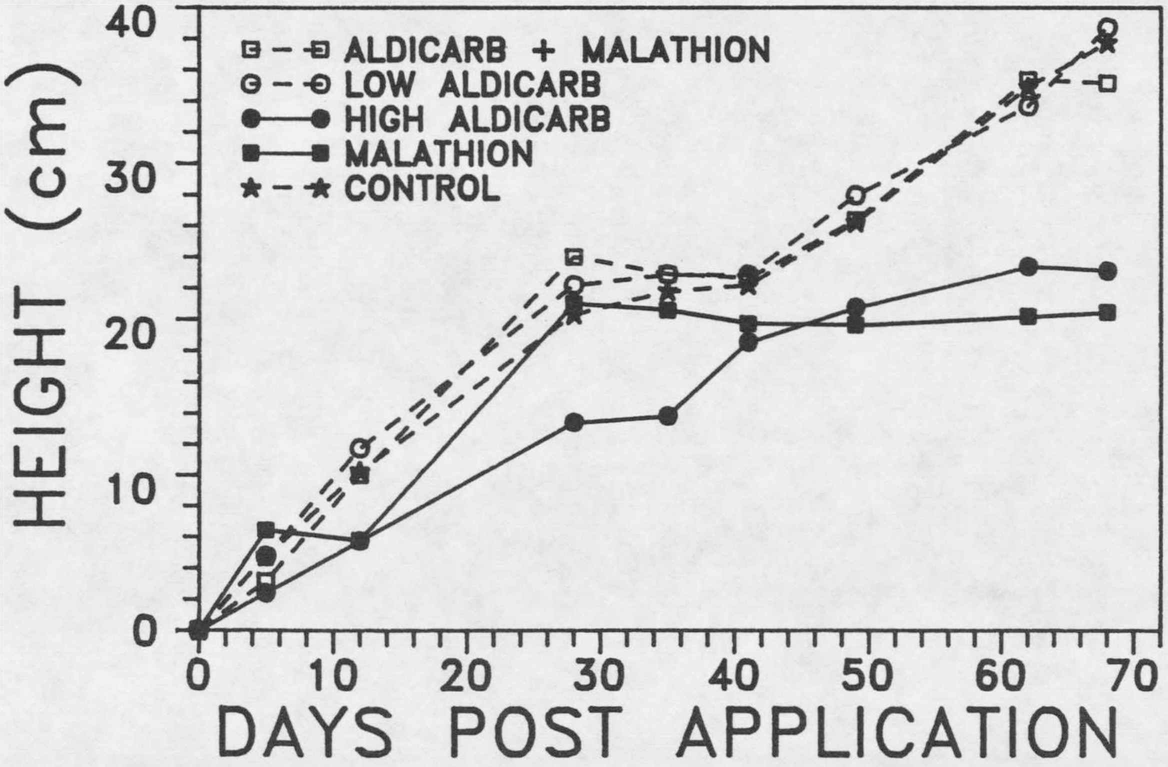

Figure 2. Growth of greenhouse grown musk thistle plants under different insecticide treatments (Bozeman, MT 1985-86).

Table 15. Regression parameters for musk thistle growth response to five different insecticide treatments.

Treatment n = 9	y-intercept (a)	slope (±SE) (b)	Correlation coefficient
Control	2.42	0.52 ±0.028a	0.99
High aldicarb	1.47	0.36 ±0.026b	0.98
Low aldicarb	3.21	0.52 ±0.037a	0.98
Aldicarb-plus-malathion	2.84	0.51 ±0.048a	0.97
Malathion	5.23	0.29 ±0.069b	0.85

aSlopes without a letter in common were significantly different using a students t-test (P < 0.01).

reduced immediately and was reduced by 31% during the entire post-treatment period. In contrast, the malathion-treated plants continued growth at approximately the same rate as the control plants for 28 days, then ceased vertical growth for the remainder of the experiment suggesting a hormonal rather than a poison impact (Figure 2). Alfalfa plants treated with a combination of malathion and methoxychlor showed a similar reduction in stem growth (Fick, 1977).

Differences in the rate of growth of musk thistle given above show growth reduction by high (but not low) aldicarb and an effect by malathion (countered by low aldicarb). Plants receiving the low aldicarb-plus-malathion treatment achieved the same height and produced the same growth pattern as the control and low aldicarb-treated plants. Therefore, aldicarb either blocked the inhibitory affect of malathion or the low aldicarb-plus-malathion combination resulted in a synergistic effect, compensating for any growth inhibition caused by the malathion. Malathion has also produced synergistic effects on insects when combined with BHC and plant extracts (Sharma and Saxena, 1983).

Vegetative biomass

Both the low aldicarb and malathion treatments reduced total plant biomass below control levels, although not significantly ($P > 0.05$, Table 16). Plants treated with high levels of aldicarb weighed significantly less (49%) than control plants ($P < 0.05$, $df = 16$, Table 16). Potted plant mixtures containing aldicarb have been shown to cause phytotoxic effects, especially at high dosages (Romanow, et al., 1984). In contrast, the biomass of low aldicarb-plus-malathion-treatedplants was slightly higher than that of control plants ($P > 0.05$) and significantly higher than that of plants treated with high aldicarb ($P < 0.05$, $df = 16$). Since both the low aldicarb and the malathion treatments alone had lower biomass than the control group, a synergistic effect is again indicated.

Differences in total plant biomass were not due to differences in main shoot biomass among treatments ($P > 0.05$, Table 16).

Table 16. The effect of insecticide treatment on the growth of musk thistle in the greenhouse, 1986.

	Control	High Aldicarb	Low Aldicarb	Aldicarb-plus-malathion	Malathion
Total biomass[ab] (gms)	17.1 ± 1.5b	8.7 ± 1.5a	14.5 ± 2.1ab	18.7 ± 2.3b	13.0 ± 1.7ab
Vegetative biomass (gms)					
Main stem	7.4 ± 0.6a	5.4 ± 0.7a	6.6 ± 0.6a	7.2 ± 0.8a	6.3 ± 0.7a
Lateral branches	3.9 ± 0.5bc	1.1 ± 0.0a	4.1 ± 1.0bc	5.0 ± 0.9c	2.1 ± 0.4ab
Reproductive biomass (gms)					
Terminal heads					
Mass/head[c]	0.9 ± 0.2ab	0.3 ± 0.1a	0.7 ± 0.2ab	0.9 ± 0.2ab	1.0 ± 0.2b
Mass seeds/head[b]	0.3 ± 0.1a	0.1 ± 0.0a	0.3 ± 0.1a	0.3 ± 0.1a	0.4 ± 0.1a
Lateral heads[b]					
Mass/head	3.3 ± 0.6b	1.4 ± 0.7a	2.5 ± 0.6ab	4.0 ± 0.7b	2.2 ± 0.5ab
Mass seeds/head	1.2 ± 0.3b	0.4 ± 0.2a	0.8 ± 0.2ab	1.3 ± 0.2b	0.9 ± 0.2ab
No. lateral branches	3.6 ± 0.6a	2.2 ± 0.7a	3.4 ± 0.7a	4.0 ± 0.8a	3.7 ± 0.4a
No. Lateral flowers[b]	8.6 ± 1.6b	4.1 ± 1.6a	5.6 ± 1.3 ab	7.2 ± 0.8ab	7.4 ± 1.7ab
No. seeds[b]					
Total	670.0 ±131.0b	240.5 ± 93.0a	475.6 ±105.0ab	713.4 ±128.0b	571.1 ±101.0ab
Terminal	112.8 ± 37.0a	30.6 ± 16.0a	109.1 ± 32.0a	120.6 ± 38.0a	168.7 ± 31.0a
Lateral	557.2 ±147.0b	210.0 ± 88.0a	366.5 ± 90.0ab	592.7 ±121.0b	402.4 ± 88.0ab

[a] Values within a row without a letter in common are significantly different ($P < 0.05$, Tukey's studentized range test).

[b] P-value from ANOVA significant at 0.01 level

[c] P-value from ANOVA significant at 0.05 level

No demonstrable difference was observed among treatments for the number of lateral branches but branch biomasses were affected. Low aldicarb-treated thistles had an insignificant 3% increase in lateral branch biomass. Lateral branch biomass in the high aldicarb treatment was, however reduced by 73% when compared to the control plants ($P < 0.01$, Table 16). Malathion-treated plants had 46% less lateral branch biomass when compared to control plants. Plants treated with low aldicarb-plus-malathion had the greatest lateral branch biomass, although only significantly greater than that observed under the malathion treatment ($P < 0.05$, df = 16). These results again support the synergistic or inhibition blocking hypothesis. They also indicate that the lack of late growth in malathion-treated plants mentioned earlier, was due to a reduction in the size of their lateral branches.

Reproductive biomass

Insecticide application controlled reproductive biomass among treatments primarily through its effect on lateral flowers ($P < 0.01$, Table 16). Neither low aldicarb nor malathion were influential. The high aldicarb treatment significantly reduced both lateral head biomass and lateral seed biomass relative to control plants ($P < 0.05$, Table 16). This is consistent with other growth and biomass results obtained in our study. The low aldicarb-plus-malathion treatment increased lateral seed biomass, and seed yields were significantly greater than under the high aldicarb treatment ($P < 0.05$, Table 16), while the low aldicarb and the malathion treatments were not ($P > 0.05$, and $P > 0.05$, respectively; Table 16), again the synergistic or inhibition blocking effect previously mentioned for growth and vegetative biomass.

Malathion-treated plants had the greatest terminal head biomass, but were only significantly greater than those plants treated with high aldicarb. All other terminal head biomass comparisons were not significant (Table 16). This suggests that malathion-treated plants have compensated for reduced lateral branch biomass by increasing terminal head biomass.

Reproductive numbers

No effect on flower numbers due to low aldicarb or malathion was observed (Table 16). A significant reduction in lateral flower numbers was observed for the high aldicarb treatment compared to the other treatments ($P < 0.05$, Table 16). This was consistent with results obtained in other aspects of this study. Their was no interactive (malathion and low aldicarb) increase in flower numbers.

Total seed numbers among treatments were also influenced by insecticide treatments ($P < 0.01$, Table 16), apparently due to a difference in lateral flower seed production ($P < 0.01$, Table 16). Plants treated with low aldicarb-plus-malathion had the highest number of lateral seeds and were significantly more fruitful than those treated with high aldicarb ($P < 0.05$, Table 16), unlike plants treated with these insecticides individually. The synergistic effect of low aldicarb-plus-malathion was demonstrated in increased lateral seed production as in total plant biomass.

Note that the malathion-treated plants had the highest number of terminal seeds. Since malathion treated plants had reduced lateral branch production, it seems likely that nutrients were reallocated from branches to seeds after malathion application.

Plants treated with aldicarb had reduced terminal seed production (Table 16). These two insecticides appeared to have opposite effects and it is possible that within low aldicarb-plus-malathion-treated thistles a reallocation of nutrients allowed compensatory growth responses which overcame the direct effects of the insecticides. Additional studies using more levels of the various treatments are necessary to clarify this interaction.

Summary

The implications of insecticide effects on plant growth and reproduction are far-reaching. Toscano, et al. (1982a, 1982b) have demonstrated inhibitive effects of pesticides (applied for Lepidopterous pest control) on lettuce physiology and yield. We have shown that high rates of aldicarb reduced growth rates, terminal flower biomass, and seed production in musk thistle. Malathion was also shown to reduce musk thistle growth by inhibiting the production of lateral branches.

If insecticides are used in biological control studies to exclude insect natural enemies of weeds in the future, their effects on weed growth and reproduction must be acccounted for before insect impacts can be properly assessed. Failure to do so will generally result in an under-estimate of the impact of natural enemies on the target weed.

In contrast to the negative effects of insecticides on plant growth and reproduction, application of aldicarb and malathion together increased total plant biomass, lateral stem biomass, and lateral flower biomass in musk thistle.

CHAPTER 6

SUMMARY

Musk thistle is an economically important weed on disturbed sites in the Gallatin Valley and throughout North America. The persistence of this weed despite chemical and biological control methods prompted a two year study of the integrated effects of _R_. _conicus_ and relieved grazing on control of this plant.

Interactive effects of a variety of environmental factors on the growth, reproduction, and spatial dispersion pattern of _C_. _nutans_ were suggested by initial measurements of coverage and standing crop. This initiated three more studies related to the biology of the thistle.

During the dry year of 1985, increased plant competition caused thistles to concentrate nutrients within terminal and secondary flower heads. In 1986, when precipitation was higher, thistles grown under relieved grazing allocated nutrients to tertiary seed head production. _R_. _conicus_ developing within the flower heads of thistles stressed by plant competition were more common in heads receiving more nutrients.

Relieved grazing enhanced flower damage by the seed head weevil _R_. _conicus_ during the dry summer of 1985. Under higher precipitation in 1986, weevil damage was not substantially different between ungrazed and grazed sites.

Relieved grazing did not reduce total musk thistle seed production. Over longer periods of time grazing relief will have greater effects because thistles which had established prior to relieved grazing were less effected than those presently establishing under relieved grazing. Grazing relief played a significant role in reducing thistle establishment because increased ground coverage reduced establishment sites for germinating seedlings. Increased plant competition also increased the competitive stress on seedlings reducing their ability to establish as rosettes.

The clumped distribution of musk thistle was controlled by microsite preferences of seedlings and established rosettes. Seedlings were more common under larger adult thistles in both grazed and ungrazed areas. Rosettes preferred small canopied adults growing in grazed areas.

Predatory cropping of a large number of tagged musk thistles during 1985 prompted a comparative study to determine the effects of terminal loss on musk thistles grown under varying degrees of environmental stress. Thistles were found to be adversely affected by the combination of terminal loss and increased grass competition. Since the seed head weevil attacks primarily terminal seed heads the potential for increased biological control by integrating relieved grazing and weevils was demonstrated.

Insecticide treatments used to eliminate weevils from thistles were unsuccessful. Concurrent greenhouse studies on the effects of insecticides on musk thistle revealed negative effects for malathion and high concentrations of aldicarb but positive effects for some mixtures. Compensatory growth and reproduction of the weed caused by chemical interaction complicates the use of insecticides for biological control studies and could increase thistle populations.

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APPENDIX

Appendix A. Species codes and scientific and common names of plants used in Table 1. Nomenclature follows Hitchcock and Cronquist, 1973.

Code	Scientific name	Common name
Grasses (including sedges)		
Agrsmi	Agropyron smithii Rydb.	Western wheatgrass
Broine	Bromus inermis Leys.	Smooth brome
Brotec	Bromus tectorum L.	Cheatgrass
Carste	Carex stenophylla Wahl.	Narrow-leaved sedge
Carpra	Carex praegracilis W. Boott.	Clustered field sedge
Dacglo	Dactylis glomerata L.	Orchard-grass
Koecri	Koeleria cristata Pers.	Prairie Junegrass
Poapra	Poa pratensis L.	Kentucky bluegrass
Stivir	Stipa viridula Trin.	Green needlegrass
Forbs		
Achmil	Achillea millefolium L.	Yarrow
Alyaly	Alyssum alyssoides L.	Pale alyssum
Andsep	Androsace septendrionalis L.	Northern androsace
Artlud	Artemisia ludoviciana Nutt.	Cudweed sagewort
Astpan	Aster pansus (Blake) Cronq.	White prairie aster

Code	Scientific name	Common name
Forbs (Cont'd)		
Carnut	Carduus nutans L.	Musk thistle
Chrvil	Chrysopsis villosa (Pursh) Nutt.	Hairy golden-aster
Cirarv	Cirsium arvense (L.) Scop.	Canada thistle
Cirvul	Cirsium vulgare (Savi) Tenore	Bull thistle
Cynoff	Cynoglossum officinale L.	Common hound's-tongue
Erocic	Erodium cicutarium L.	Crane's-bill
Grisqu	Grindelia squarrosa (Pursh) Dunal	Curly-cup gumweed
Lepcam	Lepidium campestre (L.) R. Br.	Field pepperweed
Medlup	Medicago lupulina L.	Black medic
Meloff	Melilotus officinalis L.	Yellow sweetclover
Phllon	Phlox longifolia Nutt.	Long-leaf phlox
Silcuc	Silene cucubalis Wibel	Bladder campion
Solmis	Solidago missouriensis Nutt.	Missouri goldenrod
Taroff	Taraxacum officinalis L.	Common dandelion
Tradub	Tragopogon dubius Scop.	Yellow salsify
Equi spp.	Equisetum spp.	Horsetail