Seed versus microsite limitation of Dalmation toadflax (Linaria genistifolia ssp. dalmatica), extension of biological control agents for yellow toadflax (Linaria vulgaris), and a conceptual Dalmation toadflax life history model

by Matthew James Donovan Grieshop

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

Montana State University

Abstract:

Seed versus microsite limitation of Dalmatian toadflax was examined in order to establish whether or not the weed might be readily controlled by limiting its seed production. The extension objective of the thesis was done in order to facilitate both the establishment of natural enemies as well as producer understanding of the biological control process. Finally, a life history model was created as a means of better understanding Dalmatian toadflax population dynamics beyond seed versus microsite limitation.

Experimental methods included two years of repeated observations on plant quadrats at two field sites and partial addition series experiments. The observational field study examined treatments that added additional Dalmatian toadflax seeds to quadrats, excluded interspecific plant competition, and excluded insect herbivory from Dalmatian toadflax. Extension methods included attendance of regular meetings with the Blackfoot Challenge, release of natural enemies of yellow toadflax, and the creation of a brochure. The life history model was created using a pre-existing model as a framework and two simulations were run using data collected from the two field sites.

Dalmatian toadflax was determined to be more microsite than seed limited in dry rangeland conditions. Plant competition was identified as the major factor limiting seedling recruitment of new Dalmatian toadflax plants, while additional seeding and insect herbivory did not appear to affect seedling recruitment.

Extension objectives were met through producer cooperation and the creation of an eight page full-color brochure highlighting the biological control of yellow toadflax.

Model output suggested that Dalmatian toadflax density was increasing at one site and decreasing at the other. Model output was corroborated by independent plant-transect readings performed at both sites. ' A discussion of the implications of these results suggested that Dalmatian toadflax would probably be best managed using tactics that increase adult stem mortality as opposed to tactics which limit the number of seeds per adult stem. In the context of biological control, the results suggested that natural enemies of Dalmatian toadflax that attack reproductive structures were likely to be less effective than natural enemies that attack stem or root structures.

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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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CHAPTER 1

INTRODUCTION

Dalmatian toadflax, *Linaria genistifolia* ssp. *dalmatica* (Maire and Petitmengin Fam: Scrophulariaceae), has become a serious weed of recreation and rangelands in Montana and other Northwestern states (Nowierski 1995). Chemical management of the weed has had limited success and has generally not been cost effective (Lajeunesse et al. 1993). This is largely due to the fact that the weed prefers coarse, well-drained soils which do not permit systemic herbicides adequate time to act, nor provide an economic return high enough to pay for herbicides. Cultural control is also rarely feasible, since the weed has a deep taproot, excluding simple pulling or mowing as effective control techniques (Lajeunesse et al. 1993). In contrast to its tenacity in Western American rangelands, Dalmatian toadflax is not of significant economic importance in Eurasia, its point of origin, in part because it suffers from attack by a number of arthropods not found in the New World (Alex, 1962). This suggests that classical biological control of Dalmatian toadflax in North America should be a feasible weed management strategy (Nowierski 1995). Hence, biological control of the weed is being developed as an alternative toadflax management strategy to be used in conjunction with other weed management approaches.

The major questions of integrated weed management are how and when to implement management strategies in order to best manage weed populations. Invariably, weed management strategies take the form of physical, chemical, or biological manipulation of the agroecosystem. Weeds tend to be highly adapted to disturbed systems and take ready advantage of resources freed by disruption of "normal" ecological function (Tilman 1997). Proper management should therefore provide a balanced disturbance that puts weeds at a disadvantage while it promotes desired species, so that they can exploit freed or floating resources. In order to accomplish this one needs to have an understanding of not only the weed's biology, but also its behavior as a population. More importantly its population interactions within the plant community should be well understood. All too frequently, we proceed in research as well as actual management practices without taking the population dynamics of the weed and plant community into account (Sheley 1996). If biological control is going to be a successful part of an integrated weed management program of Dalmatian toadflax the plant's ecology and response to management strategies need to be well understood.

Currently, seven species of herbivorous insects are approved for release by the USDA Animal Plant Health Inspection Service-Plant Protection and Quarantine (APHIS-PPQ) for the management of Dalmatian and yellow toadflax. The defoliating moth *Calophasia lunula* (Hufnagel) was the first agent to be released (1968), with varied success, mostly due to its susceptibility to cold and predation (Nowierski, 1995). In addition, two species of beetles accidentally introduced along with Dalmatian and yellow toadflax (*Linaria vulgaris* Miller) also have been approved for release (Hervey 1927). These include the ovary-feeding nitidulid, *Brachypterolus pulicarius* (L.), and the seed capsule feeding weevil, *Gymnetron antirrhini* (Paykul). Both beetles primarily feed on yellow toadflax although they also have been shown to feed on Dalmatian toadflax (Lajeunesse, et al, 1993). More recently, two species of root boring moths, *Eteobalea intermediella* (Riedl) and E. *serratella* (Treitschke); two additional cuculionids, the stem galling weevil, *Mecinus janthinus* (Germar) and the root galling weevil, *Gymnetron linariae* (Panzer); and the Dalmatian toadflax-adapted strain of *Gymnetron antirrhini* have been approved for release.

Two of the seven approved biological control agents for Dalmatian toadflax directly affect seed production. Of these two, *Brachypterolus,* is also the most widely established of the approved natural enemies. In theory, the lowered level of seed production resulting from insect predation should lead to lowered seedling recruitment and an eventual reduction of the weed population, as older individuals die and are not replaced. In one scenario, seedling emergence microsites for Dalmatian toadflax are readily available and every seed removed from the environment is one less adult plant. In this scenario seed feeding natural enemies are well suited for biological control. However, in a second scenario, seed emergence microsites are scarce and already saturated by Dalmatian toadflax seeds. In this situation a seed feeding natural enemy will most likely not have much of an effect on an existing weed stand, since the reduced level of seed production will probably be enough to maintain the weed population. Given the incredible reproductive capacity of Dalmatian toadflax, and the fact that it can also reproduce vegetatively, it is not clear whether or not seed production is an appropriate target for its management.

My masters thesis focused on three main areas of Dalmatian toadflax ecology and management. The three objectives were as follows; 1) to examine seedling recruitment in existing Dalmatian toadflax stands in the context of seed and microsite limitation in the presence and absence of insect herbivory and interspecific plant competition; 2) to develop a producer-run yellow toadflax biological control program with the Blackfoot Challenge noxious weed program; and 3) to collect and quantify life history data in order to initiate the construction of a "boxcar" type mechanistic model of Dalmatian toadflax population dynamics. Life history data collected included seed production, presence of seed in the seedbank, and seedling recruitment.

Seedling Recruitment in Dalmatian Toadflax

Seedling recruitment in Dalmatian toadflax is a research topic that needs to be addressed in order to develop functional integrated management systems. Two of the seven biological control agents for Dalmatian toadflax directly affect seed production. If Dalmatian toadflax seedling recruitment is not directly limited by the amount of seed present in the environment, then biological control agents that focus on other elements of the plant's physiology and life history may be more appropriate for management of Dalmatian toadflax populations.

The first goal of this thesis was to evaluate Dalmatian toadflax seedling recruitment in its natural habitat and in the presence and absence of natural enemies and plant competition. Questions addressed in this study were: Is Dalmatian toadflax seedling recruitment limited by seed production?; does feeding by *Brachypterolus pulicarius* have a negative effect on seedling recruitment?; and does interspecific competition by grass and forbs have a negative effect on seedling recruitment? I addressed these questions through a combination of studies at established toadflax sites as well as in a partial addition series experiment.

Hypotheses tested in this portion of the thesis are:

1: H_o: Additional seeding of existing stands of Dalmatian toadflax will not significantly increase seedling recruitment in the following year.

2: H_o: Insect herbivory by *Brachypterolus pulicarius* will not have a significant negative effect on seedling recruitment.

3: H_o: Interspecific plant competition will not have a negative effect on new seedling recruitment.

Producer Education through the Extension of Biological Control of Dalmatian Toadflax

The second objective of this thesis was to begin a producer-operated biological control program for yellow toadflax. The site for this program was the Blackfoot Valley utilizing the already existing Blackfoot Challenge group as the producer group.

Traditional extension from Land Grant Universities has followed a path similar to a patient-doctor relationship where the producer clientele asks a question and the university replies with an answer often researched without producer involvement. This approach, while well suited to past situations, is inflexible when presented with agroecological challenges specific to a particular region or ranch. Involving the producer in the research and innovation of a new agricultural technology has the potential to incorporate the "later" stages of producer adaptation of the technologies into the earlier developmental phases of the technology (Hildebrand, 1988). In an idealized sense this would result in the producer performing his/her own experiments with scientific and technical support from the Land Grant University.

Biological control is the weed management technology involved in the extension component of my thesis. Like any ecologically based strategy of weed management, it requires that the specific environmental and ecological factors of a region or farm be understood in order to be successful.

Involving the producers at the beginning of a biological control of weeds program has two primary advantages. The first advantage is that producers with large infestations of the weed are in a perfect position to foster new natural enemy populations, eliminating the need for a weed garden or greenhouse rearing facilities. The second advantage is that once natural enemies are established at one or two weed sites on participating landowners' properties, they are easily spread to other weed sites through producer cooperation.

For the purposes of managing yellow toadflax in the Blackfoot Valley the three natural enemies selected were the defoliating moth, *Calophasia lunula*, the ovary feeding beetle, *Brachypterolus pulicarius*, and the stem boring weevil, *Mecinus janthinus*. The three natural enemies are appropriate agents from a biological control standpoint because they attack yellow and Dalmatian toadflax, and they impact different plant parts. *B. pulicarius* adults feed on plant meristematic tissue causing increased branching, while the larvae feed on plant pollen and ovaries, causing decreased fertilization and seed capsule abortion. *Calophasia lunula* caterpillars defoliate toadflax plants decreasing the amount of resources the plant can put into growth and reproduction. *Mecinus janthinus* adults girdle plant stems in the process of oviposition, causing the terminal stem portion to wilt, while the larvae are stem and lateral shoot miners. Utilizing natural enemies with different types of impacts should lead to better management of toadflax than simply focusing on seed production or plant vigor alone.

B. pulicarius is adventive to North America and likely was introduced when Dalmatian and yellow toadflax plants were brought from Europe as ornamentals. This beetle species has become widely distributed in North America on yellow toadflax and is less commonly found on Dalmatian toadflax (Harris 1961). Reports of 74% to 90% reduction of viable seed in yellow toadflax have been reported as a result of feeding damage by *B. pulicarius* ((Harris 1961, McClay 1992). *C. lunula* was the first toadflax natural enemy to be approved for release and has been established at a number of toadflax sites in the United States and Canada, West of the Continental Divide (Nowierski 1995). *M. janthinus* was approved for release within the last three years making the Blackfoot Challenge area one of the first release sites of this natural enemy in the United States.

The second and more traditional extension aspect of this thesis goal was producer education through presentations to the Blackfoot Challenge group and the production of simple supplementary extension materials. Presentations were performed in conjunction with the involvement of producers in the process of initiating and monitoring the establishment of natural enemies of yellow toadflax. A full color brochure style report was produced and presented to the Blackfoot Challenge, highlighting the progress made over the two year period of study.

Modeling Population Dynamics Of Dalmatian Toadflax

The final objective of this thesis was to begin the development of a population dynamics model of Dalmatian toadflax. Such models have been used extensively to describe the dynamics of plant populations and examine the intricacies of weed and management strategy interactions (Sheley 1994b, Lindquist 1995, Maxwell 1997). Boxcar type models are fairly simple models well suited to simulating weed population dynamics. The model consists of a set of "boxes", with each box containing a population value for a specific stage of the weed's life history. Between the boxes lie equations that process the value from the previous box, and transfer it to the next box. In this way, specific field data regarding a weed population can be plugged into the model and run through simulated generations to suggest likely weed population trends.

This style of model has good potential as a management tool, because the user can enter disturbance or mortality pressures representative of control methods, and get a prediction of what might result. In short, the model can help identify probable weak points in the weed 's life history. An added benefit to modeling range weed population dynamics is that smaller species-specific box car models can be incorporated into larger models that might be used to guide ecological succession on infested rangeland (Sheley 1996).

To create a model for Dalmatian toadflax populations, data had to be collected for each stage in the plants life history. Seed production and dispersal, seed load in the soil, seedling recruitment, and expected mortality data are all needed to create such a model (Radosevich, 1984). Some life history data for Dalmatian toadflax have been collected previously and include yearly emergence rates, seed production, early plant phenology, and yearly toadflax population monitoring at a number of research sites (Nowierski, Zeng, FitzGerald, unpublished data). Currently, detailed information is lacking on seed dispersal and seedling recruitment. I addressed these data gaps by taking measurements of the seed bank and setting up a series of permanent ground frame sites at two different locations. Later studies will need to address vegetative reproduction and adult plant mortality in order to complete the model.

CHAPTER 2

LITERATURE REVIEW

Dalmatian Toadflax Biology and Distribution

Dalmatian toadflax is a robust, broad-leaved, perennial herb native to the Mediterranean region, between the former Yugoslavia and Iran. The plant is characterized by glaucous green foliage, bright yellow snapdragon like flowers, and ovoid to nearly spherical fruit (Nowierski, 1995). Dalmatian toadflax stems are robust and woody at the base and are one to three feet tall. It has been cultivated as an ornamental plant in Europe for at least four centuries, and was introduced to the Americas by 1874 along with its close relative, yellow toadflax (*Linaria vulgaris*) (Alex, 1962). Since its introduction, Dalmatian toadflax has become a serious weed in rangelands in a number of Western States including, Montana, Wyoming, Washington, Oregon, Idaho, and California, mostly within the last 50 years (Nowierski, 1995).

Dalmatian toadflax seeds germinate in either the spring or fall, and first-year seedlings, if established, will flower and produce seed. Dalmatian toadflax blooms from June through September, with bumble bees and other robust insects serving as its primary pollinators. The weed releases seed by the end of August and dies back by the end of fall. Seeds are small, angular, possess irregular wings, and are primarily wind dispersed. Plants put up new shoots and flower in the spring by using root reserves and non-stem rosettes (Lajeunesse et al. 1993).

The root system of Dalmatian toadflax includes a deep taproot with secondary lateral roots. The taproot can reach a depth of six feet or more, while lateral roots can extend up to ten feet away from the parent plant and are usually two to eight inches deep (Lajeunesse et al. 1993). The deep taproot of Dalmatian toadflax provides it with considerable energy reserves which allows rapid regrowth after herbivory. The lateral roots of the weed contain vegetative root buds, which are capable of producing flowering shoots, or if fragmented, a new plant.

Dalmatian toadflax has three main characteristics which make it a "problem weed". 1) It is a prolific seed producer and can reproduce vegetatively; 2) It prospers on coarse, well drained soils, especially on sites that have been recently disturbed and interspecific competition is low; and 3) it is unpalatable, if not toxic, to livestock.

Dalmatian toadflax has a very high sexual reproductive capacity. Under favorable conditions, a large plant is capable of producing 500,000 seeds per year. Furthermore, toadflax seeds can remain viable in soil for up to 10 years, allowing high levels of seed accumulation in the seedbank (Robocker 1970,1974). Dalmatian toadflax also reproduces vegetatively from secondary crown points located along the lateral root system, and the shoots produced from these lateral root-buds also may produce seed capsules (Nowierski 1995).

The soils favored by Dalmatian toadflax are coarse textured and best described as well drained and "poor". The weed can often be found on depleted rangelands and recently disturbed sites. As a seedling, the weed is not a good moisture competitor compared to established grasses and herbs, but once established, toadflax can have a significant effect on the plant community surrounding it (Robocker 1974). As a result, Dalmatian toadflax is especially prevalent on rangelands with low interspecific competition (i.e., on sites with impoverished soils or sites that have been overgrazed).

Dalmatian toadflax may be toxic to livestock (Polunin 1969), although cattle and horses will reportedly graze on floral stocks. It is possible that the weed's seeds are dispersed, in part, through the feces of livestock and small rodents (Reed 1970). Possible toxicity of Dalmatian toadflax to livestock may result because the plants contain a gluoside antirrhinoside and the quinoline alkaloid, peganine (Polunin 1969). Beside of its possible toxic effects, the weed can significantly lower range quality by replacing higher quality forage species.

Seed Versus Microsite Limitation of Dalmatian Toadflax

The concept of seed limitation is that plant recruitment is limited by the amount of seed present in the environment. While this is usually true at some critical point, there are really two interdependent factors which may limit recruitment in plant populations. Both seed availability and the availability of microsites limit the recruitment of new plants into a population (Eriksson 1991). While recruitment is usually dependent on a combination of both of these factors, it is possible to determine which plays a bigger role in specific plant populations.

Insect herbivory tends to have a negative effect on the supply of seeds to the environment. Studies on the effects of inflorescence feeding insects on seedling recruitment of plants have shown that seed predation by insects can have a dramatic effect on seedling recruitment or little to no effect at all. Extensive experimentation by Louda et. al (1990, 1995) in the Nebraska sand hills prairie has shown that recruitment of the Platt thistle, *Cirsium canescens*, (Nutt.) is severely limited by insect seed predators (Louda 1990, 1995). Seedling recruitment also was found to be limited by seed predation in the perennial shrub *Haploppappus squarrosus* (Hall) (Louda 1982), and in wild parsnip, *Pastinaca sativa* (L.) (Hendrix 1989). In contrast, for other plant species such as *Senacio jacoboaea* (L.) and *Cytisus scoparius* (L.), seedling recruitment was not reduced by insect herbivory (Crawley 1989) or seed predation (Bossard and Rejmanek 1994).

Interspecific plant competition affects the availability of seedling emergence microsites, which in turn may effectively limit seedling recruitment. Putwain et al. (1968) showed that recruitment of *Rumex acetosella* (L.) in established grasslands was entirely dependent on reduced grass competition. Similarly, *Oputia Fragilis* (Haw.) has been shown to have a higher rate of recruitment when interspecific competition is excluded (Burger et al. 1995). In another study, initial recruitment of several biennial plant species was shown to be inversely correlated with levels of ground cover (Gross, 1982).

Given the prolific seed production of Dalmatian toadflax and its ability to reproduce vegetatively I propose that, in situations where seed predation is not a factor and plant competition is negligible, seedling recruitment of Dalmatian toadflax is not primarily limited by seed production. Whether or not it might be limited under high levels of seed predation and/or plant competition is a more complex question. Given the poor competitive ability of Dalmatian toadflax seedlings for soil moisture, under competition from forbs and grasses it seems reasonable to expect seedling recruitment to be limited by micro-site availability (Robocker 1970, 1974).

In this study a combination of field observation studies and controlled field experiments were used to explore seed versus microsite limitations in Dalmatian toadflax. While field studies that add additional seeds to or remove insect predation or interspecific plant competition from pre-existing plant stands remain the most common methods of testing hypothesis regarding population dynamics of plant populations, controlled experiments may enable one to collect accurate data regarding the colonization of a disturbed habitat as a function of seeding rates. Examples of plant population dynamic studies that have involved alteration of standing plant populations through the addition or exclusion of seeds, predation, and interspecific competition include those of Louda (1982, 1991, 1995) and Crawley (1985, 1989). Partial addition series studies of *Bromus tectorum* (L.) and *Centaurea solstitialis* (L.) by Sheley and Larson (1994) and the invasiveness of biennial plants in unpopulated versus populated farmland (Gross, 1982), provide good examples of controlled field experiments.

CHAPTER 3

MATERIALS AND METHODS

Field Study of Dalmatian Toadflax Seedling Recruitment and Mortality

Experimental Design

The field experimental design consisted of a fixed block, three factor design with eight treatments replicated across four blocks at two sites. The first factor consisted of overseeded or non-overseeded treatments, the second factor consisted of plant competition allowed or excluded, and the third factor consisted of natural enemies present or excluded. The two sites chosen for this study had received previous releases of *B. pulicarius*. Four blocks were established at the two research sites to block against obvious differences in vegetative cover. Each of the factor/treatment combinations was established once in each block through the use of permanent quadrats.

Site And Block Descriptions

The study took place during the 1997 and 1998 growing seasons. The two study sites were located at the Crow Reservation, 12 miles North of Wyola, Big Horn County, MT and adjacent to the Canyon Ferry Reservoir (about three quarters of a mile North of the dam) approximately ten miles SE of Helena, Broadwater County, MT. Sites were chosen because they reflected different habitat types infested with Dalmatian toadflax and both sites had had previous releases of *B. pulicarius* for at least eight years. Each site consisted of four blocks with eight treatments representing eight possible combinations of experimental factors. Blocks were fixed previous to treatment assignment through the use of total plant cover measurements across a spatial gradient. The experiment was laid out in a randomized fashion across the fixed block design, with each treatment occurring once in each block.

The Wyola site had a higher density of Dalmatian toadflax plants than the Canyon Ferry site in addition to having a long history of cattle grazing. Cows, bulls, as well as some horses were present at the Wyola site during both study seasons. The area where the plots were laid out, and where toadflax density was highest was an old unfilled gravel pit. The soil tended to have a high clay content with rocks and gravel throughout. Blocking was laid out across a basin, up a north-facing slope, along the top of a slight hill, and then down a south-facing slope, with each described region receiving a single block of treatments. Other significant plants at the study site included cheatgrass (*Bromus tectorum* L.), yucca (*Yucca glauca* Nutt.), ragweed (*Ambrosia artemisiifolia* L.), western salsify (*Tragopogon dubius* Scop.), and yellow sweet clover (*Melilotus officinalis* (L) Lam).

The site located at Canyon Ferry was markedly different than the Wyola site and consisted of a hillside adjacent to the BLM's Riverside Campground. Grazing pressure at the Canyon Ferry site did not compare to the Wyola site as it consisted of only occasional browsing by white-tail and mule deer. The soil at this site was rocky and gravely with a lower clay content than that at the Wyola site. Environmental conditions were somewhat cooler than at the Wyola site with frequent thunderstorms. Blocking was laid across the flat before a hillside and then in three progressively decreasing plant cover levels up the hillside. Each described region received a single block of treatments. Other significant plants at the study site included cheatgrass, prickly pear (*Opuntia polyacantha* Haw.), yellow sweet clover, leafy spurge (*Euphorbia esula* L.), and spotted knapweed (*Centaurea maculosa* Lam.).

<u>Quadrat Frame Construction and Sampling Procedure</u>

Seedling recruitment, plant cover data and seed production rates were collected using four blocks of eight 60 x 60 cm permanent quadrats at both sites. Thirty-two individual parent plants in four blocks of eight treatments per site, were randomly selected for the duration of the study. Plants selected for data collection were marked with two pieces of rebar at the NW and SE corners of the quadrat. A portable quadrat-frame consisting of a 60x60 cm square divided into nine 20x20 cm squares, was used to demarcate the observation arena. The frame had adjustable legs at each corner, which could extend to 30 cm in height to minimize plant disturbance during frame placement and removal. The frame consisted of 3.81 cm (1.5") PVC pipe, 0.315 cm (0.125") ready-bolt used make the smaller squares, and 0.635 cm (0.25") ready-bolt used for legs. The ready-bolt consisted of steel bars that were threaded along their entire length. A two-dimensional conceptual diagram of the quadrat frame can be seen below in Figure 1.