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RESPONSES OF CANADA THISTLE TO DEFOLIATION
AND TO DAMAGE FROM A STEM-MINING
WEEVIL IN UTAH

by

Wendy Sue Halsey

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Biology

UTAH STATE UNIVERSITY
Logan, Utah

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Wendy Sue Halsey

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ABSTRACT

Responses of Canada Thistle to Defoliation and to
Damage from a Stem-mining Weevil in Utah

by

Wendy Sue Halsey, Master of Science
Utah State University, 1992

Major Professor: Dr. Edward Evans
Department: Biology

The responses of Canada thistle stems to damage by two types of herbivores were investigated to determine the potential role of these herbivores as biological control agents. Canada thistle stems at a cattle enclosure in Rich County, Utah were cut at one to two centimeters aboveground in June, 1991, to mimic grazing by cattle. Neighboring stems within 30 centimeters were also cut in some treatments to investigate the effects of physiologically connected ramets on the growth and reproductive responses of individual focal stems. I measured plant height, stem diameter, and number of flowerheads for each of the focal stems during the growing season and obtained dry weights in late September. Cut stems had reduced survival, and were shorter, lighter, and less successful at producing flowerheads than were uncut stems. Cutting neighboring stems did not significantly affect survival or growth of the focal stem when the focal stem was also cut. When the focal stem was left intact,

however, those stems with uncut neighbors grew significantly taller and produced more flowerheads than did stems with cut neighbors. These results suggest that neighboring Canada thistle stems assist each other by translocating nutrients or by changing the microhabitat in the absence of defoliation.

A stem-mining weevil, Ceutorhynchus litura, was released into eight 4 X 6-m plots at three exclosures in Rich County, Utah in 1990. I compared stem density, height, stem diameter, and flowerhead production of individual stems in weevil-infested versus control plots during the 1991 growing season. The presence of weevils did not affect the density of thistle stems, nor did it affect their growth or reproductive responses in weevil-infested plots. Weevil infestation declined from 1990 to 1991 in release plots but increased slightly in control plots, which suggests that emigration caused reduced infestation in release plots.

These experiments illustrate some of the complexities of Canada thistle's responses to grazing; they also reinforce that biological control is generally a gradual process with rather subtle effects over the short-term.

(74 pages)

CHAPTER I
LITERATURE REVIEW AND INTRODUCTION

Plants face a wide variety of hazards in their lifetimes, including fire, drought, floods, disease, herbivory, and competition. Plant success depends on the ability to compensate for these hazards. The genetic composition of local populations of plant species may be altered by selection acting on differential responses of individual plants to each type of hazard. Certain genotypes may be better suited to survive fire, drought, and other adversities than other genotypes because of particular plant or seed characteristics. The better-adapted genotypes become more common and the other genotypes die out, thereby changing the genetic makeup of the population as a whole. Species composition of a community is also often affected by the aforementioned hazards; new species become established, original species die out or are dominated by the new species.

Herbivory is a major selective pressure on plants and has received much attention in recent years. Herbivores can affect the fitness of an individual plant by killing it outright, by reducing its ability to compete with its neighbors, or by eliminating or reducing its ability to reproduce (e.g., Caviness and Thomas, 1980; van Leeuwen, 1983; Kinsman and Platt, 1984; MacLean, 1988; Price and Hutchings, 1992). It has been hypothesized that herbivory may also affect individual plants positively by changing their growth form, stimulating defensive responses, or increasing rate of growth or

reproductive output (Owen and Wiegert, 1976; Paige and Whitham, 1987). Paige and Whitham (1987), for example, found that when scarlet gilia, (*Ipomopsis aggregata* (Pursh) Grant), is grazed it produces multiple shoots, each with reproductive structures, rather than the one shoot that ungrazed plants produce. Maschinski and Whitham (1989), however, emphasized the importance of microsite conditions on the response of a plant to herbivory. They found different responses by the same plant species depending on the presence or absence of neighbors, level of nutrient availability, and length of recovery time after herbivory occurs. Bergelson and Crawley (1992) have challenged the conclusions of both Paige and Whitham (1987) and Maschinski and Whitham (1989).

Other authors have hypothesized that grazed plants may overcompensate for being grazed by producing more root tissue, stem biomass, flowers, and fruits than ungrazed plants (Stenseth, 1978; Hendrix, 1979; Owen, 1980; Hilbert et al., 1981; McNaughton, 1983). Not only may overcompensation result from the plant's basic growth response, but components of the saliva of insect herbivores may be plant growth stimulators for grasses (Dyer and Bokhari, 1976). The weight of present evidence, however, does not support this hypothesis (Detling and Dyer, 1981). Light herbivory invokes defensive responses in plants which may deter herbivores in the future (Coley et al., 1985; Pullin and Gilbert, 1989).

Herbivory affects plant community structure by selectively eliminating some or all members of individual species or by changing the relative fitnesses of individual plants. Overgrazing of preferred grass species allows annual weeds to invade pastures and grasslands.

Cattle and sheep usually graze heavily on the most palatable species, thus allowing many less palatable and poisonous plants to spread on rangelands (Hanson and Churchill, 1961). Herbivory may reduce the amount of plant cover, thus allowing light to reach the surface and induce germination of new seedlings (Wesson and Wareing, 1967, 1969). It also may speed the rate of nitrogen cycling in the community (Harper, 1977).

Herbivory can often affect the outcome of both inter- and intraspecific competition. The effects of herbivory on plant community structure are closely related to interspecific competition. Jeffries (1988) found that grazing by Lesser snow geese in arctic intertidal flats eliminates dicotyledonous plants, allowing the formation of grazing lawns of Carex subspathacea Wormsk. and Puccinellia phryganodes (Trin.) Scribn. and Merr. The survival and growth form of individual plants are also affected by the degree of competition to which they are exposed (Thrasher et al., 1963; Kok et al., 1986; Weiner et al., 1990; Berntson and Weiner, 1991).

Many plants occur in a single microhabitat and are restricted to the space, water, and nutrients available at that site. Clonal plants, however, can mitigate the effects of competition, limited resources, or grazing by spreading over a large area of land. Clonal plants are able to expand by means of stolons, rhizomes, rootstock, and branch layering. Each stem (i.e., ramet) of a clonal plant is merely another unit of the plant's modular growth form. A single genet (i.e., genetic individual) of a clonal species may consist of hundreds of ramets, all connected together to form a plant that covers

many square meters of ground. A genet can live many years, either via perennial stems (e.g., Populus tremuloides Michx., Agave deserti Engelm.) or via annual stems that die back to the perennial rhizome or rootstock after each growing season (e.g., Cirsium arvense (L.) Scop., Smilacina stellata (L.) Desf., Typha latifolia L.). New shoots are then produced by the rhizome or rootstock the following spring.

Vegetative propagation of clonal plants may result in a genet of physiologically connected ramets; alternatively, the ramets may become independent of each other after they become established (Harper, 1977; Cook, 1979; Ashmun et al., 1982; Price and Hutchings, 1992). Ramets may be independent of each other while maintaining the physical connection, or the connection may be lost entirely sometime after the ramet becomes independent of the parent plant for its nutrients and water, as in Ranunculus repens L. (Lovett Doust, 1981) and Aster acuminatus Michx. (Ashmun et al., 1982). Independence may be gained shortly after shoot development (St. Pierre and Wright, 1972) or it may not occur until years after shoot growth and establishment (Ashmun et al., 1982; Cook, 1983; Raphael and Nobel, 1986). Such independence causes the stems to compete with each other for light and nutrients as physiologically distinct individuals. Independence may also allow portions of the genet to survive an injury or disease that kills some of the stems but spares others, thereby increasing the survivorship of the genet as a whole (Hutchings and Bradbury, 1986).

Physiological integration can benefit a clonal plant by allowing it to sample its surroundings and produce ramets in areas where they have the best chance of survival, thereby taking some of the

randomness out of shoot development (Pitelka and Ashmun, 1985). Each ramet can use the available resources for its own growth and development as well as send some resources or photoassimilates to its neighbor ramets for their benefit. This sharing helps ramets that are experiencing shading or loss of nutrients to survive, thereby increasing the survival of the genet (Ashmun et al., 1982; Hartnett and Bazzaz, 1983; Alpert and Mooney, 1986; Raphael and Nobel, 1986; Alpert, 1991; Landa et al., 1992). Some genets maintain physical connections between ramets, but ramets are physiologically distinct until one or more of them become shaded or subject to grazing or nutrient depletion. When shading or nutrient depletion occurs, the physiological pathways are reestablished (Ashmun et al., 1982; Hartnett and Bazzaz, 1983; Pitelka and Ashmun, 1985; Jonsdottir and Callaghan, 1988).

Objectives of the Present Study

This study was designed to investigate responses of Canada thistle (Cirsium arvense (L.) Scop., Asteraceae) to herbivory. In particular, I have examined how simulated damage from cattle and actual damage from the stem-mining weevil, Ceutorhynchus litura (Fab.) (Coleoptera: Curculionidae), affect survivorship, growth, and reproduction of Canada thistle stems. Canada thistle is an aggressive, perennial, clonal plant that is difficult to control or exterminate once it becomes established and is therefore listed as a noxious weed in several states in the U.S. (Hodgson, 1968; Dewey, 1991). The Bureau of Land Management (BLM) is trying to control

Canada thistle in riparian habitats on western rangelands without resorting to herbicides. Biological control is an alternative that could be self-sustaining and relatively inexpensive once the control agent is established. Cattle grazing might be used for thistle control but little is known about the responses of Canada thistle to grazing. Among the several insects that have been brought to the United States and Canada from Europe as biological control agents against Canada thistle, the weevil, Ceutorhynchus litura, appears the most promising (e.g., Rees, 1990).

The first experiment presented here (Chapter II) was performed to study the effects of complete defoliation of Canada thistle early in the growing season, as happens naturally when cattle graze on young thistle stems in the spring. The second experiment (Chapter III) was designed to study Canada thistle's responses to the presence of a stem-mining weevil, Ceutorhynchus litura, and the success of the weevil in affecting thistle patches after two years of infestation.

These experiments were conducted at three BLM exclosures along creeks in Rich County, Utah. The exclosures were bordered by rangelands dominated by sagebrush scrub. They were established to study the results of preventing cattle from grazing (and walking) immediately adjacent to a streambed and in the associated riparian area. All of the field work for the first experiment (on the effects of defoliation) was done at the BLM Big Creek exclosure. Established in 1972, it encloses 0.8 km of the Big Creek streambed. Experiments involving the weevil were done at the Big Creek exclosure and at two exclosures in a nearby canyon (Dead Moose Meadow and Lower Otter Creek

exclosures). Big Creek is a perennial stream. The streambed at Dead Moose Meadow is dry most of the year; Lower Otter Creek is fed by a spring within the exclosure but has very little waterflow most of the summer.

Study Organisms

Canada thistle is a perennial weed in the family Asteraceae that often forms dense stands through clonal growth. The plant is native to Europe, western Asia, and northern Africa and is thought to have been brought to the United States by settlers in the late 1800's in bags of crop seeds. Canada thistle now occurs throughout the northern half of North America from approximately 35° N to 58 or 59° N latitude (Moore, 1975; Dewey, 1991). It prefers moist, well-aerated soil with a relatively stable temperature regime. As with many weeds, Canada thistle is intolerant of deep shade and establishes best in areas disturbed by human or natural activity.

Seeds germinate in spring, summer, or fall and produce a rosette that will manufacture sugars and proteins necessary for the expansion of the root system. The plant overwinters as a rosette and produces a reproductive shoot during the second growing season. This shoot dies back to the root crown during the winter and is replaced by a new shoot the following spring (Detmers, 1927; Hodgson, 1968; Moore, 1975; Rees, 1990). The new shoot's growth pattern differs from that of a true rosette in that the terminal bud of the new shoot is extended as it emerges from the ground and the shoot is capable of forming inflorescences the same year. In contrast, the terminal bud of a

rosette remains near the root collar until the shoot bolts to form a flowering stem, usually during the second growing season after it germinates. Every germinated seedling and established ramet of Canada thistle is capable of producing an extensive lateral root system. Buds on the rootstock of a single seedling are able to produce an extensive colony of many ramets (Hodgson, 1968; Carlson and Donald, 1989; Nadeau and Vanden Born, 1989).

The adverse effects of competition from different species in the adjacent area, and of local differences in resource availability, may be lessened for each ramet of a clone such as in Canada thistle because each stem is often attached to its neighbor by stem or root tissue. Each stem may, therefore, share nutrients and photosynthetic assimilates with its clonal neighbors, forming a cooperative network (Lauridson et al., 1983; Hartnett and Bazzaz, 1985; McAllister and Haderlie, 1985; Carlson and Donald, 1989; Landa et al., 1992). Competition occurs between stems that are not attached via rootstock and between connected stems when resources are limited or when all stems are grazed. Canada thistle stores nutrients in its roots during periods of dormancy and uses them to gain a competitive edge over other plants early in the next growing season (Hodgson, 1968). This often allows the thistle to dominate annual plant species within the stand.

Canada thistle is not always the most effective competitor in a community. In the rare event that it is found growing in the understory of a forest, it grows tall and gangly with light green foliage, and does not produce many inflorescences or rootstocks

(Moore, 1975). Alfalfa is able to outcompete and eradicate Canada thistle in irrigated fields as long as the field is mowed on a regular basis (Mather, 1951; Hodgson, 1968). Thrasher et al. (1963) found Alta tall fescue (Festuca arundinacea Schreb.) and Ladino white clover (Trifolium repens L.) to be quite competitive against Canada thistle.

Canada thistle is grazed by both insects and mammals despite the spines on its leaf margins. Maw (1976) found 80 phytophagous insects associated with Cirsium arvense in Canada. In addition, several insects have been introduced to North America from Europe as biological control agents for Canada thistle. These include Ceutorhynchus litura, a weevil that attacks the rosette stage of the thistle, and then tunnels through the stem toward the root crown (Zwolfer and Harris, 1966; Peschken and Beecher, 1973; Peschken and Wilkinson, 1981; Rees, 1990); Urophora cardui L., a gall fly that attacks the stems (Maw, 1976; Peschken, 1984); and Rhinocyllus conicus Froelich, a seed-eating weevil originally introduced for control of musk thistle (Carduus nutans L.) (Kok, 1974; Hodgson and Rees, 1976).

Sheep will graze on thistle stems (Silvertown and Smith, 1989), as will goats and cattle (Wood, 1987; K. Launchbaugh, pers. comm.; W. Halsey, pers. observation). Detmers (1927) found that cattle in Ohio will feed on Canada thistle rosettes when the leaves are covered with a salt solution. van Leeuwen (1983) found that rabbits will feed on stems of Cirsium vulgare (Savi.) Ten. and Cirsium palustre (L.) Scop. in the Netherlands. The American goldfinch readily eats the seeds of Canada thistle (Detmers, 1927) and blue grouse may lightly forage on Cirsium species in the winter (Pekins et al., 1989).

Mechanical and chemical control measures are not effective and/or practical against Canada thistle in many situations. Biological control agents are another option to be considered. The stem-mining weevil, Ceutorhynchus litura, was originally studied by Zwolfer and Harris (1966) for its usefulness as a biological control agent for Cirsium arvense in North America. The weevil was introduced into Canada in 1967 from Europe after it was determined that its host range is limited to members of the genera Cirsium and Carduus, with Cirsium arvense being its preferred host. Zwolfer and Harris (1966) and Peschken and Beecher (1973) describe the basic life history of the weevil, highlights of which are reproduced here. The adult stem-mining weevils feed on leaves of the rosettes in spring, resulting in the formation of punctures in the epidermis that are 2 to 4 mm in diameter. Copulation and oviposition also occur in the spring. The female oviposits 1 to 5 eggs in a cavity she makes with her rostrum on or near the midvein on the underside of a young rosette leaf. Oviposition most often occurs in the proximal one-third of the lowest leaves. Leaves must be longer than 5 cm to be suitable for oviposition.

The larvae hatch within 4 to 9 days, then mine through the leaf to the midvein, to the stem, and down to the root crown. The mined leaf turns yellow and dies several days after mining occurs. The larvae undergo two molts in the stem then exit at or near the root crown to enter the soil and construct a cocoon made of small soil particles. New adults emerge from the cocoons 2 to 3 weeks later and feed until fall on the leaves and, to some extent, stems of the distal

portion of the thistle. Adults may copulate in late summer but do not oviposit. They overwinter in the litter below the host plants.

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CHAPTER II
RESPONSES OF CANADA THISTLE
TO STEM SEVERING

ABSTRACT.--The growth and reproductive responses of Canada thistle (*Cirsium arvense* (L.) Scop.) to simulated grazing were investigated by cutting individual stems early in the growing season in a cattle enclosure in Rich County, Utah. Conspecific stems growing within 30 centimeters were also cut to investigate the effects of neighbors on the growth and reproductive responses of focal thistle stems. Height, stem diameter, and number of flowerheads were recorded for each focal stem during the growing season of 1991 and dry weights were obtained in late September. Cut stems had reduced survivorship, and were shorter, lighter, and less successful at producing flowerheads than were uncut stems. Cutting neighboring stems did not significantly affect survival or growth of the focal stem when the focal stem was also cut. When the focal stem was left intact, however, those stems with uncut neighbors grew significantly taller and produced more flowerheads than did stems with cut neighbors. These results suggest that neighboring Canada thistle stems assist each other in the absence of severing. The results of this experiment illustrate some of the complexity in the response of Canada thistle stands to grazing.

Introduction

It has been well documented that vertebrate herbivores can have a major impact on plant community structure (e.g., Tansley and Adamson, 1925; Hope-Simpson, 1940; Milton, 1940, 1947; Ellison, 1960; Jeffries, 1988). Individual species of plants respond to grazing in different ways, leading to complex changes in plant community structure. A plant's growth form affects its response to grazing and can also affect the frequency with which it is grazed (McNaughton, 1984; Krueger, 1986; Wood, 1987). Many plants have evolved growth patterns (e.g., meristems at or below ground level) or defensive mechanisms (e.g., spines and chemicals) in response to grazing (Grant and Hunter, 1966; Harper, 1977; Owen, 1980). Another growth pattern for surviving defoliation by grazing is a clonal growth form; many shoots (ramets) are produced by a system of rhizomes, rootstocks, or stolons which serves to store photosynthates and often physically connects the ramets to each other for more than a single growing season (Kays and Harper, 1974; Hartnett and Bazzaz, 1983; Alpert and Mooney, 1986; Magda et al., 1988; Price and Hutchings, 1992). The anatomical connections allow translocation of water, nutrients, and/or photoassimilates between the ramets (Ashmun et al., 1982; Alpert and Mooney, 1986; Raphael and Nobel, 1986; Jonsdottir and Callaghan, 1989; Alpert, 1991; Caraco and Kelly, 1991; Landa et al., 1992); this translocation can permit stems to survive defoliation and regrow (Marshall and Sagar, 1965, 1968; Schmid et al., 1988).

Much of the western United States is rangeland grazed by cattle. The effects of cattle grazing on range vegetation have been a major

concern in the western United States. Effects on sensitive riparian habitats (where cattle tend to congregate) have recently become of particular concern (Kinch, 1989; Chaney et al., 1990). Riparian zones have been fenced off in recent years, leading to changes in the vegetative community in the absence of cattle grazing. These changes have not always been desirable, however. Among the plants that have benefitted from the absence of cattle grazing is the clonal plant, Canada thistle (Cirsium arvense (L.) Scop.), an undesirable weed that is able to outcompete and crowd out many other plants (Detmers, 1927; Hodgson, 1968; Carlson and Donald, 1989; Nadeau and VandenBorn, 1989). Canada thistle has an underground rootstock that allows the genet (i.e., genetic individual) to spread quickly over large areas. Under less than favorable conditions it produces relatively few stems, but produces many closely spaced stems when conditions become more favorable for growth (Hodgson, 1968; Carlson and Donald, 1989; Nadeau and VandenBorn, 1989).

Canada thistle's aggressive nature makes it difficult to manage. Under some circumstances, herbicides can be effective (Beuerman et al., 1984) but they have generally not proved so in many riparian zones in the western United States (Bureau of Land Management, personal communication). A possible control strategy for Canada thistle is to allow short-term, light cattle grazing in heavily-infested riparian zones in the spring. Potential management by spring grazing can be assessed in part by field experiments in which Canada thistle is artificially defoliated. There have been few experiments to study the effects of defoliation on translocation in clonal plants

in general (Schmid et al., 1988; Jonsdottir and Callaghan, 1989), and very few translocation experiments for Canada thistle in particular (Carlson and Donald, 1989). Hunter et al. (1985) studied the effects of removing Canada thistle stems from the rootstock on the release of root buds, but did not study translocation between stems.

The experiment presented here was designed to investigate the response of Canada thistle stems to artificial severing. This severing was intended to mimic grazing by cattle early in the growing season. The ability of Canada thistle stems to regrow and produce flowers was examined experimentally by severing individual stems and/or neighboring conspecific stems while they were still small.

Study Site and Methods

The Bureau of Land Management (BLM) fenced cattle out of riparian zones in several locations in Utah in the 1970's to study the effects of cattle grazing on plant communities of these sensitive ecosystems. In the absence of grazing pressure, Canada thistle now thrives in many of the enclosures. The field work for this experiment was conducted at a BLM cattle enclosure surrounding a perennial section of Big Creek in Rich County, Utah (41° 36'24"N, 111° 20'39" W, elevation 1980 m). The enclosure was established in 1972 and encloses 0.8 km of the Big Creek streambed; the current vegetation in the enclosure includes dense stands of Cirsium arvense mixed among Cirsium vulgare (Sav.) Ten., Cirsium scariosum Nutt., Artemisia spp., Ribes spp., Rosa spp., Thermopsis montana Nutt., Urtica dioica L., Potentilla spp., Smilacina stellata (L.) Desf., Aster hesperius Gray, Juncus sp., and several

grass species. The enclosure is bordered by hillsides covered with sagebrush scrub.

A transect line with 200 points, spaced 3 to 5 meters apart, was set up on the south side of Big Creek in early June 1991. The transect snaked its way through dense stands of Canada thistle, ranging from 1 to 30 meters away from the creek. One-hundred and sixty points along the transect were chosen randomly. At each of these points, a single Canada thistle stem was selected from those growing approximately 1 to 2 meters on either side of the transect line. Focal stems were arbitrarily chosen based on their height (approximately 10 to 30 cm tall) and the number of neighboring stems within 30 cm (5 to 35), as this was the range in height and number of neighbors for the majority of stems along the transect. Only second year and older stems (i.e., no rosettes) were used.

Initial measurements of height, stem diameter, number of leaves, and number of neighboring conspecific stems were recorded for each focal stem on 12 June (100 stems) and 17 June 1991 (60 stems). Height was measured from the ground to the top of the stem; stem diameter was measured with calipers at about the height of the lowest leaf node (approximately 2 cm aboveground); all leaves which had begun to open were counted; and all conspecific neighbors within 30 cm from the center of the focal stem were counted.

At the time that initial measurements were taken, each stem was randomly assigned to receive one of four treatments: (1) control (i.e., the stem and neighboring Canada thistle stems were left undisturbed), (2) neighboring Canada thistle stems within a 30 cm

radius from the focal stem (but not the focal stem itself) were cut, (3) the focal stem alone was cut, (4) both the focal stem and neighboring stems were cut. Forty stems were assigned to each of the four treatments. Treated stems were cut 1 to 2 cm aboveground, removing both the terminal bud and all leaves. This approximates grazing by cattle on small Canada thistle stems in the spring. A cow wraps its tongue around a plant, pulls it into its mouth, and cuts off the stem by pressing the incisor teeth of the lower jaw against the dental plate of the upper jaw (Webster, 1987). Observations of grazed thistles (where grazing was attributed to cattle) located outside a similar enclosure at nearby Lower Otter Creek indicate that cattle cut the stems of Canada thistle at approximately 1 to 2 cm above the ground. The clipping treatments were performed on each study plant immediately following the initial measurements on 12 June and 17 June.

At the initial census in mid-June, the focal stems had 4 to 14 leaves, and 2 to 35 neighbors. Initial heights ranged from 7 to 31 cm, while stem diameters varied from 4.7 to 11.9 mm. Measurements of height were taken every 10 to 14 days thereafter from 2 July until 28 August. Height was measured a final time on 23 September 1991. The inflorescence buds were recorded as present or absent beginning 13 July. The number of flowering heads and buds were counted at each subsequent census (26 July to 23 September). Gender of flowering focal stems was determined at the final census (23 September). Because the stands of thistle along the transect were so dense, a small number of stems (1 to 5) in each treatment could not be found at any given census; these were not necessarily the same stems each time.

The initial number of neighbors was regressed against focal stem height as a possible covariate in statistical analyses, but neighbor density was unrelated to initial height of the focal stem and was therefore not used as a covariate.

Focal stems were harvested on 23 September, brought back to the lab, dried at 60° C for 48 hours, and weighed. The vegetative portion was separated from the reproductive portion and weighed separately. Only the vegetative weights were used in the analyses because flowerheads on many of the stems had been removed by rodents and/or deer prior to harvest of the stems.

Five 1 m² plots were set up inside the enclosure but away from the transect line to determine if the stems were physically connected belowground. The central plant in each plot was treated with the herbicide Roundup^R (glyphosate) by wiping it onto the leaves. The neighbors were observed several times during the summer to check for yellowing of the leaves and death of the stem, indicating that Roundup^R had been translocated from the treated stem to its neighbors. In addition, thistle stems just outside the enclosure were excavated to a depth of approximately 30 cm to determine the extent to which neighboring stems were connected to a common rootstock.

Results

Dead thistle stems from the previous year covered the ground at the study site and delayed the appearance of new stems above the ground by one to two weeks longer than areas that were bare of old stems; new stems in bare areas were observed as early as the end of May, whereas new stems in areas of heavy litter did not appear until 7 June or shortly thereafter. While some stems began to bolt as early as 9 June, most of those that were not cut off at the base grew relatively slowly during June. A growth spurt occurred thereafter during the first two weeks of July.

Many cut stems immediately began regrowing, but others failed to survive the cutting treatment. The cut stems that regrew did so by producing one or more branches from the base of the remaining stem. The number of stems that survived in each treatment was compared to the total number of stems for that treatment that could be found on more than half of the censuses (i.e., at least four of the seven censuses). Of the uncut stems, 37 with cut neighbors and 37 with uncut neighbors (of 38 stems found in each treatment) survived to the final census. Of the stems that were cut, only 21 of 38 of those with uncut neighbors and 26 of 39 with cut neighbors survived to the final census. Cutting a stem early in the growing season thus significantly affects the stem's probability of survival ($\chi^2=39.11$, $df=1$, $p<.0001$; CATMOD procedure for two-way categorical analysis, SAS Version 6.03). The slightly lower survival of cut stems with intact neighbors (versus those with cut neighbors) is not significant ($\chi^2=0.96$, $df=1$, $p=.3273$), nor is the interaction between cutting treatments (i.e., cutting the

stem itself and/or cutting its neighbors; $\chi^2=0.96$, $df=1$, $p=.3273$).

As detailed below, most of the uncut stems produced flower buds while most of the surviving cut stems did not. Flower buds were produced just above the topmost leaves in mid-July. Thereafter, the stems elongated, becoming more slender as they did so and pushing the buds higher above the leaves. Flower buds began to open approximately 2 weeks after they appeared. Only the larger buds were viable; many of the tiny (<5 mm diameter) buds did not open. The uncut stems reached their maximum height by late July, while the cut stems continued to grow slowly through September.

Two tests were done to assess whether the thistle stems at the study site are commonly connected to each other via rootstock. An indirect indication of belowground connections came from applying glyphosate (Roundup^R) on 2 July 1991 to center stems in 1-m² study plots within the enclosure. Treated stems were dead by 26 July and several of the neighboring stems showed signs of glyphosate poisoning (yellowing and curling of the leaves and stem). It is unlikely that the yellowing was due to natural senescence since none of the nearby stems outside the plot showed similar symptoms. Ten thistle stems within a 1-m² plot outside the enclosure were excavated; each stem was connected underground to at least two others, and it is likely that all ten emerged from a single rootstock, but the roots snapped between groups during excavation, or the rootstock was situated at a depth greater than was excavated. This evidence, combined with published accounts of thistle growth habit (e.g., Detmers, 1927; Carlson and Donald, 1989; Nadeau and VandenBorn, 1989), suggests that in general,

the stems within the enclosure are physically connected to most of the other stems in their vicinity. The only stems that definitely cannot be physically connected together are male and female stems, since males and females are always separate plants (i.e., Canada thistle is dioecious).

Most of the flowering stems at the study site were females with patches of male-flowering stems interspersed. To test for sexual differences in height attained by focal stems, I compared final heights (i.e., heights as measured on 23 September) of male and female stems for treatments 1 and 2 (in which the stems themselves were not cut). I omitted treatments 3 and 4 (in which the focal stems were cut) because very few of the stems flowered in these treatments and I was therefore unable to determine the gender of most of the stems. Analysis of variance indicated no significant difference in height between genders, and no significant interaction between gender and neighbor treatment (Table 1). Since male and female stems did not differ significantly, I combined stems of both genders with non-flowering stems of uncertain gender to increase sample sizes for further analysis.

I compared stem heights among treatments over the growing season by using a repeated measures analysis of variance. Both cutting the focal stem and cutting neighboring stems had a highly significant effect on growth as reflected by stem height (Table 2). The effects of these treatments differed over time, however (note the significant interaction of treatments with date in Table 2; see also Figure 1).

TABLE 1.--Two-way analysis of variance of final heights (as measured on 23 September 1991) of flowering, uncut Canada thistle stems, classed by gender (male or female) and by treatment to neighboring stems (treatment 1, neighbors left intact, versus treatment 2, neighbors cut)

<u>Source of Variation</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>P-value</u>
Treatment	1	1505.25	7.67	.0080
Gender	1	22.42	0.11	.7368
Treat * Gender	1	48.34	0.25	.6219
Error	48	196.22	--	--

TABLE 2.--Two-way analysis of variance with repeated measures (date) on stem height of Canada thistle for four cutting treatments (stem cut or uncut X neighbors cut or uncut) over the course of one growing season. Probability is given as adjusted by the Greenhouse-Geisser method (GLM procedure; SAS Version 6.03)

<u>Source of Variation</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>P(G-G)</u>
Stemcut(S)	1	86914.41	95.10	.0001
Neighborcut(N)	1	7856.90	8.60	.0042
S * N	1	2850.71	3.12	.0805
Error	98	913.92	--	--
Date	6	19013.94	316.94	.0001
Date * Stemcut	6	250.98	4.18	.0212
Date * Neighborcut	6	217.92	3.63	.0341
D * S * N	6	80.71	1.35	.2620
Error	568	59.99	--	--

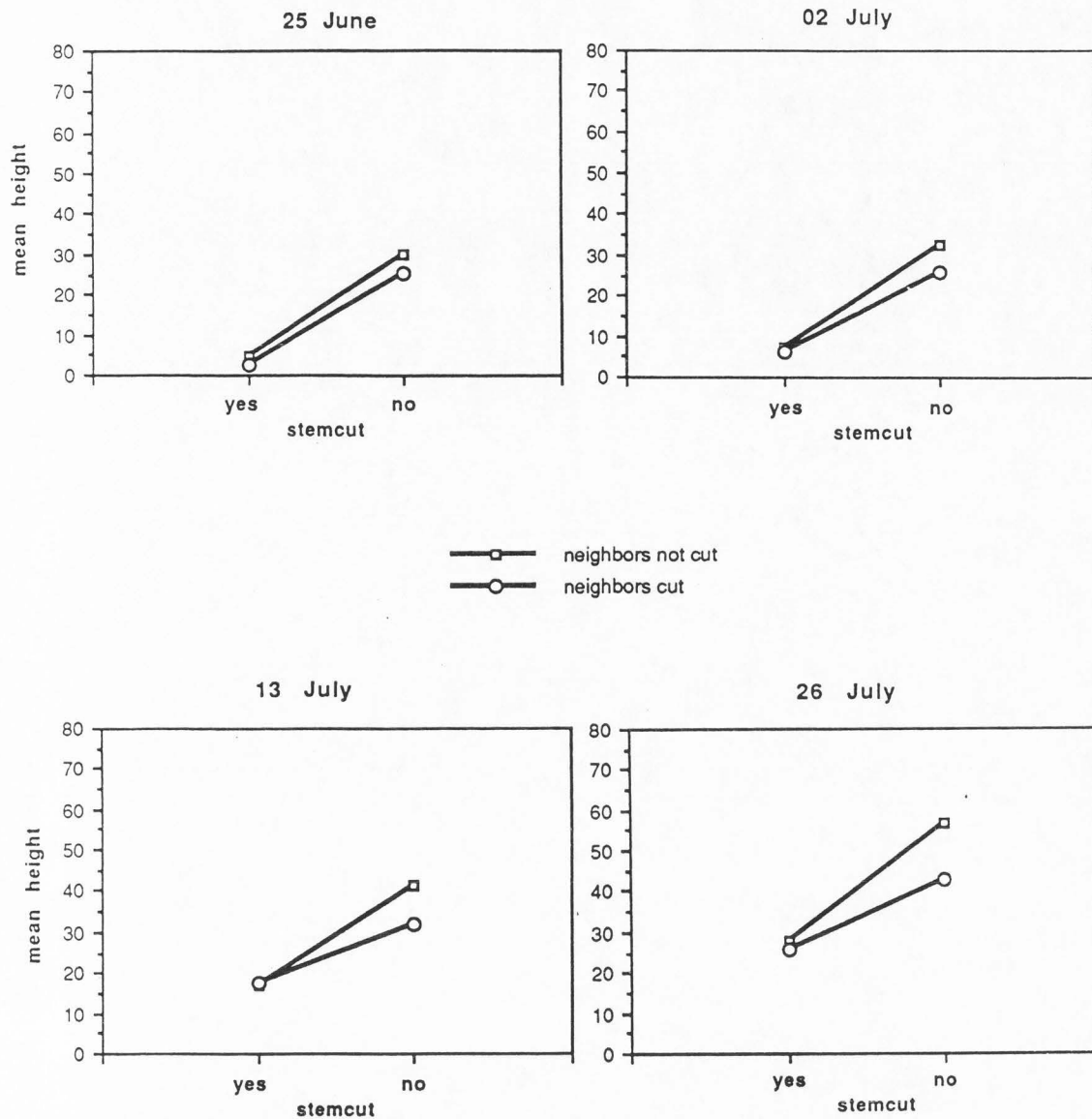


FIG. 1.--Interaction plots of mean height (in cm) of cut versus uncut Canada thistle stems with cut versus uncut neighbors for seven census dates in 1991. Stems were cut in early June 1991

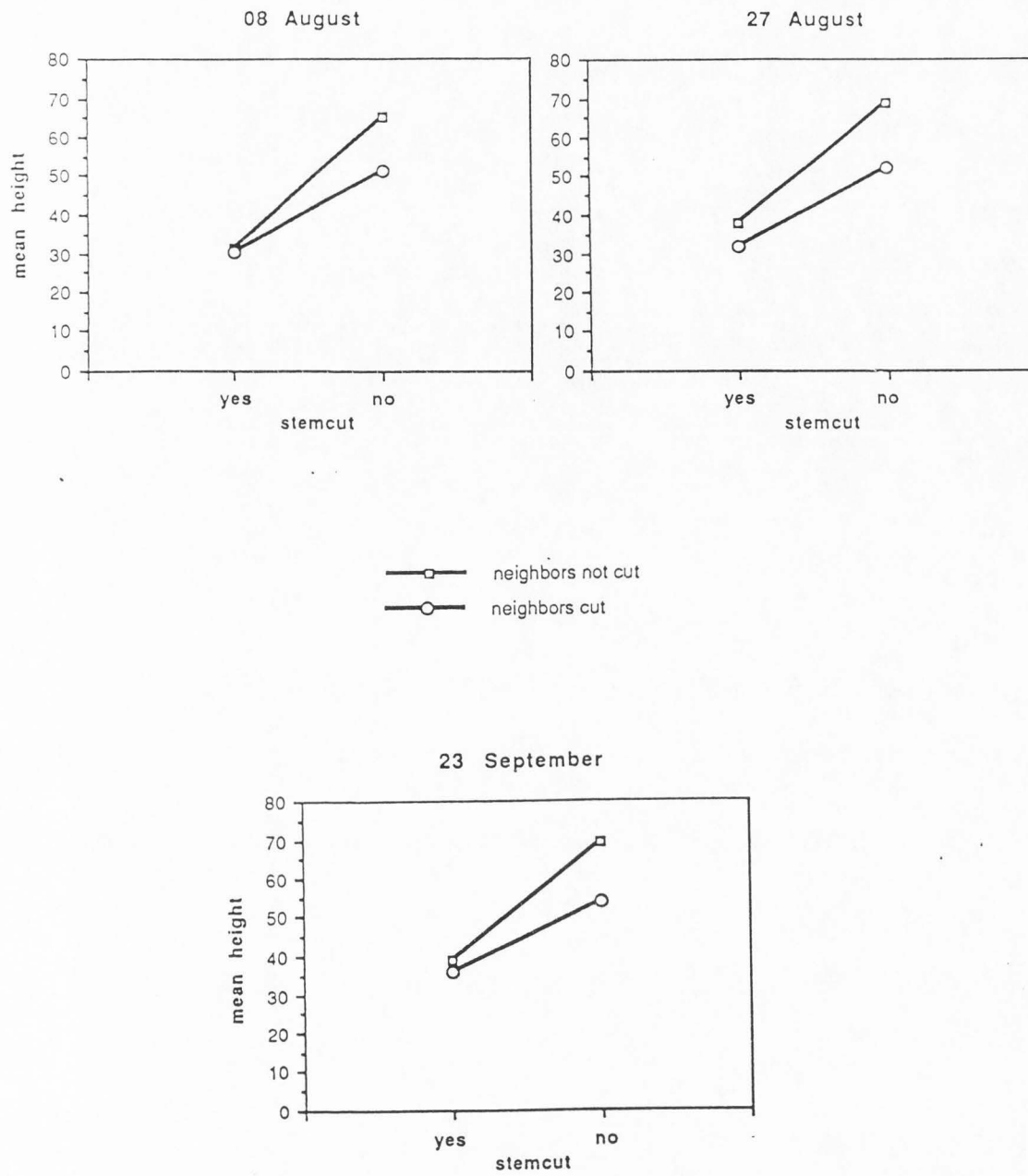


FIG. 1.--Continued

Therefore, I analyzed the effects of treatments separately for individual sampling dates.

Cutting the stem in mid-June had a highly significant effect on stem height on each subsequent sampling date throughout the growing season (Table 3). Cutting neighboring stems also had a significant effect on all dates except 8 August (when $p=.0687$). A significant interaction between cutting the stem and cutting neighboring stems occurred on four sampling occasions; the interaction was nearly significant on two of the three remaining sampling dates (only on 25 June was there little indication of an interaction; Table 3). The interaction arose because uncut stems grew considerably taller when neighbors were also uncut (treatment 1) than when neighbors were cut (treatment 2). Cut stems, however, did not differ in their subsequent growth depending on whether neighboring stems were cut (treatments 3 and 4). The interaction was most apparent in July and early August (Table 3, Figure 1).

I measured dry weight of vegetative tissues of focal stems at the end of the growing season (stems were harvested on 23 September). To test for sexual differences, I compared dry weights of male and female stems in treatments 1 and 2 (I used \log (dry weight) to correct for lack of normality in the raw data). The two sexes did not differ significantly in weight, nor was there a significant interaction between the treatment a stem received and its gender (Table 4). Therefore, I again combined sexes to increase sample size in analyzing the effect of treatment (now including all four treatments) on final weight. There was a strong effect of cutting the stems on their final

TABLE 3.--P-values associated with cutting treatments and their interaction for analyses of variance of Canada thistle stem height on individual sampling dates. The treatments were cutting or not cutting an individual stem ("stemcut"), and cutting or not cutting neighboring Canada thistle stems ("neighborcut"). Degrees of freedom are given for the error term (these vary across dates, as not all stems were located on any given sampling occasion, and some stems died between censuses)

Source of Variation	Date						
	25 June	02 July	13 July	26 July	08 Aug	27 Aug	23 Sept
Stemcut(S)	.0001	.0001	.0001	.0001	.0001	.0001	.0001
Neighborcut	.0030	.0019	.0247	.0083	.0687	.0041	.0208
S * N (N)	.1913	.0081	.0149	.0177	.0155	.0760	.0656
Error df	123	123	120	118	117	114	113

TABLE 4.--Two-way analysis of variance of vegetative dry weights (log-transformed) of uncut Canada thistle stems harvested on 23 September 1991. Classes tested were gender of the stem and treatment the neighbors received (uncut or cut)

Source of Variation	df	MS	F	P-value
Treatment	1	.0055	0.03	.8538
Gender	1	.2439	1.52	.2239
Treat * Gender	1	.3218	2.00	.1635
Error	48	.1607	--	--

dry weight (mean \pm one standard error for uncut stems = $7.77 \pm 1.91\text{g}$ (n=68), and for cut stems = $3.17 \pm 2.91\text{g}$ (n=44)), but no significant effect of cutting neighboring stems (mean \pm one standard error for uncut neighbors = $5.66 \pm 2.81\text{g}$ (n=55), and for cut neighbors = $5.28 \pm 2.34\text{g}$ (n=57)). There was also no significant interaction between cutting treatments (Table 5).

As discussed above, cutting neighboring stems substantially reduced final stem height, particularly when the focal stem had not been cut earlier in the season (Figure 1). An analysis restricted to treatments 1 and 2 (in which the focal stem was not cut) indicates no significant difference between the mean vegetative dry weights for uncut stems with uncut versus cut neighbors ($x \pm 1$ s.e. = $8.42 \pm 1.82\text{g}$ versus $7.14 \pm 2.00\text{g}$; log dry weights: N=68, F=1.11, df=1,66, p=.2964). However, the relatively large standard errors of the log dry weights (compared with standard errors for heights) may be masking an effect

TABLE 5.--Two-way analysis of variance of vegetative dry weights (log-transformed) of all Canada thistle stems (genders combined) harvested on 23 September 1991. Classes tested were stem treatment (cut or uncut, "stemcut"), and treatment of neighboring stems (cut or uncut, "neighborcut")

<u>Source of Variation</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>P-value</u>
Stemcut(S)	1	21.724	30.83	.0001
Neighborcut(N)	1	0.015	0.02	.8860
S * N	1	0.939	1.33	.2508
Error	108	0.705	--	--

of treatment on dry weight that would be detected with a larger sample size. A plot of the raw data reveals that for stems of both treatments (i.e., uncut stems with or without neighboring stems cut), taller stems tend to be heavier (Figure 2). Linear regression equations of final log dry weight against height fitted individually for the two treatments do not differ significantly in slope or elevation (Zar, 1984; pages 292-299). The common regression line has a highly significant positive slope ($y = .5454 + .0243x$; $r^2 = .5195$, $p < .0001$); in general, stems with cut neighbors tend to be shorter and lighter than stems with uncut neighbors.

To investigate the influence of cutting treatments on reproductive activity of Canada thistle stems, I estimated the percentages of stems flowering from the number of stems that were recorded with flowerheads on one or more of the sampling dates. Only 19.0% (4 of 21) of the surviving cut stems with uncut neighbors and 7.7% (2 of 26) of the surviving cut stems with cut neighbors produced flowerheads by the end of the growing season. The mean number of flowerheads (\pm one standard error) produced by cut stems with uncut neighbors ($n=21$) versus cut neighbors ($n=26$) was 3.05 ± 8.84 versus 0.65 ± 2.35 . Of the uncut stems, 89.2% (33 of 37) of the stems with uncut neighbors and 83.8% (31 of 37) of the stems with cut neighbors produced flowerheads by the end of the growing season. Thus, cutting the focal stems significantly affected the stems' ability to flower ($\chi^2 = 143.37$, $df=1$, $p < .0001$; CATMOD Procedure for two-way categorical analysis, SAS Version 5.0). The slight reduction in flowering activity when neighboring stems were cut versus uncut was not

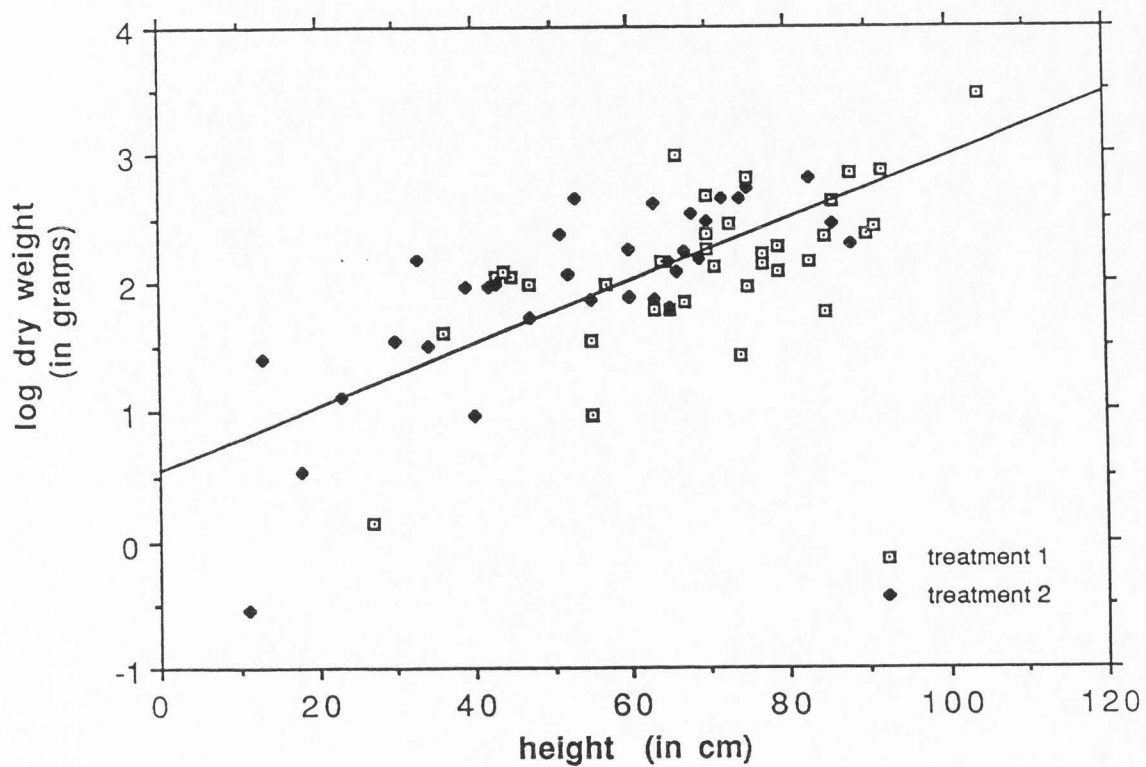


FIG. 2.--Log dry weight versus height for uncut Canada thistle stems with uncut neighbors (treatment 1) and cut neighbors (treatment 2). The fitted line is the common linear regression equation for both treatments combined ($y = .5454 + .0243x$, $r^2 = .5195$, $p < .0001$)

significant ($\chi^2=1.50$, $df=1$, $p=.2214$). There was also no significant interaction between the focal stem and neighbor treatments ($\chi^2=0.12$, $df=1$, $p=.7281$). Flowering was also delayed by two to three weeks in the cut stems that were able to produce flowerheads versus the uncut stems (Figure 3).

Since so few cut stems produced flowerheads, only uncut stems in treatments 1 and 2 were analyzed in detail for reproductive output; this was measured by using the maximum number of flowerheads censused during the growing season. Several stems had produced flowerheads between late July and the final census in September but had lost them sometime before the final census (they had either broken off or had been eaten by rodents or deer) and the gender of these stems was not determined. Those stems for which gender was unknown (but for which number of flowerheads had been counted earlier in the season) were used only in analyses in which genders were combined.

The maximum number of flowerheads for each uncut, flowering stem (square-root transformed to correct for lack of normality) in treatments 1 and 2 was subjected to analysis of variance. The gender of the stem did not significantly affect the number of flowerheads the stem produced; there was also no interaction between gender and cutting treatment (Table 6). Female and male stems were combined with stems for which gender was not determined (number of flowerheads had been recorded at earlier censuses) in treatments 1 and 2 to increase sample size for further analysis of the effect of cutting neighboring stems. The mean maximum number of flowerheads produced by uncut stems with uncut neighbors ($\bar{x} \pm \text{one s.e.} = 20.98 \pm 2.38$) was significantly

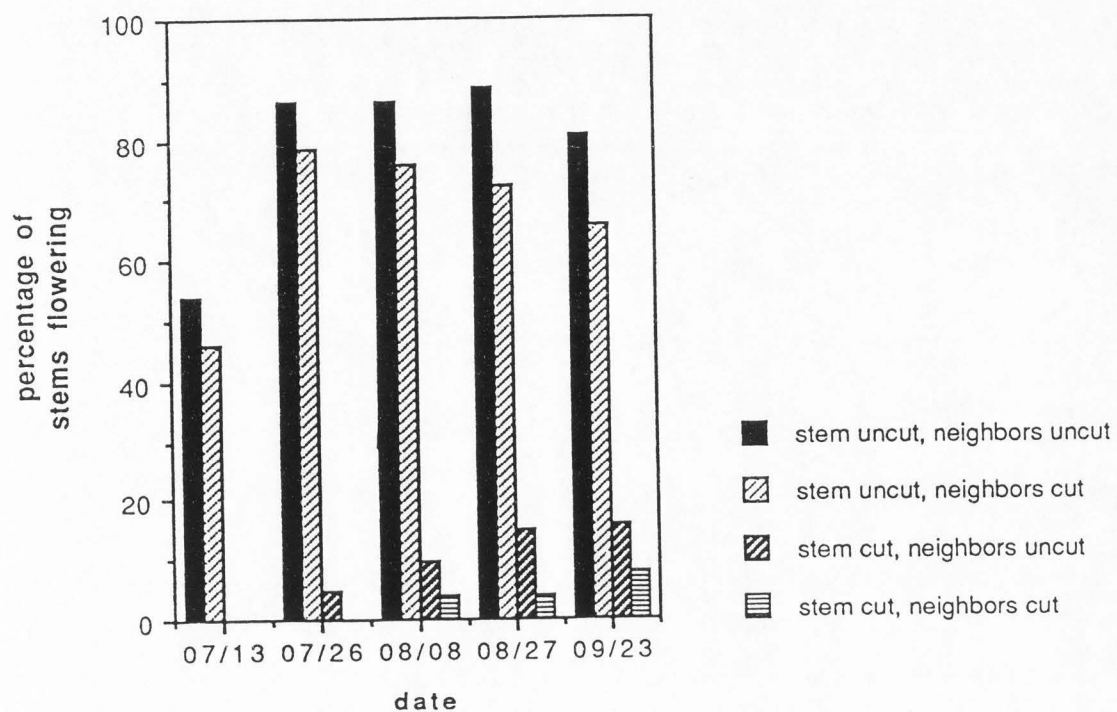


FIG. 3.--Percentage of Canada thistle stems with at least one flowerhead on different census dates in 1991 for four treatments

TABLE 6.--Two-way analysis of variance on the number of flowerheads (squares-root-transformed) produced by male and female stems of Canada thistle when the neighbors were not cut (treatment 1) and when the neighbors were cut (treatment 2)

<u>Source of Variation</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>P-value</u>
Treatment	1	2.3372	1.10	.2994
Gender	1	0.8650	0.41	.5264
Treat * Gender	1	2.5077	1.18	.2826
Error	48	2.1237	--	--

larger than the mean for uncut stems with cut neighbors ($\bar{x} \pm$ one s.e. = 14.09 ± 2.56 ; square-root transformation: $n=62$, $F=4.29$, $df=1,60$, $p=.0427$). The number of flowerheads produced by a stem, furthermore, was positively correlated with stem height (Figure 4). Linear regression equations of number of flowerheads against height for the late July census, fitted individually for the two treatments, do not differ significantly in slope or elevation (Zar, 1984; pages 292-299). The common regression line ($y=-13.4869 + .5267x$; $r^2=.5247$, $p<.0001$) reveals that for stems of both treatments (i.e., uncut stems with or without neighbors cut), taller stems produced more flowerheads.

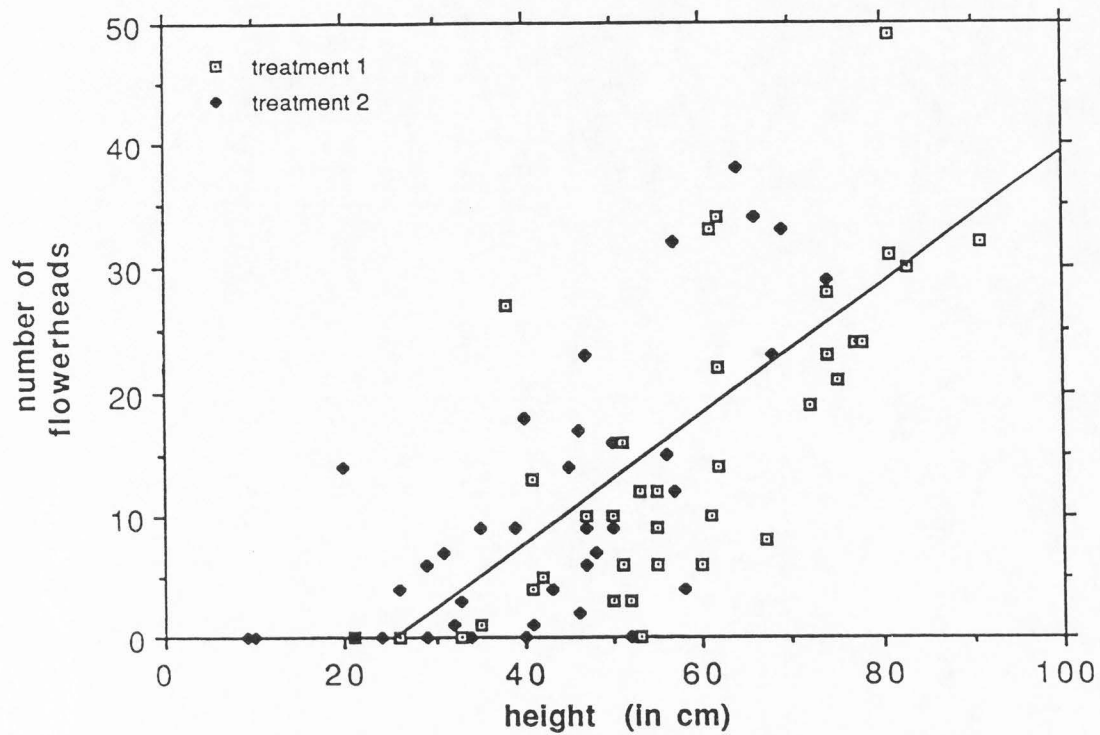


FIG. 4.--Number of flowerheads present on individual Canada thistle stems on 26 July 1991 versus stem height on 26 July for uncut stems with uncut neighbors (treatment 1) and uncut stems with cut neighbors (treatment 2). The fitted line is the common linear regression equation for both treatments combined ($y=13.4869+.5267x$, $r^2=.5247$, $p<.0001$)

Discussion

This experiment was designed to mimic several possible scenarios in which a cow grazes on small Canada thistle stems early in the growing season. The cow may graze all of the stems in a local area. Alternatively, it may eat a single stem, leaving neighboring stems intact. Finally, it may feed on most of the stems, but one or a few stems may escape. As observed in the field, the cow is likely to bite off the thistle stem at approximately one to two centimeters aboveground, removing most or all of the leaves. In this experiment, artificial severing of single stems and/or neighboring stems near ground level mimicked such situations; these treatments were compared with a "control" treatment, i.e., an absence of grazing.

The Canada thistle stems subjected to treatments presumably were, for the most part, attached to nearby conspecific neighboring stems via the rootstock. The literature concerning Canada thistle growth (Detmers, 1927; Beuerman et al., 1984), supports this assumption, as do additional observations made near the study site (i.e., the excavation of stems and application of Roundup^R). This physical connection makes the response of a single Canada thistle stem to any one of the scenarios listed above a combination of the stem's response to severing and its interactions with connected (and cut or uncut) neighboring stems.

The responses of the focal stems to being cut (leaving aside for the moment the significance of also cutting neighboring stems) were not surprising. A stem that was not severed early in the growing season had a much better chance of surviving to the end of the growing

season than did a stem severed early on. Many of the severed focal stems showed no signs of regrowth or were unsuccessful in attempting to regrow and died back. Those severed stems that were able to successfully resprout from the side of remaining stem tissue generally failed to grow as large by the end of the growing season as an unsevered stem, and had very little chance of producing flowerheads. Cutting the stems also affected the timing of flowerhead production. Uncut stems began to produce flowerheads by 13 July but cut stems delayed flowerhead production by two to three weeks. These experimental results clearly demonstrate that individual Canada thistle stems are significantly hindered in their growth, survival, and reproduction by severing early in the growing season.

The adverse effects of early spring severing of Canada thistle stems may be modified by whether or not neighboring thistle stems are also severed. The interactions of a single stem of a clonal plant with its conspecific neighboring stems are more complex than the interactions between a stem of a nonclonal plant and its neighbors. Adjacent stems may either play a competitive or a cooperative role, whether they are physically connected to each other or not. Unconnected neighbors will compete with a stem for water, nutrients, sunlight, and space. They also may assist the stem by shading the ground, thus reducing direct evaporation from the surface and increasing the humidity at ground-level. Connected ramets may similarly compete and cooperate with each other, particularly if there is no translocation through the root system (Hutchings and Bradbury, 1986). They may assist each other in additional ways, however, by

sending water, nutrients, and/or photoassimilates through the roots to connected ramets. This translocation allows ramets to grow and survive in areas that would not sustain growth of solitary plants (Hartnett and Bazzaz, 1983; Alpert, 1991). Assistance by translocation can essentially cease until it is required by one or more physically connected ramets (e.g., as the result of water stress or shading), at which time translocation resumes (Pitelka and Ashmun, 1985; Alpert and Mooney, 1986; Jonsdottir and Callaghan, 1988).

Raphael and Nobel (1986) and Alpert and Mooney (1986) found that ramets which are attached to neighboring ramets have a better chance of surviving and show increased growth over ramets which are severed from neighbors. In the present study, the role of neighboring stems in modifying the response of the focal stems to severing is not as clearcut as the response of the stems themselves. There was no clear influence of the neighboring stems on the survival of the focal stem, regardless of the treatment that the stem received. Almost all of the unsevered stems survived, whether or not their neighbors were cut, (one stem died in September in each of the treatments) and there was no significant difference in the survival of severed stems with versus without uncut neighboring stems.

Neighboring stems, however, appear to play a cooperative role in the growth of unsevered stems, as uncut stems with uncut neighbors grew to a significantly greater height than those stems with cut neighbors. The elongation of stems with intact neighbors could merely represent increased growth to compete for light with no difference in aboveground biomass between stems with cut versus uncut neighbors.

That possibility cannot be unequivocally ruled out since the weights of the stems with uncut neighbors were not statistically significantly heavier than the weights of stems with cut neighbors. Overall, however, the evidence favors the hypothesis that stems with uncut neighbors grew heavier as well as taller than stems with cut neighbors, as height and weight were strongly positively related to each other in both sets of stems in very similar if not identical fashion. Reproductive output was also strongly positively related to height, and uncut stems with uncut neighbors produced significantly more (49% more) flowerheads than did uncut stems with cut neighbors. These results are consistent with the hypothesis that stems are sharing translocates rather than just interacting as competitors for light. Two possible explanations, then, for the smaller size and lower reproductive output of uncut stems with cut neighbors are: (1) the stem received smaller amounts of translocates from its cut neighbors, and/or (2) the cut neighbors pulled more translocates from the uncut stem. Another possibility is that the neighboring thistle stems increased the humidity around the base of the stems and slowed the rate of water loss, due to evaporation, from the soil thereby creating more suitable habitat for Canada thistle.

The responses of cut stems to cutting of their neighbors are less marked than are responses of uncut stems. There were no clear effects (either cooperative or competitive) of treatment of neighboring stems on growth of those surviving focal stems that were artificially severed. Cut stems with uncut versus cut neighbors were very similar in heights and dry weights achieved by the end of the growing season,

and in their tendency to produce flowers. There was a slight tendency, however, for those stems with uncut neighbors to be taller and produce more flowerheads than cut stems with cut neighbors, again consistent with the hypothesis that the stems are sharing resources via the rootstock. But overall these results suggest that a cut stem is not able to draw sufficient resources from its intact neighboring conspecifics to improve to any great degree its capacity to recover from severing.

In summary, the results of this experiment show that Canada thistle stems that are cut off near ground level soon after they emerge (approximately two weeks) are unable to catch up during the growing season with uncut stems, both in terms of vegetative and reproductive output. Although the stems themselves were adversely affected by severing early in the growing season, the plant (i.e., genet) as a whole consists of many stems and an immense root system that was most likely little affected by the severing of one or a few stems. This experiment was designed to examine only the responses of individual stems, not the entire plant. The genet may also have responded to cut stems by producing new sprouts instead of, or in addition to, reinitiating growth at the point of cutting. Hunter et al. (1985) found that removing individual Canada thistle stems from the rootstock released the rootbuds and more stems were produced. The results also indicate that neighboring thistle stems assist each other in the absence of severing. Thus, early spring severing of a local patch of Canada thistle stems not only adversely affects the regrowth and sexual reproduction of severed stems, but also of isolated, intact

stems that escape severing. These results illustrate some of the complexities in responses of stems that can be expected were cattle to be introduced to graze lightly on riparian stands of Canada thistle early in the growing season.

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CHAPTER III
EFFECTS OF A STEM-MINING WEEVIL
ON CANADA THISTLE

ABSTRACT.--A stem-mining weevil (Ceutorhynchus litura (F.) Coleoptera: Curculionidae) was released into plots in three exclosures in Rich County, Utah in 1990 as a biological control agent. Stem density, height, stem diameter, and flowerhead production of stems in eight pairs of control versus weevil-infested plots were measured during the 1991 growing season to study the influence of the weevil on growth and sexual reproduction of the thistle. Stems were harvested at the end of the season to assess weevil infestation within the stems. Presence of weevils did not affect the density of stems within the plots, nor did it affect height, stem diameter, or flowerhead production by the stems. Weevil infestation decreased in the weevil-infested plots but increased in several of the control plots from 1990 to 1991.

Introduction

Canada thistle (Cirsium arvense (L.) Scop.) is one of the most aggressive and problematic weeds in the United States. It is listed as a noxious weed in at least 35 states (Dewey, 1991), which means it is targeted for aggressive control measures aimed at reducing the number of plants and preventing or limiting its spread (Ross and Lembi, 1985). Canada thistle's widespread distribution and perennial,

clonal nature make it difficult to control with mechanical efforts, making biological control a viable option (for details about Canada thistle's life history see Detmers, 1927; Hodgson, 1968; Moore, 1975). The basic concept of biological control of weeds is to bring a natural enemy of the weed (which is almost always native to another country or region) from the weed's native area to feed on the plant. Insects and pathogens historically have been used as biological control agents; they are studied in their native habitat, collected, tested for host specificity, released into one or several experimental plots to study their effect on the weed (and the responses of native vegetation), then released on a large scale in suitable habitats for control efforts (Rosenthal et al., 1985; Harris, 1988).

Several insects have been imported from Europe as potential control agents against Canada thistle. One such insect is Ceutorhynchus litura (F.) (Coleoptera: Curculionidae), a stem-mining weevil that feeds exclusively on the genera Cirsium and Carduus, with Cirsium arvense as its preferred host. Zwolfer and Harris (1966), Peschken and Beecher (1973), and Peschken and Wilkinson (1981) describe the biology of Ceutorhynchus; a brief synopsis is included here. Ceutorhynchus litura females will feed on the lower surface of young thistle leaves and deposit their eggs in the resultant cavity in April and May. Upon hatching, the larvae move to the leaf midvein, following that vessel down the stem to the root crown. The larvae undergo two molts within the stem, feeding on the pith tissue as they grow, and thereby hollowing out the stem. The third instar larvae then chew their way out of the stem at the root crown and pupate in

the soil at the base of the stem. Adults emerge from the soil in June or July to feed and, sometimes, to copulate. Adults overwinter in the litter below the thistle stems and emerge the next spring to feed, copulate, and oviposit.

Rees (1990) found Ceutorhynchus in Montana to be effective in controlling the aerial and subterranean parts of infested Canada thistle stems and, occasionally, the associated rootstock as well. This control was most likely facilitated by secondary organisms (i.e., other insects or pathogens) entering the damaged stem and causing more damage. Logistical difficulties, however, prevented Rees from assessing rigorously how the weevil affects entire stands (versus single stems) of Canada thistle. The objectives of the present study were to assess the rate of infestation by the weevil, and its effects on stem density, growth, and reproductive output, in stands of Canada thistle in northern Utah during the second growing season following the weevil's initial release.

Methods

Adults of Ceutorhynchus litura were released in May, 1990, into study plots at three locations in Rich County, Utah as potential biological control agents against Canada thistle. Eight 4 X 6-m plots were set up at the Big Creek cattle enclosure by E.W. Evans of Utah State University and L. Lichthardt and P. Schuler of the Bureau of Land Management (BLM). The plots were situated along a transect on the south side of the creek; typically they were positioned 10 to 30 meters from the streambed, with 20 to 50 meters separating adjacent

plots. Four additional 4 X 6-m plots each were set up at the Dead Moose Meadow (DMM) and Lower Otter Creek (LOC) exclosures in an adjacent canyon; adjacent plots at these locations were situated 10 to 50 meters apart. Exact plot locations in all three exclosures were determined by placing plots in dense stands (essentially monocultures) of Canada thistle. The plots were set up in a randomized complete block design (i.e., paired adjacent plots). For each of the four blocks (i.e., pairs) at Big Creek, one plot in each pair was randomly chosen to receive weevils; the other plot served as a control. Similarly, for each of the two blocks at DMM and at LOC, one plot in each pair randomly received weevils with the other one serving as a control plot. Weevils were obtained from established populations near Bozeman, Montana; 300 to 350 weevils were released in each treated plot at all three exclosures.

I assessed the impact of the weevils on stands of the thistle by measuring thistle density, growth, and sexual reproductive effort in weevil-infested versus control plots in 1991. Ten 0.1-m² (20 X 50-cm) subplots were arbitrarily established in each 4 X 6-m plot at the three exclosures in late June 1991. I haphazardly placed two subplots along the four sides of the plots, and two subplots in the center of the plots; the eight outer subplots were placed about one meter inside the plot. The four corners of each subplot were marked with plastic flags so that the subplots could be relocated repeatedly throughout the growing season. Densities of Canada thistle were determined by counting all stems in each subplot in early July, early August, and late September 1991. These counts were combined to estimate the

number of Canada thistle stems per square meter for each weevil-infested and control plot.

Fifteen stems growing within each 4 X 6-m plot, but outside the subplots, were marked with plastic tape in early July. The growth and reproduction of these individual stems was subsequently monitored throughout the remainder of the growing season. Height, stem diameter (measured with calipers at approximately 2 cm aboveground), and number of flowerheads for each marked stem were recorded four times during the summer (mid-July, early August, mid-August, and late September, 1991). The marked stems, plus 15 additional stems per plot, were harvested (with a portion of the underground stem) after the final census in late September to score the stems for Ceutorhynchus infestation. A stem with characteristic signs of Ceutorhynchus (black frass inside and/or a small circular to oval exit hole near the root crown; e.g., Rees, 1990) was scored as infested by the weevil. The same procedure was used in the fall of 1990 (on samples of 20 stems per plot) to estimate levels of infestation during the first growing season following weevil release (E.W. Evans, personal communication).

Because weevil-infested stems were not found in most control plots, a chi-square analysis (rather than analysis of variance) was used to test for differences in the number of weevil-release versus control plots that contained weevil-infested stems in 1990 and 1991. A paired t-test was then used to test for significant change in the level of weevil infestation in release and control plots from 1990 to 1991. Analyses of variance with repeated measures were used to determine if thistle stem density, height, stem diameter, and

flowerhead production varied throughout the growing season or were affected by the presence of weevils within the plot. The mean density, height, stem diameter, and number of flowerheads for the 15 measured stems in each plot was used as the replicate for each date. To correct for uneven variances among dates and treatments, the natural log of the stem densities, heights, and number of flowerheads were used in analyses; stem diameters did not require transformation.

Results and Discussion

The experiment was designed to assess whether stands of Canada thistle (versus individual stems) infested with Ceutorhynchus would be affected in basic properties (density, mean stem size, and sexual reproductive activity) by the presence of the weevil. My studies in 1991 were intended to test for effects of weevils early (i.e., during the second year) in the establishment process. Clearly, the rate with which such effects might manifest themselves depends in part on how rapidly weevil numbers and levels of infestation of Canada thistle stems increase in plots to which weevils were added ("weevil plots") versus in nearby control plots (which, over time, can be expected to slowly accumulate weevils also as the insects emigrate from release plots). Initial release in 1990 resulted in infestation of nearly half of Canada thistle stems in weevil plots versus only occasional infestation in control plots (Figure 5).

The rate of infestation for weevil plots was significantly different from that of control plots for 1990; weevil-infestation was found in eight out of eight weevil plots and only one of eight in

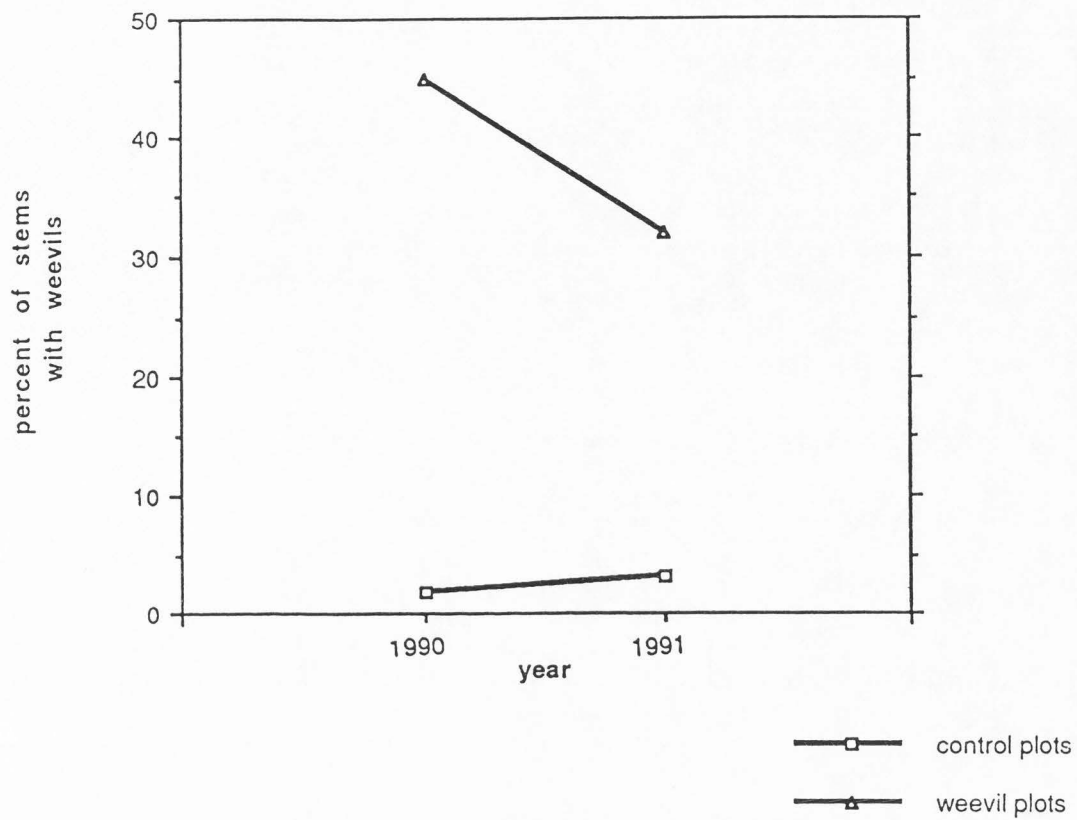


FIG. 5.--Interaction plot of mean percentage of Canada thistle stems infested with *Ceutorhynchus litura* larvae in eight weevil-release plots (i.e., weevil plots) and eight control plots in 1990 and 1991

control plots ($X^2=12.44$, $p<.0005$). Weevil plots also differed from control plots in rate of infestation in 1991; weevil-infestation was again found in all eight weevil plots but in only four of eight control plots ($X^2=5.33$, $p<.02$). The percentage of stems in the weevil plots that were infested by one or more Ceutorhynchus larvae, however, declined significantly from 1990 to 1991 (mean \pm one standard error for 1990 = 45.00 ± 13.63 , for 1991 = 31.96 ± 4.62 ; paired t-test: $t=2.74$, $p<.025$). The drop in the level of infestation in weevil plots from 1990 to 1991 may reflect either true reduction in population size of the weevil at the exclosures or slow weevil population growth combined with migration of weevils away from the release sites. The slight increase in weevil infestation in control plots, although not significant, ($x \pm$ one s.e. for 1990 = 1.88 ± 5.30 , for 1991 = 3.21 ± 4.62 ; paired t-test: $t=.533$, $p>.25$) supports the latter possibility (emigration from release sites), as do the observations of Rees (1990) in Montana. Rees found that the number of weevils in release plots in Montana tended to increase slowly, taking up to ten years to increase by 87%.

Stem densities did not differ significantly between control and weevil plots in September 1990, following the first season of weevil infestation (E.W. Evans, personal communication). Similarly, I detected no significant effect of weevils on the stem densities in study plots at any time over the 1991 growing season (Table 7, Figure 6). In particular, the mean density for the eight plots with weevils was slightly (but not significantly) higher than the density of the control plots for all three censuses. This conceivably could reflect

TABLE 7.--Repeated measures analysis of variance of the natural log of Canada thistle stem densities in weevil-infested versus control plots (n=8 blocks or pairs of plots), as determined three times during the summer of 1991. Probabilities are given as adjusted by the Greenhouse-Geisser method (GLM procedure; SAS version 6.03)

<u>Source of Variation</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>P(G-G)</u>
Block (B)	1	1.1486	2.81	.1178
Treatment (T)	1	0.0730	0.18	.6798
Error	13	0.4094	--	--
Date (D)	2	0.0337	3.32	.0535
D * B	2	0.0156	1.54	.2341
D * T	2	0.0009	0.09	.9126
Error (Date)	26	0.0102	--	--

an attempt by the plant to compensate for stems damaged by the mining of the weevil, but the issue cannot be resolved at present and may only become so as the infestation increases in future years (it is noteworthy that the mean density was similarly slightly, but not significantly, higher in weevil versus control plots in September 1990). Stem density did change within the plots over the course of the growing season ($p < .06$; Table 7); density at first increased, only to decrease by the end of the season. This probably reflects early senescence of those stems that emerged relatively late and were unable to catch up with, and escape shading by, earlier emerging, taller stems. The lack of an interaction between date and treatment simplifies interpretation of the data, as it indicates that the changes in density over the course of the season were very similar in

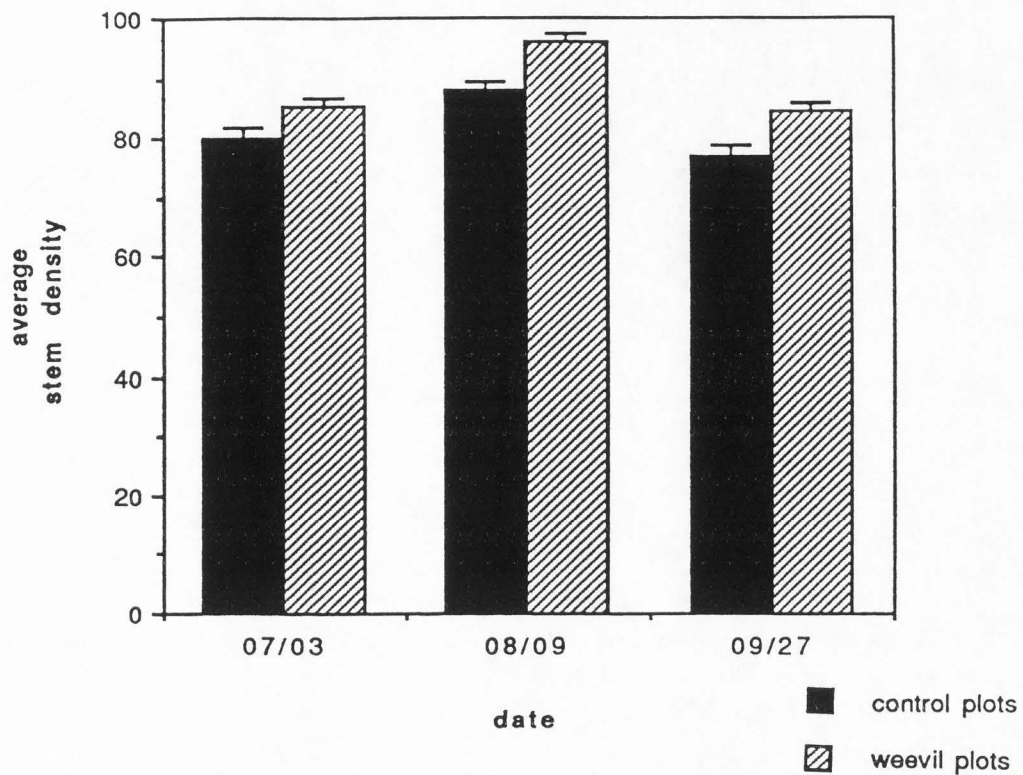


FIG. 6.--Mean number of Canada thistle stems/m² in 1991 for eight plots without Ceutorhynchus added (i.e., control plots) and eight plots with Ceutorhynchus added (i.e., weevil plots). Error bars are one standard error

weevil and control plots (i.e., the weevils did not contribute significantly to early death of stems).

I also found no significant difference between weevil and control plots in the mean height (Table 8), stem diameter (Table 9), and flower production (Table 10) of Canada thistle stems. Only height (and not stem diameter or number of flowerheads) changed significantly over the growing season, and there were no significant interactions between weevil treatment and date. Thistle stems in both treatments on average grew rapidly early in the season (July and August) and then slowed in their growth rate in late August and September (Figure 7). Stem diameter decreased slowly (although not significantly) throughout the growing season as the stems extended upward (Figure 8).

TABLE 8.--Repeated measures analysis of variance of the natural log of mean Canada thistle stem heights in weevil-infested versus control plots (n=8 blocks or pairs of plots), measured four times during the summer of 1991. Probabilities are given as adjusted by the Greenhouse-Geisser method (GLM procedure; SAS Version 6.03)

<u>Source of Variation</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>P(G-G)</u>
Block (B)	1	0.2627	2.89	.1129
Treatment (T)	1	0.0176	0.19	.6672
Error	13	0.0909	--	--
Date (D)	3	0.0532	19.65	.0002
D * B	3	0.0089	3.28	.0787
D * T	3	0.0007	0.25	.6907
Error (Date)	39	0.0027	--	--

TABLE 9.--Repeated measures analysis of variance of the mean Canada thistle stem diameters in weevil-infested versus control plots (n=8 blocks or pairs of plots), measured four times during the summer of 1991. Probabilities are given as adjusted by the Greenhouse-Geisser method (GLM procedure; SAS Version 6.03)

<u>Source of Variation</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>P(G-G)</u>
Block (B)	1	13.2150	7.94	.0145
Treatment (T)	1	3.9452	2.37	.1477
Error	13	1.6652	--	--
Date (D)	3	0.2086	1.96	.1432
D * B	3	0.2423	2.27	.1023
D * T	3	0.1601	1.50	.2329
Error (Date)	39	0.1066	--	--

TABLE 10.--Repeated measures analysis of variance of the natural log of the mean number of flowerheads produced by Canada thistle stems in weevil-infested plots and control plots (n=8 blocks or pairs of plots), as determined four times during the summer of 1991. Probabilities are given as adjusted by the Greenhouse-Geisser method (GLM procedure; SAS Version 6.03)

<u>Source of Variation</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>P(G-G)</u>
Block (B)	1	1.5647	2.37	.1477
Treatment (T)	1	0.1774	0.27	.6129
Error	13	0.6603	--	--
Date (D)	3	0.4355	3.01	.0980
D * B	3	0.2539	1.96	.1812
D * T	3	0.0880	0.61	.4733
Error (Date)	39	0.1446	--	--

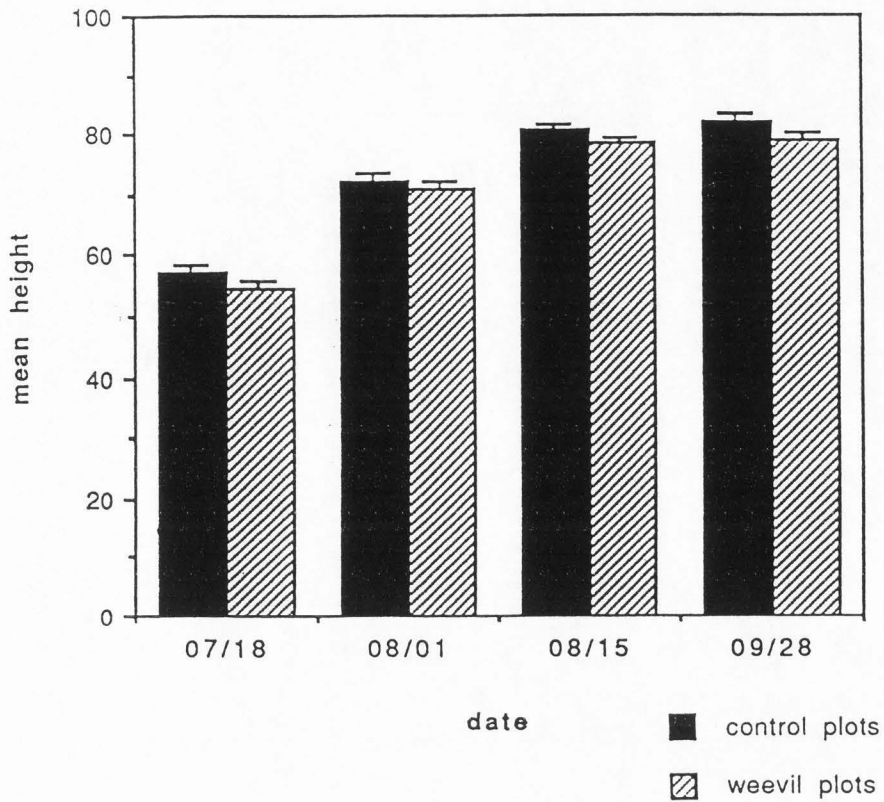


FIG. 7.--Mean height of Canada thistle stems for four census dates in 1991 for eight plots without *Ceutorhynchus* added (i.e., control plots) and eight plots with *Ceutorhynchus* added (i.e., weevil plots). Measurements were taken on 15 stems in each plot. Error bars are one standard error

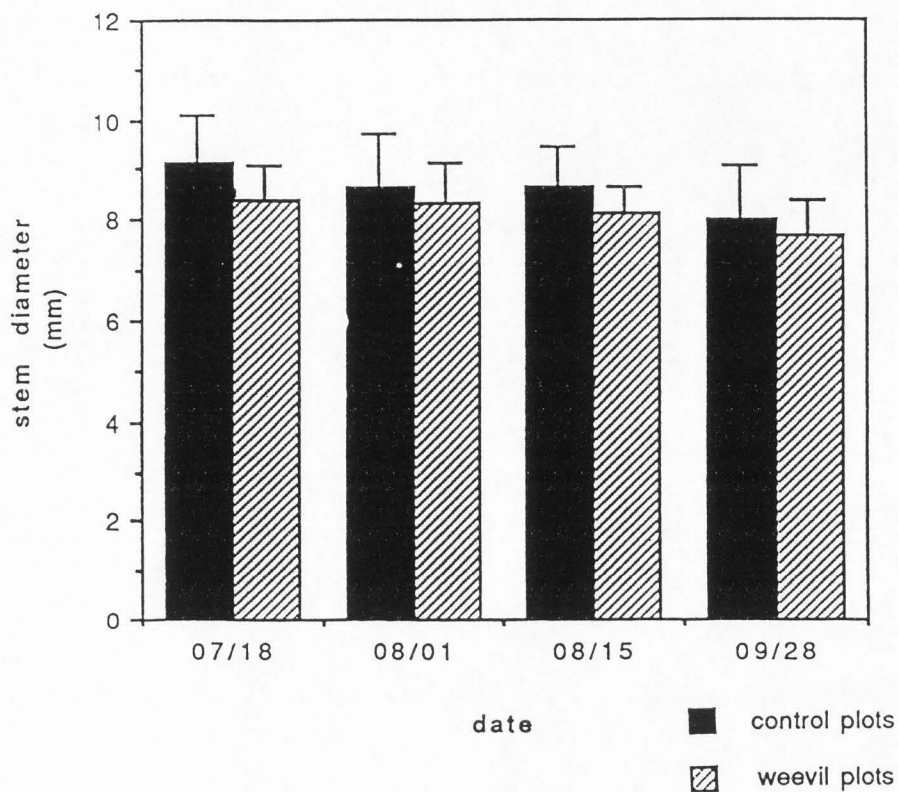


FIG. 8.--Mean stem diameter of 15 Canada thistle stems for four census dates in 1991 in each of eight plots without *Ceutorhynchus* added (i.e., control plots) and eight plots with *Ceutorhynchus* added (i.e., weevil plots). Error bars are one standard error

Flowerhead production was concentrated in late July and continued through August (Figure 9). The large (but not significant; $p=.0980$ for date in Table 10) decrease in mean number of flowerheads per plot observed in September reflects the activities of deer and/or rodents, which consumed a large number of flowerheads throughout the exclosures.

In summary, field data from the 1991 growing season reveal no clear, measurable effects of weevil infestation on local stands of thistle stems in the exclosures. These results are not unexpected, however, as the studies were conducted in only the second year following initial release of weevils. Biological control of weeds by insects is generally a slow process, taking several to many years to result in measurable depression of weed populations (Rosenthal et al., 1985). Populations of the weevil near Bozeman, Montana have taken up to ten years to become established, and slightly longer to have a definite negative effect on the thistle stems and entire plants (i.e., genets; Rees, 1990, 1991). Rees found that the underground portions of infested stems generally do not survive the winter, and lateral roots of infested stems produce fewer shoots the following spring, probably due to loss of nutrient reserves in the roots. Such phenomena may well be occurring at the Utah study plots as well; their cumulative effects on Canada thistle populations may only gradually become evident in coming years.

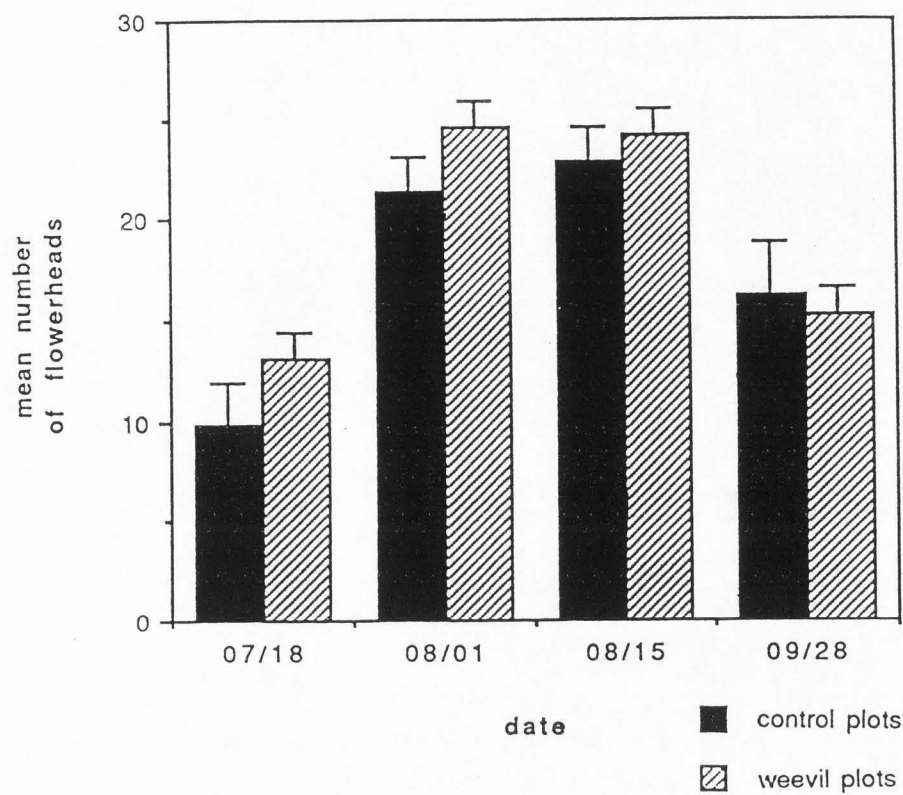


FIG. 9.--Mean number of flowerheads produced in 1991 by 15 Canada thistle stems in each of eight plots without Ceutorhynchus added (i.e., control plots) and eight plots with Ceutorhynchus added (i.e., weevil plots). Error bars are one standard error

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CHAPTER IV
GENERAL DISCUSSION AND CONCLUSIONS

Canada thistle (Cirsium arvense (L.) Scop.) is a very aggressive plant. A single seedling is capable of producing a rootstock that spreads up to four meters in its first year of growth (Detmers, 1927) and extends to a depth of more than 20 centimeters (Nadeau and Vanden Born, 1989). The rootstock is perennial and produces ramets each spring that form a dense stand of thistle stems. Canada thistle is widely considered to be a weed; it competes with crops for nutrients, light, and space, reduces the amount of available forage for livestock on rangelands, and reduces the enjoyment of hiking through a field or meadow.

Various control measures are available for Canada thistle, including chemicals and mechanical devices. Both chemical and mechanical methods are effective under some circumstances, particularly for cultivated crops or permanent grasslands (Detmers, 1927; Hodgson, 1968; Carlson and Donaldson, 1989). Chemical and mechanical control methods are not often practical, however, in native rangelands and meadows; biological control may be a more useful method in these areas. Biological control is generally an ongoing process in that the control agent is a living organism that feeds on or infects the weed and is able to reproduce itself, increasing the population to take advantage of the abundance of the weed. The

control agent is often an insect, but vertebrate herbivores and pathogens may also be used (Rosenthal et al., 1985; Harris, 1988).

Canada thistle stems are relatively immune to grazing by most vertebrate herbivores because of spines on the leaf margins. Spines are not a foolproof defense, however, as livestock in Europe will graze Canada thistle on a regular basis (Detmers, 1927). Similarly, rangeland cattle in North America will eat young, tender stems in spring and also tall stems in late summer if forage is scarce. Regular grazing of thistle stems by cattle can have the same negative effect on stem survival and growth as regular mowing, but cattle are more erratic in what they eat and in the number of stems they eat. Insects are relatively unaffected by the spines, as the thistle stems themselves are free of spines and the spines are only on the margins of the leaves. Many insects native to North America, including weevils and aphids, utilize Canada thistle as a food source (Maw, 1976). Several other insects have been introduced from Europe as agents to control Canada thistle (Peschken, 1984; Rees, 1990).

The results of the experiment presented in Chapter II indicate that spring grazing by cattle can negatively affect survival and growth of Canada thistle stems. The greatest effect occurs when the stem itself is severed; severing of a stem's nearby neighbors can also reduce its growth and reproductive output, although survival is not affected. Repeated spring grazing of stems within the enclosures by cattle on a yearly basis could eventually reduce the nutrient reserves of the associated rootstock, thereby reducing its ability to produce aerial stems and eventually killing the plant (i.e., genet). The

number of cattle and length of time they spend in the enclosure would have to be closely monitored to prevent damage by the cattle to the streambed and bank, thereby defeating the purpose of the enclosure.

Ceutorhynchus litura (F.)(Coleoptera: Curculionidae) is a very promising control agent for Canada thistle. It is a stem-mining weevil that is host-specific for the genera Cirsium and Carduus, with Cirsium arvense its preferred host (Rees, 1990). During the study presented in Chapter III, Ceutorhynchus litura was in the second year of establishment in the three enclosures in Rich County. The level of infestation of Ceutorhynchus within the release plots decreased from the first year of infestation to the second. The infestation rate of control plots increased, however, suggesting that the weevils are spreading throughout the enclosures rather than remaining within the release plots. There was no detectable effect of the weevils on survival, growth, or reproductive output of stands of Canada thistle stems within the weevil-infested plots. Thus it appears that, as in other biological control efforts, effects on the survival and growth of the thistle, if they occur, will manifest themselves only after a longer period of weevil infestation.

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