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BIOLOGICAL CONTROL: EFFECTS OF *TYRIA JACOBABAEAE* ON THE  
POPULATION DYNAMICS OF *SENECIO JACOBABAEA* IN NORTHWEST MONTANA

By

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Dissertation

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for the degree of

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in Wildlife Biology

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Biological control: effects of *Tyria jacobaeae* on the population dynamics of *Senecio jacobaea* in northwest Montana

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Abstract

Biological control, using introduced, specialist insects is a common strategy for controlling plant invasions. However, the efficacy of biological control agents in controlling their host plants is rarely quantified population level. I quantified the impact of a specialist biological control agent, the cinnabar moth (*Tyria jacobaeae*) on its host plant, tansy ragwort (*Senecio jacobaea*) in northwest Montana. Cinnabar moth damage and its effects on important plant vital rates were tested with and without specialist herbivores. The presence of moth larvae corresponded to a reduction in population growth rates to less than one, compared to herbivore-free controls, indicating the potential for successful biological control by this insect. However, delayed effects of cinnabar moth herbivory on tansy ragwort vital rates were realized during the year following moth herbivory, after the moths had disappeared from the system. Individual damage to flowering plants in 2005 led to increased survival of these plants in the following year compared to controls, by reverting back to a vegetative state. In addition, seed set was reduced in plants that were damaged as juvenile rosettes in 2005 that went on to flower in 2006. When these delayed effects were combined in matrix models, gains in adult survival did not outweigh the decreases in fecundity or transition rates in terms of population growth and our initial conclusions remained unchanged. However, further study revealed that moth larvae were more likely to be depredated by carpenter ants in xeric sites suggesting that moth populations may not be sustained in these areas. Cinnabar moth larvae can be effective in this system provided they consume a large number of seeds (>90%) in consecutive years, but requires that moth populations are established and sustained from year to year. While herbivores do show the ability to control an invasive plant species, this relationship is strongly contextual in this system. This work emphasizes the importance of recognizing the influence of habitat context on the outcome plant-herbivore interactions, specifically in invaded ecosystems.

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## **CHAPTER 1**

### **GEOGRAPHIC PATTERNS OF PLANT SIZE AND DENSITY IN *SENECIO* *JACOBAEA* (L.): ANALYSIS OF EXISTING LITERATURE FROM THE NATIVE AND INVADED RANGE**

## ABSTRACT

Invasive plant species are often assumed to be larger and more abundant where they are invasive compared to where they are native. However, studies conducted in both the native and invaded range of invasive plant species (i.e., biogeographic comparison studies) suggest that these assumptions are not always met. Recent reviews of such studies indicate that the failure to include spatial and temporal covariates could produce misleading results. In lieu of designing a costly comparative study, we conducted a meta-analysis for one invasive species that has been studied intensively in both its native and invaded range in an effort to verify the basic assumptions of greater abundance and size. We reviewed existing literature for tansy ragwort (*Senecio jacobaea* L.), to find measures of size and abundance. We found 21 studies that reported values of size and/or abundance of tansy ragwort in either the native or invaded range. We did not detect any significant differences in size or abundance measures between ranges after standardizing for units within and between studies. Abundance measures were not associated with latitude or minimum residence time within or between ranges. However, after removal of one extreme outlier, we found that plant size among all sites had a strong negative association with minimum residence time. However, adjusting for this association did not reveal significant differences in plant size between ranges. While measures of plant size were also strongly correlated with latitude, plants showed only a weak tendency toward larger size in the invaded range. We conclude that the assumptions of greater size or abundance in defining a species as invasive may not always be met, as comparative studies with other species have shown. This suggests that some species may be considered locally invasive but may not be considered invasive at larger spatial scales. We recommend this

type of literature review for other invasive plant species as a useful tool for comparatively assessing general geographic patterns of size and abundance in invasive plant species so long as the limitations of the available data are adequately addressed.

## **INTRODUCTION**

Invasive species are non-native species that become more abundant outside of their native range (Daehler 2001). In plants, some have hypothesized that greater abundance is achieved because plants are more vigorous, realized by greater size, growth, or fecundity, in the invaded versus the native range. A recent profusion of biogeographic comparison studies have sought to determine how often, and to what extent, invasive plants differ in size from their native conspecifics (e.g., Joshi and Vrieling 2005, Stastny et al. 2005, Paynter et al. 2003) to isolate mechanisms that promote invasiveness. A majority of such studies rely on the assumption that the non-native species occurs at higher densities (Hierro et al. 2005), but surprisingly few studies quantify this basic measure (but see Lonsdale and Segura 1987, Woodburn and Sheppard 1996; Edwards et al. 1998, Grigulis et al. 2001, Paynter et al. 2003, Jakobs et al. 2004, Erfmeier and Bruehlheide 2004). Additionally, results have been inconsistent between studies that compare plant size measures between ranges, even within the same species (e.g., Willis et al. 2000, Stastny et al. 2005, Joshi and Vrieling 2005). Despite the prevalence of literature focusing on particular invasive species, there is still a dearth of studies that quantify basic measures of size and abundance for species where they are invasive and native. Existing published data for many well-studied invasive species from many locations could prove as a source from which to compile such information.

Ideally, researchers would conduct large-scale studies, stratified at a global scale, to ask how consistently particular species are truly invasive, in order to develop specific questions as to what traits differ between areas where species become invasive, their native ranges, and where they do not become invasive. However, such experiments would be logistically challenging, even for relatively straightforward responses such as individual size and plant density. At the same time, based on current evidence, general conclusions regarding invasiveness remain elusive. In this paper, we explore the ability of previously-published studies to inform biogeographic understanding of a widely introduced invasive plant, *Senecio jacobaea* L. (Asteraceae) (tansy ragwort). Specifically, we use 19 published studies from throughout its range to test a major assumption of invasion theory: Is tansy ragwort consistently larger and more abundant in areas where it is considered invasive, relative to its native range?

From an ecological perspective, this analysis tests whether species considered invasive are consistently different between native and invaded ranges. From a methodological perspective, this study informs how well we can infer range-wide traits from manipulative studies over a small part of species ranges, and how much past research can inform current questions, in lieu of extensive and expensive new investigations.

## **METHODS**

### *Natural history*

Tansy ragwort (*Senecio jacobaea*) is a biennial to short-lived perennial (Bain 1991). The species spends its first season as a basal rosette and then bolts a flowering stalk during the second growing season. Inflorescences consist of disk and ray achenes,

mature seeds are most commonly gravity- or wind-dispersed. Colonization and establishment occurs via seeds or vegetative growth from the root crown. The plant has shown persistence in disturbed areas due to the persistence of an abundant seed bank which is positively correlated with the historical abundance of flowering plants (McEvoy et al. 1991). It has a capacity for regrowth after damage (van der Meijden et al. 2000), and produces a complex and variable profile of pyrrolizidine alkaloids acting constitutive defenses against herbivory (Witte et al. 1992, Macel et al. 2002).

The plant is native to Europe and Asia minor and introduced to North America, Australia, and New Zealand. It is distributed in North America, from northwestern California north to British Columbia, east to Montana and south to Colorado, and in Canada's maritime provinces. Tansy ragwort was first recorded in North America in 1913 from Vancouver Island (Harris 1971), later recorded in Oregon in 1922 (Isaacson 1973), and anecdotal evidence suggests it was present in Montana as early as the 1970s (G. Markin, personal communication). The plant was introduced to Australia in the 1880s (Bornemissza 1966) and New Zealand in 1874 (Poole and Cairns 1940).

#### *Literature Search*

We searched for studies of tansy ragwort size and abundance using Web of Science and Agricola databases (ISI Web of Knowledge (CITE, from 1970-Aug 2008), for studies with *Senecio Jacob\**, *Senecio*, or "tansy ragwort" in the topic field. Duplicates were removed and papers were sorted based on the type of data presented. We expanded our search by following references within the existing articles that went beyond our search dates, or were from non-journal or obscure journal sources such as conference proceedings, government technical reports, and theses and dissertations. We included all

types of studies (e.g., randomized experiments, non-randomized experiments, and observational studies) in this review. The data available were notably unbalanced due to the clustered distribution of tansy ragwort as well as to research interest and effort in particular locations.

### *Data analysis*

We found a total of 21 studies that reported measures of plant density and/or plant size. In studies where herbivores were experimentally manipulated to measure effects of damage on plants, we used only the values from control plots in order to assess natural abundance and size of tansy ragwort at each study location. Many of the studies contained a number of abundance counts at different points in time. We entered these into our database and then used the average per study, which required averaging across different years within studies. We averaged across sites within studies to avoid complications of dealing with within study variation so that we could focus on the general geographic patterns.

Across all measures of plant size and abundance, sample size was reported for 20% of estimates (7/34), and standard errors for 26% (9/34) estimates. Therefore, we analyzed the overall effects of native vs. invaded range on size and abundance using the point estimate from each study. In addition, studies differed in the units used to measure size and the life stages used to measure density (Table 1). Therefore, we analyzed proportional differences among sites using generalized linear models with log-link functions and fixed effects of measurement units. As outlined by Ricketts et al. (2008), the exponential transformation means the slope ('treatment' term) in the model refers to proportional differences in abundance, and the intercept accounts for differences in units

among studies. Eight studies included more than one measure of size (e.g., number of capitula and height measures) or abundance (e.g., some studies had both rosettes/m<sup>2</sup> flowering plants/m<sup>2</sup>). We used study as a random factor in the model to account for this within study variation. As an additional precautionary measure, we randomly chose one value from those studies that reported two or more values and repeated the analysis with this reduced data set to compare results to the full data set.

We added simple covariates to adjust for variation in plant abundance and size over space and time. Including latitude is simple and can correct for among-population variation within one or both ranges (Colautti et al. 2008). We used broad estimates of degrees of latitude corresponding to each study location either by country (Australia, New Zealand, The Netherlands, United Kingdom), state within country (USA), or province within country (Canada). We used published year of first arrival to calculate the minimum residence time (MRT) of tansy ragwort for each study. Documentation typically consisted of arrival estimates at the state, provincial, country, or continental scale. The MRT value was simply the year of introduction subtracted from the year of study. We used zero to intuitively represent plants in the native range. (Conclusions were identical if we set MRT to 200 years for sites in the native range; K. Crider unpubl.).

## **RESULTS**

In total, we found 120 studies in our literature search of which 21 reported measures of size and/or abundance. We found 20 estimates of plant abundance, including 7 that reported flowering plant densities (5 from the native range, and 2 from the invaded range); 4 that reported total plant densities (3 from the invaded range and 1 from the native range); and 9 studies of rosette densities (4 from the invaded range and 5 from the native range). Of studies that reported plant size, 9 reported capitula per plant, 4 from the

invaded range and 5 from the native range. Five studies reported plant height, 4 from the invaded range and 1 from the native range. Three studies from the invaded range reported seeds per capitulum. We included only studies that reported capitula per plant or plant height in the statistical analysis of plant size vs. range (native vs. invaded), because seeds per capitulum were only reported from the invaded range. Cameron (1935), Harper and Wood (1957), Dempster (1971), Schmidl (1972), Nagel and Isaacson (1974), Forbes (1977), Dempster and Lakhani (1979), and Cox and McEvoy (1983) reported multiple values within one or both categories. We randomly chose values from each group and excluded remaining values from the analysis, reducing the number of studies to 13 abundance measures and 12 size measures. Analyses with these reduced data sets did not change results (not shown), hereafter results refer to entire data sets for both size (n=14) and abundance (n=20) (Table 1).

Neither average plant abundance nor average size differed significantly between the native and invaded range (Table 2A). One large outlier showed the potential to skew comparisons of plant size; Cameron (1935) measured 886 capitula per plant in the native range. We repeated the analyses after removing this outlier to determine its effect on skewing the results, but this did not change our conclusions ( $P=0.902$  vs.  $P=0.557$ , outlier removed, Table 2A).

As a covariate, estimated minimum residence time (MRT) was not strongly correlated with abundance within or between ranges (Table 2C, Figure 1B, top) but was positively correlated with plant size only after excluding the outlier ( $P=0.149$  vs.  $P=0.045$ , outlier removed; Table 2C, Figure 1A, top) meaning that plants in the invaded range generally increased in size with increasing MRT. Adjusting for this variation

revealed a weak, nonsignificant difference in size between ranges ( $P=0.181$ ;  $P=0.147$ , outlier removed; Table 2C, Figure 1A, top). Considering latitude as a covariate yielded similar results as MRT (Table 2B). Plant abundance tended to decrease with latitude, but this relationship was not significant ( $P=0.295$ , Table 2B, Figure 1B, bottom). That being so, including latitude did not reveal any differences in abundance between ranges ( $P=0.898$ , Table 2B, Figure 1B, bottom). There was a negative correlation between latitude and plant size that became larger, and significant, when the outlier was removed ( $P=0.159$  vs.  $P=0.022$ , outlier removed, Table 2B, Figure 1A, bottom). After correcting for the latitudinal gradient, there was only a weak tendency for plants of greater size in the invaded range, and this difference was marginally significant ( $0.05 < P < 0.10$ ) only with the removal of the outlier ( $P=0.184$  vs.  $P=0.091$ , outlier removed, Table 2B, Figure 1A, bottom).

## **DISCUSSION**

Plants were slightly larger but not more abundant in the invaded as compared to native ranges. Abundance was highly variable within each range, and abundances overlap among ranges. This result supports cumulative results from comparative studies that have measured abundance. Most found larger populations or higher density in the invaded range compared to the native range (Eckert et al. 1996, Jakobs et al. 2004, Prati and Bossdorf 2004, Vilà et al. 2005, Bastlova-Hanzelyova 2001, Paynter 2003), some found no differences in abundance (Wolfe 2002, Erfmeier and Bruelheide 2004), and some found lower abundance in the invaded vs. native range (Sheppard et al. 1996, Lonsdale and Segura 1987). Similarity between ranges might indicate that plants are not more dense in the invaded range as one would hypothesize. However, it is also possible

that tansy ragwort occurs at similar densities in the native range because it is classified as a ruderal species, implying higher abundance in disturbed areas (Wardle 1987). Natural fluctuations in abundance, leading to markedly patchy distribution are common in species like tansy ragwort that are short-lived, have light-weight seeds that can disperse relatively far, or can form seed banks that readily germinate given amenable biotic and abiotic conditions. In dune populations of tansy ragwort in The Netherlands, patches of plants fluctuate in density corresponding to both the spatial and temporal distribution of herbivores, the frequency of disturbance, the density of vegetation, and availability of sunlight (van der Meijden and van der Waals-Kooi 1979). However, natural variation in abundance may be associated with traits common to many weedy plant species (Baker 1974), e.g., high capacity for population growth and plastic growth form (c.f., Crone and Taylor 1996, Buckley et al. 2003, Pardini et al. 2009).

Our results suggest a potential tendency of plants to increase in size over time in the invaded range. The evolution of increased competitive ability hypothesis (EICA) is a potential explanation for this phenomenon (Blossey and Nötzold 1995). It posits that, in the absence of their native herbivores, invasive species experience strong selection for genotypes that allocate less to chemical herbivore defenses, and more to growth (Blossey and Nötzold 1995). In our study, accounting for the correlation with time since introduction resulted in a very weak difference in size between the native and invaded range (Table 2C), corroborating other studies that assess plant size between ranges. To date, tests of the EICA hypothesis show mixed results—no clear pattern has emerged (see Bossdorf et al. 2005, Hinz and Schwarzlaender 2004, for review). There are many cases where differences in plant size between ranges seem to favor acceptance of EICA, but

lack the ability to link this to a true genetic tradeoff of allocation between defense and growth (Bossdorf et al. 2005). The EICA hypothesis is consistent with our observations of changes in plant size over time in the invaded range; plants may start small in the invaded range, but evolve to be larger as growth is favored over defense. Three existing biogeographical comparison studies use tansy ragwort to test the EICA hypothesis. Willis et al. (2000) did not find significant differences of size between common garden plantings of tansy ragwort from the invaded and native ranges, whereas Joshi and Vrieling (2005) and Stastny et al. (2005) found that tansy ragwort plants were larger in the invaded range. We calculated the mean MRT of sampled invaded range locations for these three studies to determine whether the mean MRT is lower in Willis et al. (2000) compared to Joshi and Vrieling (2005) and Stastny et al. (2005) which would indicate younger populations that have not had as much time to experience genetic changes. Our calculations revealed the opposite of our speculation. The Willis et al. (2000) populations were much older (MRT $\approx$ 128 yrs) but there was no discernible difference between ranges. While the younger populations presented by Joshi and Vrieling (2005) (MRT $\approx$ 58 yrs), and Stastny et al. (2005) (MRT $\approx$ 81 yrs) were significantly larger than their native conspecifics. This result could reflect a tradeoff of increasing defensive compounds in the presence of increasing generalist herbivore pressure over time at the expense of increased growth or reproduction (e.g., Hawkes 2007).

Correcting for latitude resulted in a slight difference in size between ranges (when the large outlier was removed), where plants were larger in the native range than in the invaded range (Table 2A, bottom). Theory predicts the tendency for plants to decrease in size along an increasing latitudinal or elevation gradient. Numerous studies have shown a

strong relationship between traits associated with growth and latitude in invasive plant species (Weber and Schmid 1998; Kollmann and Bañuelos 2004, Maron et al. 2004, 2007, Friedman et al. 2008, and Montague et al. 2008). A recent review of common garden experiments that compared traits between native and invasive plant populations found latitudinal clines in 14 out of 34 species (Colautti et al. 2008), including tansy ragwort.

Our results highlight high among-site and among-range variation in measures of both plant size and abundance. These results should be interpreted with great caution, as our analysis included many assumptions and potential biases that should be addressed. Among these, we assumed the value for year of introduction as absolute, while in reality species can be introduced at multiple times in multiple locations. Fine tuning our estimates with historical introduction information would likely not be a feasible solution in this case, as documentation is generally lacking, purely anecdotal, or difficult to find for most species. Another solution would be to conduct these analyses using values of time that vary within a range of possible values to determine the sensitivity of measures of size and abundance to minute fluctuations in MRT. In addition, our use of the year of study to calculate the time since introduction was not ideal because the published date of the study cannot be assumed to be equivalent to the date that the data were collected, resulting in over-estimation of population age. Our confidence was also limited by small sample sizes representing clustered areas of tansy ragwort research, rather than randomly distributed over a larger geographic area. Finally, the decision to omit an outlying data point is always subjective to some degree. In this case it was especially so as we have no ancillary with which to justify our decision. Therefore, we must emphasize that results

based on the omission of this data point are speculative. If nothing else, these results illustrate that careful consideration and adequate justification of any data modification is crucial in conveying the sensitivity of results to such modification.

Overall, this study illustrates that striking differences in plant abundance and size between native and invaded ranges may not be as common or as obvious as is often assumed. While adjusting for natural variation in space and time was important, it did not change the overall result. That being said, the lack of expected differences in abundance or size between ranges is a compelling result in itself. While not without its limitations, meta-analyses of natural variation, such as this study, cannot replace direct experiments, but they can be valuable companion for assessing patterns of invasions at large scales in space and time. But, how important is meeting these two assumptions of invasiveness at such a large scale? From a theoretical perspective, these results are intriguing and could initiate support for an argument that tansy ragwort is not an invasive species and should not be continually studied as such. However, from a management perspective such broad conclusions are probably not particularly useful. Invasive species traits are variable over relatively small spatial and temporal scales due to complex interactions between species traits, community traits and abiotic conditions (e.g., Lambrinos 2002). Therefore, resource management decisions based on local observation of species, rather than designations made from large scale analysis, is a much more practical approach.

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Table 1. Studies containing abundance and size measures of tansy ragwort used in the data analysis.

Author(s)	Year	Time since introduction <sup>1</sup>	Latitude <sup>2</sup>	Location of study	Variable	Abundance	Size	Reported se	n
Native Range									
Forbes	1977	0	54	UK	Mature Plants/m <sup>2</sup>	1.6		x	x
Harper and Wood	1957	0	54	UK	Mature Plants/m <sup>2</sup>	1.8		x	x
Dempster	1971	0	54	UK	Mature Plants/m <sup>2</sup>	5.3		x	x
Cameron	1935	0	54	UK	Mature Plants/m <sup>2</sup>	26.9		x	x
Cameron	1935	0	54	UK	Plants/m <sup>2</sup>	9.9		x	x
Forbes	1977	0	54	UK	Rosettes/m <sup>2</sup>	4.6		x	x
Dempster	1957	0	54	UK	Rosettes/m <sup>2</sup>	21.5		x	x
Dempster and Lakhani	1979	0	54	UK	Rosettes/m <sup>2</sup>	29.2		x	x
Harper and Wood	1957	0	54	UK	Rosettes/m <sup>2</sup>	37.5		x	x
Cameron	1935	0	54	UK	Rosettes/m <sup>2</sup>	37.7		x	x
Prins and Nell	1990	0	52	The Netherlands, Europe	Height (cm)		29.0	x	x
Crawley and Gillman	1989	0	54	UK	Capitula/plant		67.9	x	x
Van der Meijden and Van der Waals-Kooi	1979	0	52	The Netherlands, Europe	Capitula/plant		124.9	x	x
Harper and Wood	1957	0	54	UK	Capitula/plant		213.8	x	x
Islam and Crawley	1983	0	54	UK	Capitula/plant		230.8	x	x
Cameron	1935	0	54	UK	Capitula/plant		886.3	x	x

Table 1 (cont.)

Author(s)	Year of study	Time since introduction <sup>1</sup>	Latitude <sup>2</sup>	Location of study	Measured variable	Abundance	Size	Reported se	n
Invaded Range									
Nagel and Isaacson	1974	52	42	Oregon, USA	Mature Plants/m <sup>2</sup>	1.3		0.04	x
Harris et al.	1978	55	49	British Columbia, Canada	Mature Plants/m <sup>2</sup>	17.5		x	x
Pemberton and Turner	1990	78	39	California, USA	Plants/m <sup>2</sup>	15.9		x	x
Hawkes and Johnson	1978	61	39	California, USA	Plants/m <sup>2</sup>	18.0		x	x
Crider unpubl.	2009	34	48	Montana, USA	Plants/m <sup>2</sup>	35.7		2.55	96
Thompson	1985	61	54	New Zealand	Rosettes/m <sup>2</sup>	1.34		x	x
Nagel and Isaacson	1974	52	41	Oregon, USA	Rosettes/m <sup>2</sup>	10.4		1.68	19
Harris et al.	1978	57	54	Nova Scotia, Canada	Rosettes/m <sup>2</sup>	15.7		x	x
Bauer	2006	32	48	Montana, USA	Rosettes/m <sup>2</sup>	33.6		3.33	84
Crider unpubl.	2009	34	48	Montana, USA	Capitula/plant		39.67	3.31	300
Cox and McEvoy	1983	61	42	Oregon, USA	Capitula/plant		133.5	11	40
Bornemissza	1966	85	37	Australia	Capitula/plant		326.0	x	x
Schmidl	1972	87	37	Australia	Capitula/plant		393.0	x	x
McLaren et al.	2000	115	37	Australia	Height (cm)		75.0	2.8	50
Cox and McEvoy	1983	61	42	Oregon, USA	Height (cm)		84.0	3	40
McEvoy and Cox	1987	65	42	Oregon, USA	Height (cm)		84.0	2.31	155
Schmidl	1972	87	37	Australia	Height (cm)		89.0	x	x

<sup>1</sup>Calculated by subtracting the year of study from published year of introduction.

<sup>2</sup>Degree of latitude as approximated by country (The Netherlands and United Kingdom (UK)), state (California, Montana, Oregon), province (Nova Scotia and British Columbia) or continent (Australia).

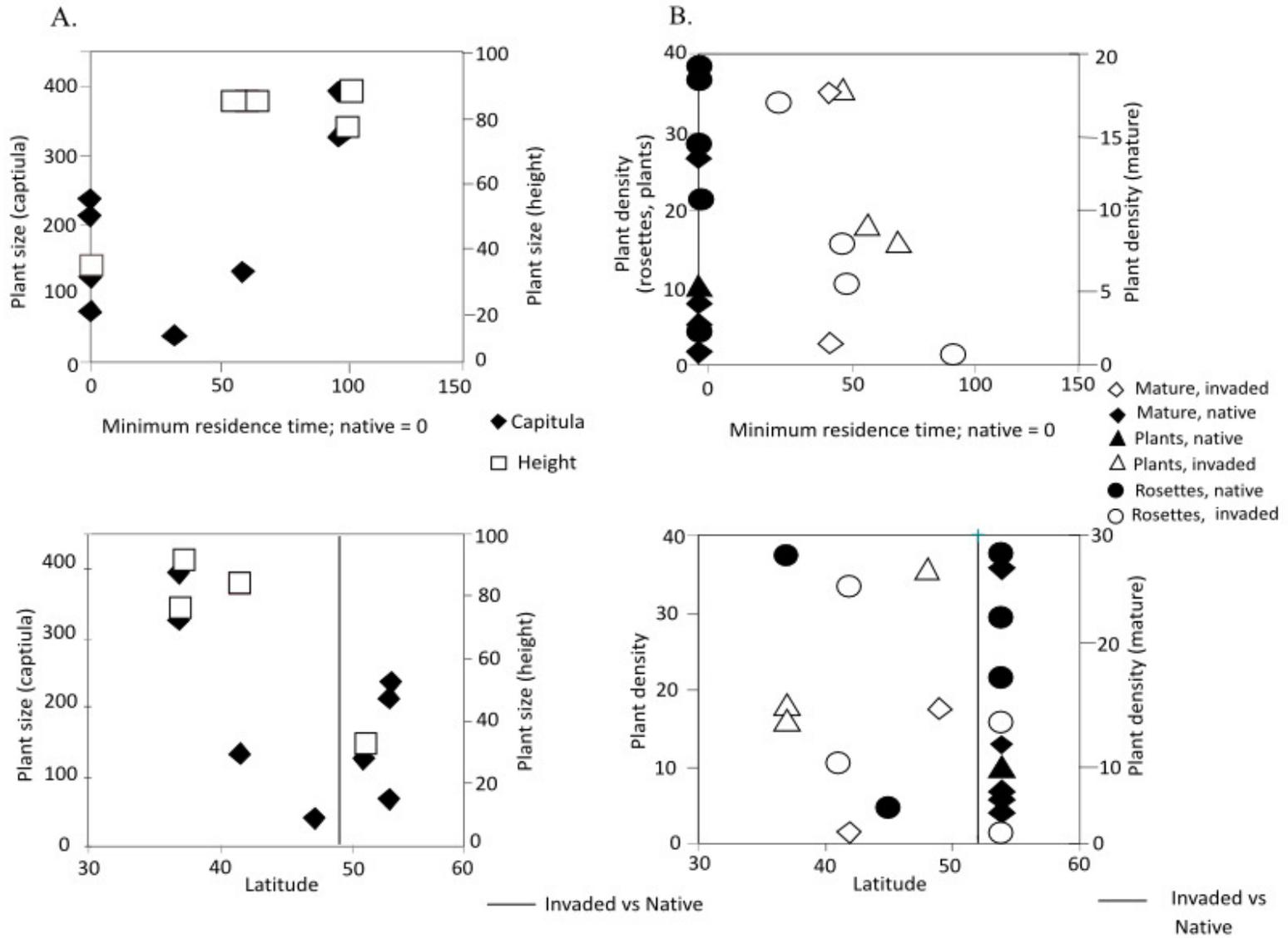
Table 2. Generalized linear model analysis results for comparisons of size and abundance of tansy ragwort between native and invaded ranges. (A) Comparisons with no covariates, (B) Latitudinal degrees of study sites as a covariate, (C) Estimated minimum residence time at study sites as a covariate.

Covariate	Native vs invaded (native=1)			
	t	P	t	P
<b>A. No covariate</b>				
Abundance <sup>1</sup>	na	na	0.149	0.884
Size <sup>2</sup>	na	na	0.125	0.902
Size (outlier removed) <sup>3</sup>	na	na	-0.629	0.537
<b>B. Latitude</b>				
Abundance	-1.078	0.295	0.130	0.898
Size	-1.469	0.159	1.383	0.184
Size (outlier removed)	-2.511	0.022 *	1.868	0.091 †
<b>C. Estimated minimum residence time</b>				
Abundance	-1.093	0.289	-0.983	0.339
Size	1.506	0.149	1.392	0.181
Size (outlier removed)	2.156	0.045*	1.516	0.147

<sup>1</sup> N = 20 studies; <sup>2</sup>N = 14 studies; <sup>3</sup>N = 13 studies ; \* P < 0.05; † 0.05 < P < 0.10

## **FIGURE LEGEND**

Figure 1. Graphs depicting relationships of tansy ragwort between native and invaded ranges. Panels represent: (A) Plant size and minimum residence time (top), and plant size and latitude (bottom), (B) Plant abundance and minimum residence time (top) and plant abundance and latitude (bottom). Points that overlapped were jittered slightly for visibility. Outlying point from Cameron (1935) for capitula is excluded from (A).



## **CHAPTER 2**

DEMOGRAPHIC MECHANISMS OF BIOLOGICAL CONTROL SUCCESS:

CONTEXT-DEPENDENT EFFECTS OF CINNABAR MOTHS ON TANSY

RAGWORT

## ABSTRACT

Invasions are driven at the level of populations. Biological control using specialist herbivores that target important life stages to weed population growth are commonly introduced, but assessment of such programs is sorely lacking. In this study we tested the whether an invasive plant (*Senecio jacobaea* L., tansy ragwort) could be controlled by a specialist biological control agent, (*Tyria jacobaea*, cinnabar moth) using an experimental demographic approach. We used matrix population models with experimental addition of moth larvae to quantify the demographic responses of tansy ragwort to herbivory in two different environments. In both xeric and mesic sites, we estimated that tansy ragwort population growth rates ( $\lambda$ ) would be greater than one in the absence of herbivory, and less than one in the presence of herbivory, as expected for an invasive species. In agreement with our prediction, the presence of moth larvae corresponded to a reduction in population growth rates less than one, compared to herbivore-free controls, indicating the potential for successful biological control by this insect. Our results suggest that if herbivory is high (> 90% of seeds destroyed), tansy ragwort can be controlled in this system, and cinnabar moths might be effective in other areas where tansy ragwort is invasive. However, lower rates of herbivory may not be effective in reducing the population growth of tansy ragwort, and, as noted in previous studies, juvenile rosettes, the most important life stage for persistence of tansy ragwort, remain largely unaffected by herbivory from moth larvae.

## INTRODUCTION

Biological control of invasive plants is now a common practice; over 300 nonnative species of insects and pathogens have been introduced worldwide to control over 50 exotic plant species (Malakoff 1999). Biological control of invasive plant species is based on the assumption that specialist herbivores are important in regulating plant populations in the native range and should therefore be successful at controlling the same species in invaded ranges (Debach and Rosen 1991). While several striking successes of biological control programs exist (Harper 1977, Huffaker and Holloway 1949), many ecologists would argue that the jury is still out as to whether herbivores can substantially depress or regulate plant populations in general (Maron and Crone 2006). However, published research that quantifies the effects of biological control agents on invasive plants, while once rare, is becoming more common, allowing for increased accuracy in estimating the success of biological control.

Recently, demographic matrix models have been used to analyze the population dynamics of invasive plant species to determine their potential responses to biological control (e.g., Shea and Kelly 1998, McEvoy and Coombs 1999, Raghu and Dhileepan 2005, Koop and Horvitz 2005). Prospective analyses emphasize the potential for biological control to be effective by identifying vital rates that are important for rapid population growth. The most basic measure of population analysis, the asymptotic population growth rate,  $\lambda$ , can be a useful measure for predicting the invasiveness of a particular plant species under various management scenarios (e.g., Shea 2002, Schutzenhofer and Knight 2007, Davis 2006). Successful control of an invasive plant requires host-specific control agents able to reduce this rate below one, the minimum rate

at which the population can replace itself. In this context, it is possible for a biological control agent to consume its host and reduce plant population growth rates, but not successfully control its host, if this reduction is not large enough to result in population growth rates below one. Summaries suggest that this scenario may be relatively common; most biological control agents are now screened to ensure they consume the host plant, but the estimated percent of successful suppression of invasive plants ranges from 20% (Williamson and Fitter 1996) to 41% (OTA 1995) of biocontrol projects in the United States.

Demographic data from invasive plant populations before release of biological control agents can be combined with sensitivity and elasticity analysis (i.e., prospective analyses) to reveal what vital rates are most important for population growth (McEvoy and Coombs 1999; Shea and Kelly 1998). These vulnerable stages are often referred to as “Achilles’ heels”, because they are the points in the plant’s life cycle where control agents can have large impacts (Lonsdale 1993; Rees and Paynter 1997, Hendon and Briske 1997; Shea and Kelly 1998; McEvoy and Coombs 1999; Parker 2000; Buckley et al. 2004). Biological control agents that affect traits with higher sensitivity and elasticity should tend to have larger effects on population growth rates (Schutzenhofer & Knight 2007). While prospective analyses do not typically incorporate estimates of the impacts of potential biological control agents, retrospective analyses can then be used in the same way to determine the magnitude of impacts of a particular biological control agent on each vital rate, and, cumulatively on  $\lambda$ . In other words, pre- and post- analyses can reveal whether some agents may successfully control invasive species if they have a very large

effect on a vital rate with low sensitivity, or fail to control invasive species if they have a tiny effect on a vital rate with a high sensitivity (c.f., Crone et al. 2009).

Here, we take a prospective approach, using population matrix models to test whether an introduced biological control agent, cinnabar moth (*Tyria jacobaea*; Arctiidae) can control the abundance of its host plant, tansy ragwort (*Senecio jacobaea*; Asteraceae), in northwest Montana, an area invaded only ~ 11 yrs prior to this study. McEvoy and colleagues extensively studied demographic effects of three insect herbivores as biological control agents on tansy ragwort in western Oregon (McEvoy and Rudd 1993; McEvoy et al. 1993; McEvoy & Coombs 1999). These studies indicated that cinnabar moths alone had minimal impacts on tansy ragwort populations, and were unlikely to be effective biological control agents. In addition, the cinnabar moth showed the propensity to switch to native congeneric host plants (Diehl and McEvoy 1989). Contrary to recommendations of these studies (Diehl and McEvoy 1989, McEvoy et al. 1993), cinnabar moths were released in northwest Montana in 1997. In the more mesic half of the release area (Flathead National Forest), cinnabar moth introductions appeared to control tansy ragwort. However an adjacent, relatively xeric part of the release area (Kootenai National Forest) still harbors high densities of the plants and a lower success of established cinnabar moth populations. To test the qualitative observation that moths appear to effectively suppress tansy ragwort in northwest Montana, we conducted an experimental study of tansy ragwort demography in the presence and absence of cinnabar moth larvae in mesic and xeric sites. If cinnabar moths are responsible for tansy ragwort population declines, estimated population growth rates should be below one in the presence of cinnabar moths, at least in mesic environmental conditions. In the absence of

cinnabar moths, population growth rates should be above one, indicating that populations would increase in the absence of cinnabar moths.

## **METHODS**

### *Study system*

The native range of tansy ragwort extends from Norway south through Asia Minor and from Great Britain east to Siberia. It was first recorded in North America in 1913 from Vancouver Island (Harris et al. 1978). It is a biennial or short-lived perennial herb that grows as a basal rosette during the first growing season and reproduces via dimorphic achenes borne on inflorescences of a bolting shoot produced during or after the second growing season. In NW Montana, plants emerge in spring, inflorescences begin to bolt in July, flowering occurs in August, and seeds are mature by the beginning of September.

Cinnabar moth, a *Senecio*-specific lepidopteran species, was introduced as a larval-stage seed and leaf predator of tansy ragwort, first to northern California in 1959, and to Montana in 1997. Pupae overwinter and adults emerge in late spring (May-June) as adult and juvenile plants begin to grow and flower. Female moths lay eggs on the underside of basal rosette leaves, or on the underside of leaves on the adult bolting stems. Early larval instars mainly feed on the leaves from which they emerge but later feed on inflorescences. Larvae develop and pupate within 4 weeks of hatching. Larvae can remain on the same plant during their entire development, or if food resources are depleted they will move to an adjacent rosette or adult stem.

### *Study area and experimental design*

Study sites were established in the Kootenai National Forest, 40 km east of Libby, Montana in Lincoln County. Experiments in the Flathead National Forest were not possible because tansy ragwort has been nearly extirpated in this area. Two main study areas (“sites”) were chosen for experiments (Table 1). The xeric Little Wolf (LW) site is on a large, southwest facing slope in the Little Wolf Creek Drainage that was burned in 1994, and salvage-logged in 1995. This site is characterized by dry soils, with an early successional lodgepole pine (*Pinus contorta*) forest with an understory of bunchgrasses, forbs, and shrubs. It typifies most areas invaded by tansy ragwort in the Kootenai National Forest, where cinnabar moth control appears poor. The mesic site, Island Lake, is located about 3 km west of LW. This site has a north to east aspect, with flat areas characterized by mesic soils. This area was not burned in the Little Wolf Creek fire; it supports sod-forming forage grasses, shrubs, a few forbs, and sparsely spaced, mid-successional pines. This site more resembles areas in the Flathead National Forest where cinnabar moths appear to have successfully controlled tansy ragwort.

We monitored plants annually from 2005 to 2006 in four macroplots at each site. In the mesic site, we used four 30-40m x 30-40 m macroplots; macroplots varied in size based on existing barbed wire fence to exclude cattle (Trainor 2003). In the xeric site we randomly selected 4 locations, based on random selection from 5 potential dead-end logging roads (with replacement), and a random distance based on the length of the chosen road. Next, we randomly selected a side of the road (north or south) on which to place a macroplot. We chose four similar-sized macroplots by finding the nearest populations with  $> 5$  mature plants / m<sup>2</sup> at four random locations. This area had been

closed to motor vehicle and cattle use since 1994, so fencing was not necessary. At each of the 8 macroplot locations we established 12 randomly located 1 m x 1 m plots. Ten plots had wood borders on all sides (25 cm high x 2.5 cm thick) around their perimeters resting on the ground to minimize soil disturbance. Borders were used as a base on which to secure netting over the herbivore exclusion plots (C).

We randomly assigned plots to each of the following four treatments: 1) High density herbivore (cinnabar moth larvae) addition (H), 2) Low density herbivore addition (L), 3) Control with wood borders, herbivore exclusion, no herbivore addition (C), and 4) a neutral control with no borders and no herbivore exclusion or addition (N). Three replicates of each treatment were established in each of the 4 locations at each of the 2 sites yielding a total of 24 plots for each treatment for a total of 96 m<sup>2</sup> plots).

We collected third and fourth instar cinnabar moth larvae from the Flathead National Forest (FNF) in areas where the moths have been established in large populations for a number of years. We chose a low density (150 per m<sup>2</sup>) and a higher density of larvae (250 per m<sup>2</sup>) that corresponded roughly to, but were slightly lower than, median densities that McEvoy and colleagues (1993, their Figure 9) found at study sites in Oregon. We added 250 larvae to tansy ragwort stems in each plot in the H treatment plots (6,000 total larvae), and 150 larvae to each of the L treatment plots (3,600 total larvae). Five to ten larvae were first added to flowering stem inflorescences or buds. Remaining larvae were added to the leaves of juvenile (i.e., not flowering) rosettes. Due to the sedentary nature of the larvae (Crawley 1989) and the potential for undesirable cage effects, we did not enclose larvae in the larvae treatment plots, but left plots open so as to not alter their behavior.

We enclosed the control (C) plots with tents of fabric netting (1mm<sup>2</sup> mesh) which was stapled around the plot border and supported in the plot center by a ~2 cm diameter piece of PVC pipe approximately 91 cm tall. We compared these plots to those with no mesh netting to test for shading effects of the netting at the end of the study (see Results). This height allowed for normal height growth of tansy ragwort flowering stems. Netting was added during the time of maximum hatching of cinnabar moth larvae, and removed approximately 3-4 weeks later, depending on the timing of the site.

#### *Demographic monitoring*

We monitored individual tansy ragwort plants in each 1m x 1m plots using standard demographic methods (following Williams and Crone 2006). We recorded stage (seedling, juvenile, rosette or reproductive adult) of each plant in August in 2005 and 2006. In 2005, plants were individually numbered, tagged and mapped to facilitate relocation. We recorded the number of leaves for seedlings and rosettes, and the number of flowers for adult stems.

We visually estimated damage to each plant by cinnabar moth larvae during each annual census. We estimated damage differently for flowering adult plants and juvenile rosettes. For adult stems that were damaged by cinnabar moth larvae, we estimated how much of the inflorescence had been damaged. Because larvae tend to congregate on the flowers and buds, and we were most interested in the effects of damage on fecundity of these plants, we did not measure leaf damage to adult plants. Adult plants were defined as 100% damaged if all of flowers or buds were consumed with a single, stripped stalk remaining. For partially eaten adult plants, we counted the number of undamaged and damaged buds or flowers to calculate the total proportion of damage. For rosettes,

cinnabar moths generally ate the leaf tissue leaving a bare petiole behind. If a petiole was the only part of the plant remaining, we counted this as an entirely consumed leaf. We estimated partially eaten leaves to the nearest 0.25 of total leaf area consumed based on the size of the remaining portion of the leaf. The total damage to a rosette was calculated as the sum of the proportion of each leaf eaten divided by the total (original) number of leaves.

#### *Matrix model analysis*

We constructed a 4x4 annual stage-structured transition matrix using estimates of survival, growth and fecundity for seeds, seedlings (first-year germinants), rosettes (vegetative plants), and adults (flowering plants) (Figure 1 and Table 2). Vital rates were calculated from our experiments and ancillary data as follows:

#### *Seed bank (Sb)*

Trainor (2003) conducted a seedbank longevity study for tansy ragwort in the same general study area. Trainor estimated mean seed survival in the soil over three years for a variety of sites in the Flathead and Kootenai National Forests. We used the estimated mean annual survival rate of seeds in the soil from Trainor's study (2003) as a constant for the seed bank (Sb) variable in all matrix simulations in this study.

#### *Seed production (Fs)*

Seed production was calculated from the number of capitula for each flowering plant, counted in each annual census. We calculated the average number of seeds produced by taking a random sample of 10 capitula per site in 2005 (n=80 total). Seed number did not differ between sites so we multiplied the mean seed number per capitula

by the total number of capitula produced per adult plant to estimate the total seed production per plant.

### *Germination (G)*

Seedling emergence in experimental plots includes two components: (1) germination from the existing seed bank (of unknown size), and (2) germination from new seeds produced the previous year (hereafter, new recruitment, or new recruits). New recruitment more specifically represents the proportion of each new seed crop that does not enter the existing seed bank, but immediately germinates. In order to distinguish new recruitment from seed bank recruitment, we used a seed addition experiment from 2005-06. We harvested 1000 mature tansy ragwort seeds from plants adjacent to each macroplot at each site in August 2005. We haphazardly chose three 25 cm x 25 cm seed addition plots within each macroplot. These seed addition plots were complimented by three randomly placed control plots where seeds were not added. Plots were chosen to be at least 5 m apart and did not contain any flowering tansy ragwort plants. Seeds were scattered over the ground to simulate seed rain. We used generalized linear regression models (with site as a random factor and gamma distributed error) of seedlings vs. seeds; the resulting model slope is an estimate of seedlings per sown seed, i.e., seed germination.

### *Survival: Seedlings (Ss), Rosettes (Sr), and Adults (Sa)*

We analyzed survival of each above-ground life stage as a binomial process. Survival is defined as the probability a plant in year  $t$  is alive in year  $t+1$ , regardless of its stage class in the next year (see Table 2).

### *Transitions to flowering (Tra, and Taa)*

For rosettes and adult plants, we analyzed transitions to flowering, conditioned on survival. In other words, we analyzed whether plants that did not die during a time interval ( $t_0$  to  $t+1$ ) were flowering in year  $t+1$ . We analyzed this conditional probability as a binomial process, then calculated transition rates between rosette and flowering stage classes as the product of the appropriate binomial probabilities (Table 2).

We analyzed plant damage and all demographic variables using generalized linear mixed models (lmer procedure in R; R Foundation for Statistical Computing 2005). Because each macroplot contained three plots of each treatment, we had to account for variance or error created between the plots within macroplots in order to illuminate true treatment effects between sites. The resulting model included macroplot and plot within macroplot as random effects, and treatment and site as fixed effects. We analyzed herbivore effects by comparing H, L, and C treatments, and assessed cage effects by comparing C and N plots in one set of analyses. In each analysis, we tested statistical significance of factors using likelihood ratio tests of models with the appropriate factor, relative to reduced models without that factor (analogous to Type III hypothesis tests in ANOVA). We estimated those vital rates that were significantly different between treatments, sites, or the interaction of both treatment and site in matrix models. We tested binomial and Poisson-distributed variables for overdispersion. Capitula production per plant was overdispersed with a high mean, so we approximated this variable with a log-normal distribution. No other variables were overdispersed (scale parameter  $< 1.5$  for all other variables).

### *Perturbation analyses*

We conducted sensitivity and elasticity analyses to compare the results of our experiments with prospective analyses that might be used to estimate herbivore impacts. We calculated elasticity values for each separate matrix in the C treatment (using mean values for vital rates) to determine the whether the sensitivity of  $\lambda$  differed in which transitions are most important for population growth. Calculations were made in MATLAB® (The MathWorks 2007) using code modified from Morris and Doak (2004).

## **RESULTS**

Cinnabar moths consumed both foliage on rosettes and foliage and capitula on flowering plants. In the H treatments 29% of individuals were damaged at the mesic site; whereas 66% of plants were damaged at the xeric site (Figure 2a). Damage was slightly lower in the L treatment at both sites (20% mesic and 54% xeric; Figure 2a). A very small proportion of the total plants in these plots were damaged in control plots (0.6%; Figure 2a). The proportion of total plants damaged in neutral controls (N) was also very low (1.1%) and did not differ statistically from C treatments ( $\chi^2 = 0.72$ ,  $df = 1$ ,  $P > 0.99$ ), demonstrating that wooden borders did not affect plant damage. Amount of damage per plant was largest in the H treatment overall (estimated proportion of plant consumed 96.4% mesic; 58.7% xeric, Table 3, Figure 2b), and slightly lower in L treatments overall (77.8% mesic, 60.8% xeric; Table 3, Figure 2b).

We tested differences in vital rates using mixed models (Figure 3). The number of capitula per plant was highest in C plots and lowest in H at both sites (Table 3, Figure 3). Herbivore addition did not significantly affect rosette or adult survival (Table 3), although adult survival tended to be higher in herbivore addition treatments ( $P = 0.07$ ,

Table 3, Figure 3). In the xeric site, seedling survival was lowest in L plots, intermediate in H plots and highest in C plots (Figure 3). Tests of vital rates in caged herbivore exclusion controls (C) versus neutral controls (N) did not indicate that any vital rates were affected by the wood plot borders during 2005-06 (Table 4).

Germination rates were low overall. Seed addition plots had a higher number of new recruits than did the control plots (Figure 4), with an average of 3.3 germinants per seed addition plot. Based on regression of seed input vs. seedling recruitment in these plots, 1.37% of seeds germinated directly as new recruits.

#### *Population projection matrices*

The herbivore addition experiment revealed two kinds of effects. First, cinnabar moths dramatically reduced seed production, and this reduction corresponded with larva density. Second, herbivore addition more weakly affected seedling and adult survival, with effects that did not vary with larva density, and were therefore more difficult to attribute to herbivory *per se*. Therefore, we analyzed two sets of matrix models: one in which herbivores affected only seed production, and one in which herbivores affected growth and survival, as well as seed production (Table 5).

In both cases, matrices predicted growing populations ( $\lambda > 1$ ) in the absence of herbivory (C), and declining populations ( $\lambda < 1$ ) in the presence of herbivory (H and L, Figure 5). Expected growth rates were slightly lower (~ 3-4%) in H than L treatments, but this effect was negligible relative to differences between treatments and controls. Adding treatment effects on survival did not change these conclusions except that it removed the difference between H and L  $\lambda$ 's at the xeric site. Across all treatments, population growth rates were higher in the xeric than in the mesic site in this year,

although these differences were most pronounced in the absence of herbivory, where  $\lambda$  averaged about 20% higher in xeric compared to mesic habitats (Figure 5).

#### *Perturbation analyses*

Sensitivity analysis suggested that  $\lambda$  would be most affected by changes to seedling recruitment from the seedbank ( $G$ ) and the transition rate from rosette to adult plants ( $Tra$ ), a stage that is conditional on rosette survival ( $Sr$ ) (Figure 5). Converting these values to proportional changes (i.e., elasticity) between rates still indicated that  $\lambda$  would be most affected by changes to survival of plants in the rosette stage, although seedling recruitment, a very small rate, did not have a high elasticity. More specifically, rosette stasis ( $Sr - Tra$ , Table 6) had the highest elasticity values in both xeric and mesic sites (Figure 5), while the rosette transition to adult ( $Tra$ ) had the second-highest values.

## **DISCUSSION**

Our experiments demonstrate that cinnabar moth can control tansy ragwort populations in northwest Montana. This result suggests that managers are correct in attributing declines of tansy ragwort in the Flathead National Forest to cinnabar moths, and is consistent with large observational studies that have associated cinnabar moth abundance with reductions in tansy ragwort abundance in northern California (Pemberton and Turner 1990, Hawkes 1973, Hawkes and Johnson 1978). Our results contrast with McEvoy's research in Oregon (e.g., McEvoy et al. 1993), which concluded that cinnabar moths could not control tansy ragwort. In Oregon, cinnabar moths occurred at similar densities to those in the Flathead National Forest and our experimental treatments (150-250 larvae/m<sup>2</sup> in our study; median of about 200-300/m<sup>2</sup> in McEvoy et al. 1993, their Fig. 9). However, plants were somewhat less damaged in Oregon (82% reduction in capitula)

than Montana (99% reduction in capitula). We tested whether this difference was sufficient to explain the discrepancy between our conclusions by recalculating  $\lambda$  using vital rates from our control plots, with an 82% reduction in seed production. With this reduction, populations would remain invasive in Montana, growing at 12% year ( $\lambda=1.12$ ; reduction of 0.40) in mesic habitats and 23% ( $\lambda=1.23$ ; reduction of 0.51) in xeric habitats.

Our experimental approach was strong in its ability to mimic realistic field densities of herbivores vs. studies where clipping of plants is used in lieu of herbivores. However, treatment and response was measured over a short time interval (one year). Therefore, we could not incorporate environmental or demographic stochasticity that might change vital rates and the overall predictions of our model. We assess this limitation by drawing on a five-year demographic study of tansy ragwort across three habitat types in the Kootenai National Forest where cinnabar moths have not successfully established (Trainor 2003, Bauer 2006). Bauer estimated mean vital rates separately for each year (2001-2005) in logged and unlogged areas similar to our xeric sites (Bauer 2006; his Appendix D). To explore the ability of cinnabar moths to control tansy ragwort more generally in northwest Montana, we calculated population growth rates for each of these matrices, with hypothetical reductions of 80, 85, 90 and 95% of seed production. Without herbivory, Bauer's  $\lambda$  values were larger than 1.00 in 5 of the 10 matrices and averaged above 1.00 in each of the two habitats over the 5 years of study. Population growth rates consistently declined to below 1.00 for > 90% seed predation; whereas predation of 80-85% of seeds did not reduce population growth rates below 1.00 (for populations with rates that were above 1.00 initially). Therefore, cinnabar moths would be effective in this area only if moths continue to consume > 90% of seeds.

Our results indicate that cinnabar moths have the potential to control tansy ragwort, because they dramatically reduce a relatively less important vital rate. However, this conclusion comes with two significant caveats. First, cinnabar moths have the potential to switch from tansy ragwort to native *Senecio* species in the study area (Diehl and McEvoy 1989). Host-switching has not been observed in our study area, but native species of *Senecio* include *S. triangularis*, tall groundsel (*S. hydrophiloides* Rydb.), rocky ragwort (*S. megacephalus* Nutt.), and tall ragwort (*S. Serra* Hook.). Therefore, if cinnabar moths continue to be used as control agents, we strongly recommend monitoring its possible impacts on native species.

Second, establishment of cinnabar moths has been problematic in some parts of northwest Montana. In the Flathead National Forest, moths are established and tansy ragwort persists at very low densities. However, moths were distributed to the adjacent Kootenai National Forest in 1999 (our specific study region; Table 1), but have not established or substantially reduced tansy ragwort abundance. One possible explanation for this difference is biotic interference by carpenter ants that are associated with logging disturbances which provide suitable nesting substrate (Chen et al. 2002). Carpenter ants are not present or present in very low numbers on the Flathead National Forest (See Chapter 3, this dissertation), but they were prolific in the salvage-logged xeric sites, and present, although much less common in the mesic sites on the Kootenai National Forest (Chapter 3, this dissertation). In our study area in the Kootenai National Forest, carpenter ant predation was observed frequently during moth larvae releases and feeding periods (Chapter 3 of this dissertation).

We observed large differences between vital rates of tansy ragwort in xeric and mesic sites. Although overall tansy ragwort abundance was highest in the mesic sites (Table 1), the xeric sites had higher values of  $\lambda$ . Higher population growth rates were due to large differences in seedling survival; the rate in the xeric area was nearly twice as high as it was in the mesic area (Figure 5). The reasons for this are not clear, as we would have expected dry soil conditions and clumped vegetation (although high cover) at the xeric sites (Table 1) to compromise seedling survival. However, total plant cover was generally high (>90%) at both sites, potentially indicating that species identity and composition is more important than density. Mesic sites were mainly comprised of sod-forming (impenetrable) forage grasses that may have compromised seedling survival to a larger degree relative to the predominance of bunch grasses and a seasonal, nitrogen-fixing hop clover (*Trifolium sp.*) at the xeric sites may prove less competitive, and potentially facilitative (Carino and Daehler 2002) in conjunction with tansy ragwort (Table 1). Given higher population growth rates and lower abundance in the xeric sites, we speculate that, although density-independent  $\lambda$ 's predict the potential for populations to grow or decline, other factors determine equilibrium abundance. We tested for intraspecific density dependence by regressing vital rates against plot density and did not find any significant relationships (K. Crider unpubl.). In his more extensive demographic data set, Bauer (2006) observed slightly positive relationships between plant density and tansy ragwort vital rates, the opposite of traditional density dependence. Bauer (2006) reported negative relationships between tansy ragwort vital rates and total plant cover, suggesting plant density ultimately reflects community-level relationships. These analyses are beyond the scope of our study, so the asymptotic  $\lambda$  of growing populations

should be interpreted with caution, as other factors may also act to limit population size. However, we believe that density independent matrix models are still robust predictors of the potential for populations to grow (in the absence of herbivory) vs. strongly decline (in the presence of herbivory).

In some places, tansy ragwort is able to compensate for herbivory by the cinnabar moth by producing new inflorescences (Bornemissza 1966; Harris et al. 1978; Cox and McEvoy 1983; Islam and Crawley 1983; Crawley and Nachapong 1985). However, in tansy ragwort, compensation is thought to be resource-limited, and is thought to be much lower in areas with summer moisture stress (Cox and McEvoy 1983). Compensatory growth can also be phenologically constrained in cooler, drier climates. Harris and colleagues (1978) found that recovery of carbohydrate reserves and successful regrowth of rosettes in eastern Canada was strictly limited by the timing of the first frost because the time of recovery necessary exceeded the date of the first frost. We did not observe regrowth during this study. However, in 2006, we monitored regrowth while monitoring the effects of carpenter ants on cinnabar moth larvae (Chapter 3 of this dissertation). Approximately 20% of plants regrew flowers, but the number of regrowth flowers was only ~30% of the original number of flowers, comparable to ~21% found by Cox and McEvoy in moisture-stressed valley populations of tansy ragwort (1983) in eastern Oregon. To test whether seeds from regrowth flowers had sufficient time to develop prior to frost, we germinated regrowth and normal seeds in the greenhouse. Thirteen percent of seeds from normal capitula germinated, but only 4% of seeds from regrowth capitula germinated under greenhouse conditions. These data are not directly comparable to our demography experiments, because larvae were added at different densities, and were

exposed to ant predation which reduced plant damage in some cases. However, the data do largely confirm that plants are not able to compensate for herbivory in this environment ( $20\% \times 30\% = 6\%$  of seeds  $\times$   $1/3$  of normal germination =  $\sim 2\%$  of predated seeds). The inability to compensate seems to reflect both resource costs of initial seed production (plants regrew many fewer flowers), and phenological limits to seed development due to the timing of the first winter frost (these seeds had much lower germination).

Finally, fitness consequences of herbivory can manifest themselves below ground and have lasting effects on resource allocation, potentially changing vital rates (namely rosette survival and adult to rosette reversion), over the long-term (e.g., Ehrlén and van Groenendael 2001, Bañuelos and Obeso 2004). In tansy ragwort, a large number of rosettes showed the propensity to remain rosettes (rather than transitioning to adults), and some adult plants reverted back to a vegetative state after flowering. In our experiment, we added larvae to plants in 2005, and saw very few moths or larvae at our site in 2006. During the 2005-2006 demographic year, plant growth and survival was not affected by herbivory. However, seed set of plants in treated plots remained lower in 2006, even though larvae were no longer present. At the same time, flowering plants exposed to herbivory in 2005 were slightly more likely to survive (Chapter 4, this dissertation). Both effects suggest that tansy ragwort is able to store and reallocate resources in response to plant damage. I explore these responses and their implications for population dynamics further in Chapter 4 of this dissertation.

Attempts to establish guidelines for biocontrol agent selection are often criticized for gross oversimplification (Cullen 1995, Sheppard 2003) and have not resulted in any

reliable strategic framework. As a result, current literature rarely provides *a priori* rationalization for agent release. Our methodology follows recent emphasis on a conceptual and quantitative modeling approach that integrates both the target species and the biological control agent(s) rather than basing criteria largely on attributes of the agent alone (Kriticos 2003). By virtue of experimentation our study serves as a detailed assessment of cinnabar moth efficacy (i.e., a 'post-release' assessment). The detail of these experiments allowed us to define the window of efficacy necessary to reduce the population growth of tansy ragwort both generally and comparatively between sites. Our results indicate that the population-dynamic impacts of plant-consumer interactions can vary dramatically in space. At the present time, we are left with the important but unsatisfying conclusion that interactions are context-dependent and releases should be monitored carefully. With more research, one would ideally predict both moth and plant population dynamics as a function of environmental and biotic variables. We strongly encourage the continued use of demographic models parameterized by the best available data in order to allow for more informed agent selection that will reduce the potential economic and ecological costs associated with biocontrol agents.

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Table 1. Habitat characteristics for xeric and mesic habitats in the Kootenai National Forest.

Site	Disturbance History	Dominant vegetation	Percent Cover Mean(m <sup>2</sup> ) 2005-2007	Proportion of moisture in soil	Number of plants sampled (2005-2006)
Little Wolf (xeric site)	11 years previous (wildfire/salvage logged)	hop clover  perennial grasses	90.79	0.07	1905
Island Lake (mesic site)	>11 years previous (unknown)	sod forming grasses	94.7	0.16	3887

Table 2. Vital rates for tansy ragwort and the projection matrix structure showing calculations for each matrix element from vital rates.

Vital Rate	Symbol
Seedling survival	Ss
Rosette survival	Sr
Rosette to adult   survival	Tra
Adult survival	Sa
Adult to adult   survival	Taa
Seeds per adult	Fs
Seedlings per seed	G
Seedbank survival (Bauer 2006)	Sb

Matrix structure	Seed bank	Seedling	Rosette	Adult
Seed bank	$Sb * Sb$	0	0	$Fs * Sb$
Seedling	G	0	0	$Fs * G$
Rosette	0	Ss	$Sr * 1 - Tra$	$Sa * 1 - Taa$
Adult	0	0	$Sr * Tra$	$Sa * Taa$

Table 3. Likelihood ratio comparisons for each vital rate and damage variables. \*\*=  
 $P \leq 0.01$ , \*  $P \leq 0.05$ , † =  $P \leq 0.10$  §= variables estimated for use in matrix models containing  
seed consumption and survival effects.

	Factor	$\chi^2$	df	P	
<b>Tests of plant damage</b>					
Proportion of plants damaged					
	Site	2.5582	1	0.1097	
	Treatment	35.439	2	0.0000	**
Proportion of buds or leaf area consumed C, N Treatments					
	Site	0.726	1	1.00	
	Treatment	10.379	2	0.000	**
<b>Tests of demographic rates</b>					
Flowering					
	Site	0	1	1	
	Treatment	66.329	2	0.0000	**
	Treatment * Site	1.8144	2	0.4037	
Rosette survival					
	Site	0.1904	1	0.6625	
	Treatment	0.7658	2	0.6819	
	Treatment*Site	0.1991	2	0.9052	
Adult survival					
	Site	1.5388	1	0.2148	
	Treatment	5.3520	2	0.06884	†§
	Treatment*Site	0.5765	1	0.7496	
Seedling survival					
	Site	9.1558	1	0.002479	**
	Treatment	7.4059	2	0.02465	*§
	Treatment*Site	0.8007	2	0.6701	
Rosette to adult transitions  survival					
	Site	0.5239	1	0.4692	
	Treatment	4.8966	2	0.08644	†§
	Treatment*Site	0.2152	2	0.898	

Table 4. Likelihood ratio comparisons between neutral controls (N) and controls (C) with wood plot borders to test for effects of barriers on vital rates (i.e., cage effects).

Vital rate	Factor	$\chi^2$	df	P
Flowering				
(Fs)	Site	0.8972	1	0.3435
	Treatment	2.5266	2	0.1119
	Treatment*Site	0	2	1.0000
Rosette Survival				
(Sr)	Site	0.6258	1	0.4289
	Treatment	0.4957	2	0.4814
	Treatment*Site	0.1741	2	0.6765
Adult Survival				
(Sa)	Site	1.9656	1	0.1609
	Treatment	0.8196	2	0.3653
	Treatment*Site	0.8915	2	0.3451
Seedling Survival				
(Ss)	Site	2.0281	1	0.1544
	Treatment	0.0176	2	0.8946
	Treatment*Site	2.606	2	0.1065
RA transitions   survival				
(Tra)	Site	3.0368	1	0.0814
	Treatment	1.0221	2	0.312
	Treatment*Site	1.8365	2	0.1754

Table 5. Vital rates for xeric and mesic habitats used to calculate matrix elements for each treatment/habitat combination for effects of only herbivores and effects of both herbivores and survival. Values were calculated from generalized linear mixed models (see Table 3).

Vital rate	Symbol	Seed consumption only		Seed consumption + survival effects	
		Mesic	Xeric	Mesic	Xeric
Seedling survival (C)	Ss	0.97	0.50	0.58	0.96
Seedling survival (L)		0.97	0.50	0.18	0.79
Seedling survival (H)	0.97	0.50	0.89	0.99	
Rosette survival	Sr	0.96	0.96	0.96	0.96
Rosette to adult   survival (C)	Tra	0.11	0.11	0.14	0.14
Rosette to adult   survival (L)		0.11	0.11	0.09	0.09
Rosette to adult   survival (H)		0.11	0.11	0.09	0.09
Adult survival (C)	Sa	0.53	0.53	0.41	0.41
Adult survival (L)		0.53	0.53	0.61	0.61
Adult survival (H)		0.53	0.53	0.58	0.58
Germination	G	0.01	0.01	0.01	0.01
Flowers per adult (C)	F	23.13	23.13	23.13	23.13
Flowers per adult (L)	F	0.27	0.27	0.27	0.27
Flowers per adult (H)	F	0.07	0.07	0.07	0.07
Seeds per adult(C)	Fs	1156.63	1156.63	1156.63	1156.63
Seeds per adult(L)	Fs	13.85	13.85	13.85	13.85
Seeds per adult (H)	Fs	3.31	3.31	3.31	3.31

Table 6. Prospective analysis, using elasticity and sensitivity values for vital rates from control plots in mesic (A) and xeric (B) sites.

Vital rate	Sensitivity	Elasticity
A. mesic sites		
Ss, seedling survival	0.53	0.18
Sr, rosette survival	0.73	0.49
Tra, transition from rosette to adult (conditioned on survival)	2.09	0.16
Sa, adult survival	0.04	0.01
G, seed germination	26.29	0.18
Fs, Flowers per adult plant	0.0002	0.18
Sb, seed bank survival	0.34	0.17
Taa, transition from adult to adult (conditioned on survival)	0.09	0.00
B. xeric sites		
Ss, seedling survival	0.35	0.21
Sr, rosette survival	0.77	0.46
Tra, transition from rosette to adult (conditioned on survival)	2.77	0.19
Sa, adult survival	0.03	0.01
G, seed germination	33.70	0.21
Fs, Flowers per adult plant	0.0003	0.21
Sb, seed bank survival	0.36	0.16
Taa, transition from adult to adult (conditioned on survival)	0.10	0.00

Table 7. Values of  $\lambda$  for matrices by Bauer (2006) where fecundity values were reduced by amounts proportional to those observed in the current study (99%), and hypothetical values from 85%.

Year	Habitat	Original $\lambda$ estimates (Bauer 2006)	Seed prod. per plant (Bauer 2006)	Resulting $\lambda$ with X% reduction in seed production				
				80%	85%	90%	95%	99%
2001	Burned, logged	1.65	1202	1.15	1.1	1.02	0.92	0.77
2002		1.11	973	0.79	0.75	0.71	0.64	0.56
2003		0.87	1271	0.67	0.65	0.62	0.58	0.54
2004		0.82	1410	0.66	0.64	0.61	0.58	0.54
2005		0.61	658	0.55	0.55	0.54	0.53	0.52
2001	Burned, unlogged	1.65	1005	1.15	1.09	1.02	0.91	0.76
2002		0.98	1134	0.72	0.69	0.66	0.61	0.54
2003		1.11	3009	0.8	0.77	0.72	0.66	0.57
2004		1.71	2537	1.15	1.09	1	0.88	0.69
2005		0.72	934	0.6	0.57	0.57	0.55	0.52

## FIGURE LEGEND

Figure 1. Life cycle diagram for tansy ragwort that corresponds to the transition matrix model. Arrows indicate all possible transitions in the model.  $F_s$  = fecundity,  $S_a$ =Adult survival (includes  $T_{aa}$  and  $1-T_{aa}$ ),  $S_r$ = rosette survival,  $T_{ra}$ = rosette to adult transitions (conditioned on  $S_r$ ),  $T_{aa}$ =adult stasis (conditioned on  $S_a$ ),  $1-T_{aa}$ = adult reversion to rosette (conditioned on  $S_a$ ).

Figure 2. (a) Estimated proportion of total plants per treatment that were damaged by cinnabar moth larvae estimated by likelihood ratio comparisons. C= control, L= Low density larvae treatment, H=high density larvae treatment. (b) Average larval damage per plant by treatment and site for larvae additions treatments only (H, L) estimated by likelihood ratio comparisons. Error bars indicate  $\pm 1$  SE.

Figure 3. Estimates of mean vital rates for each site and experimental treatment combination from maximum likelihood ratios. C= control, L= Low density larvae treatment, H=high density larvae treatment,. Error bars indicate the confidence interval of differences from means and model estimated standard errors ( $\pm 1$  se).

Figure 4. Seedlings in July 2006 after seed additions in 2005. Seedling recruitment (“new recruitment” in Methods) per seeds is estimated from a regression slope: # seedlings =  $3.1 + 0.0137[\# \text{ seeds}]$  (generalized linear mixed model, with gamma-distributed error). The intercept in this model reflects germination from seed rain, plus the seed bank.

Figure 5. Population growth rates from matrix projection models in each habitat for (a) matrices with effects on seed consumption (b) matrices with effects on seed production and survival.  $\lambda$  estimated from 500 random matrices drawn from vital rates (uniform distribution). C= control, L= Low density larvae treatment, H=high density larvae treatment. Error bars represent +/- range as calculated per treatment.

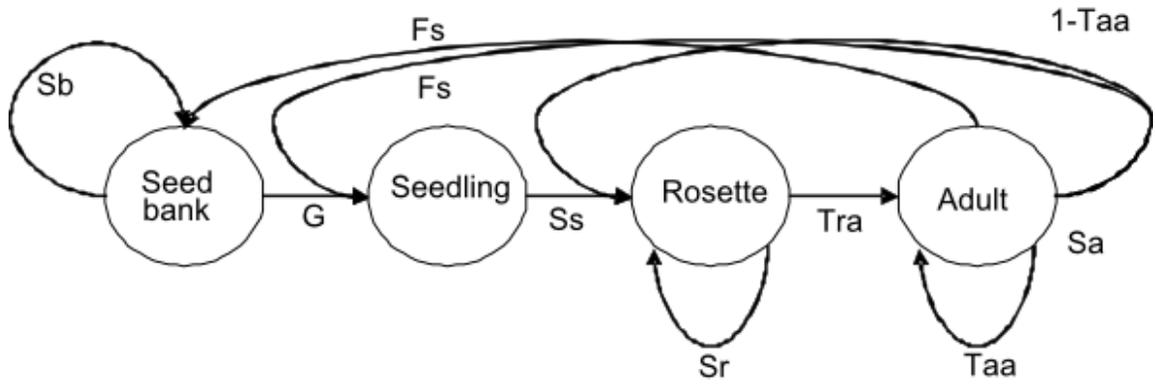


Figure 1

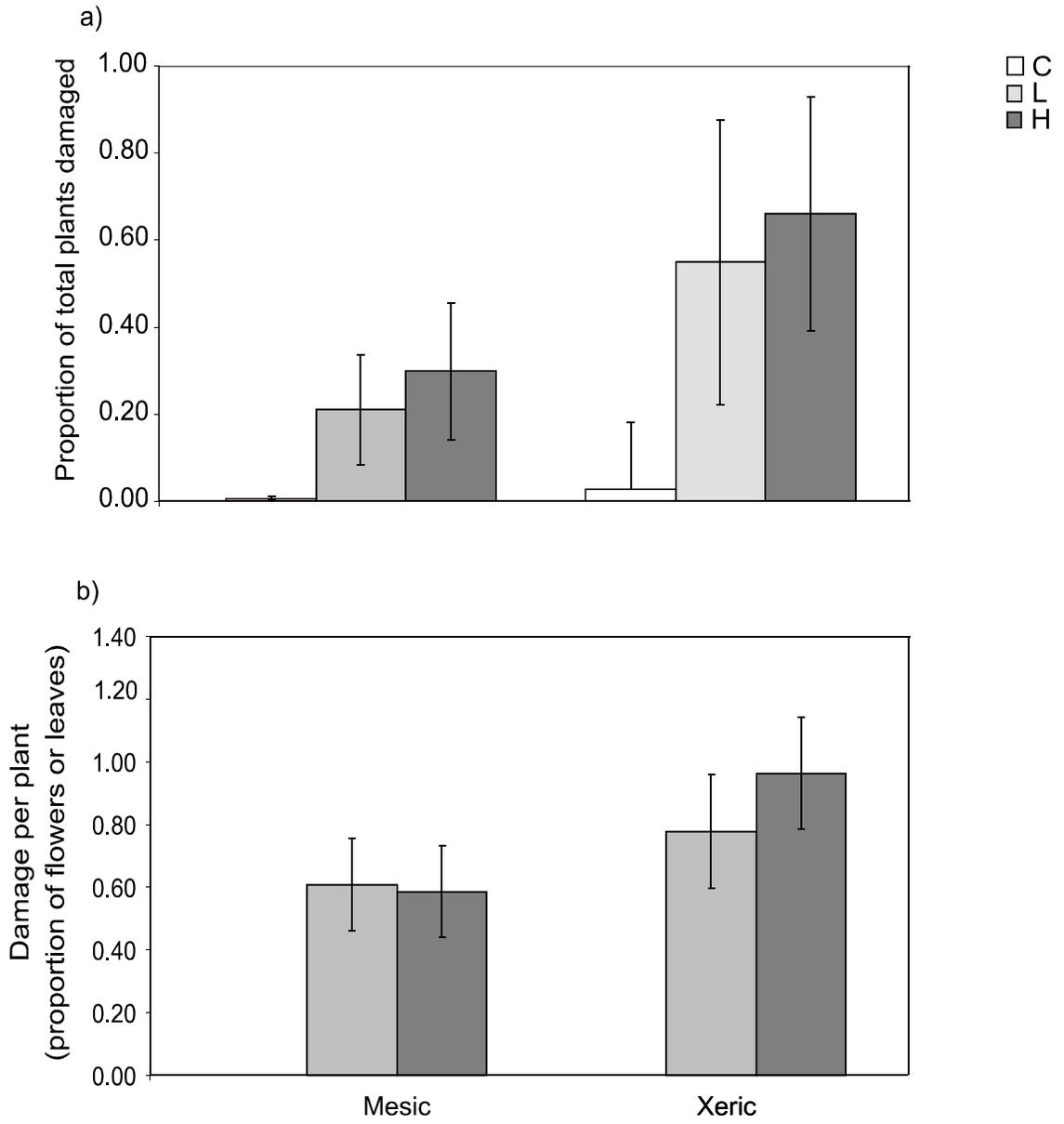


Figure 2

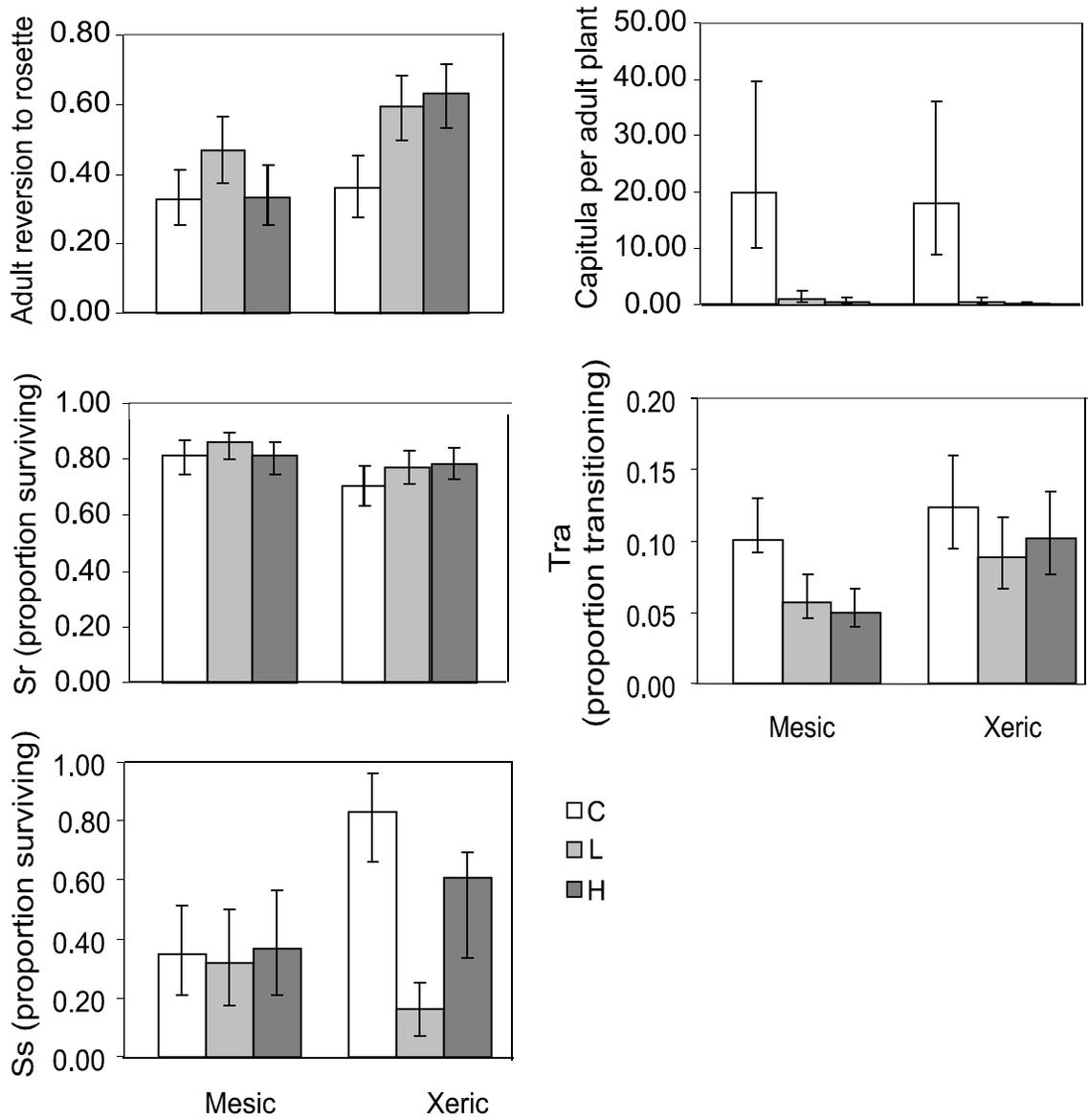


Figure 3

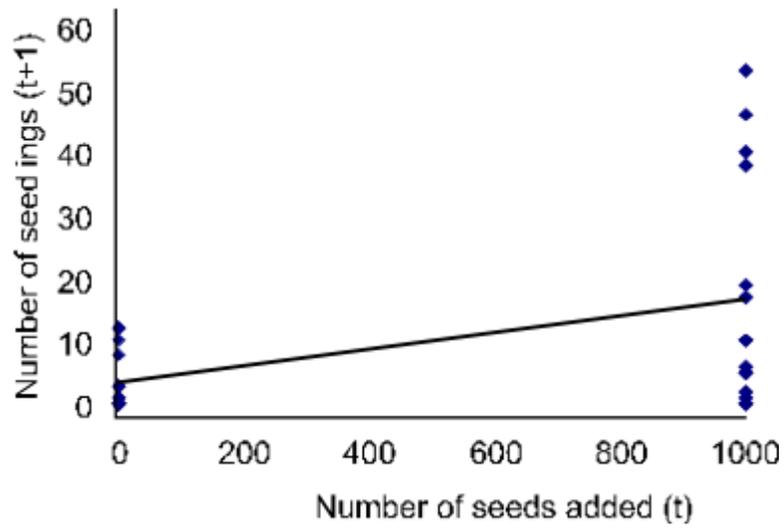


Figure 4

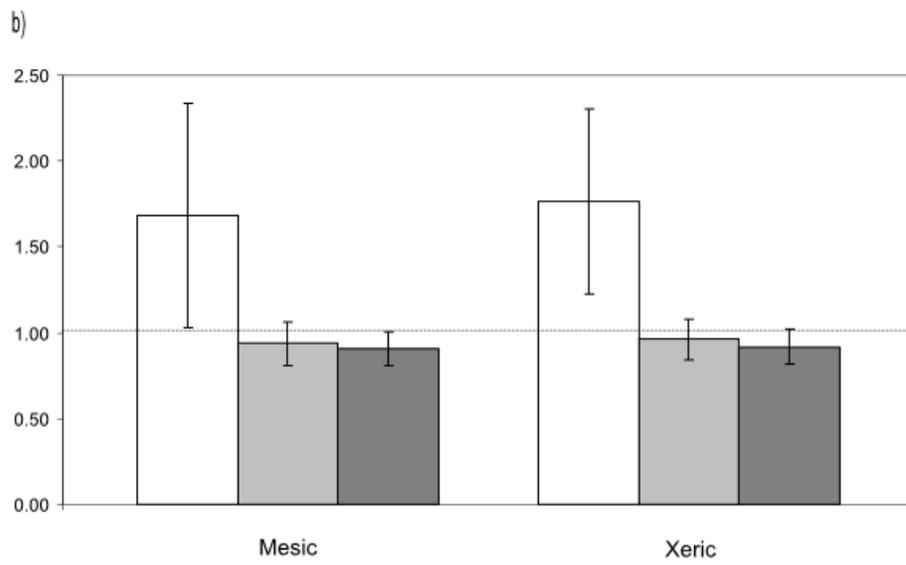
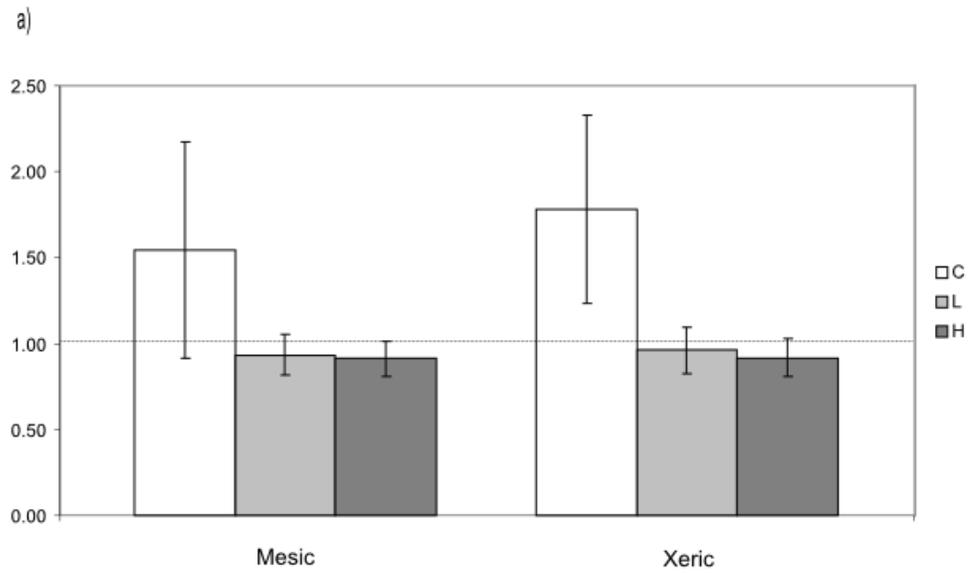


Figure 5

## CHAPTER 3

DIRECT AND INDIRECT EFFECTS OF A NATIVE PREDATOR, *CAMPONOTUS SP.*, ON A BIOLOGICAL CONTROL AGENT, *TYRIA JACOBAEA* (L.), AND ITS HOST PLANT, *SENECIO JACOBAEA*

## **ABSTRACT**

Native predators pose a substantial yet often overlooked, risk to biocontrol establishment and success. Quantifying these effects, in addition to understanding predator distribution and abundance, is important for the design of effective biological control releases. We studied predation by native *Camponotus* sp. (carpenter ants) on *Tyria jacobaea* (cinnabar moth) larvae on the invasive weed, *Senecio jacobaea* (tansy ragwort). Ant exclusion experiments revealed that more *T. jacobaea* larvae were taken from plants accessible to ants than from those where ants were excluded. In addition, more larvae were taken in dry, burned, and logged areas overall, than in the moist, less recently disturbed areas. An additional experiment in the dry, disturbed area demonstrated that the relative percent of buds or flowers consumed by *T. jacobaea* larvae was significantly higher on plants where larvae were protected from *Camponotus* sp. compared to those that were accessible to *Camponotus* sp. Ant predation reduced seed set and subsequent efficacy of cinnabar moth as a control agent. The results of this study emphasize the importance of identifying not only potential predators to biological control agents and quantifying their effects on the agent and the invasive plant, but also the environmental contexts in which they may pose the largest risk to the establishment and subsequent efficacy of a particular biological control agent.

## **INTRODUCTION**

Invasive plant management using insect biological control agents assumes that herbivores will be controlled solely by bottom-up forces, the factors that ultimately affect the abundance and distribution of their host plants. However, predation and parasitism by native generalists is suspected to play a role in about half of all weed biological control failures (Julien & Griffiths 1998). Direct biological interference with biological control

agents in the form of predation and parasitism has been reported anecdotally, but is rarely quantified (Goeden and Louda 1976; Julien and Griffiths 1998). Many cases of interference involve insect biological control used to control agricultural insect pests (Rosenheim et al. 1993, Rosenheim et al. 1999, Snyder and Ives 2001), while the frequency and severity of interference with biological control agents introduced to control invasive plants has received much less attention. Studies to date have primarily evaluated the presence and impact of predation on the biological control agents themselves (e.g., Nechols 1996, Wiebe and Obrycki 2004, Ding and Blossey 2005), but fewer have assessed the effects of such interference in terms of efficacy of the agents (but see, Bacher and Schwab 2000, Denoth and Myers 2005, Hunt-Joshi et al. 2005).

The variable establishment of biological control agents is often associated with abiotic conditions (e.g., Byrne et al. 2002, van Hezewijk et al. 2008). Disturbance generally increases invasive plant success (Elton 1958, Drake et al. 1989) so that one might expect that disturbed areas are more likely to be targeted for biocontrol agent releases. In the same way, generalist arthropod species have been shown to increase in abundance relative to specialists in response to forest disturbances (e.g., Magura 2008, Saint-Germain et al. 2005) and they are more likely (than specialists, e.g.) to switch prey as the proportion of that prey increases (Murdoch 1969). In this regard, native species interactions with biological control agents can be anticipated in disturbed areas.

In this chapter, I describe a series of observations and experiments designed to determine the impacts of a native, generalist predator, carpenter ants (*Camponotus* spp.), on the biological control of an invasive plant, tansy ragwort (*Senecio jacobaea*), by an introduced herbivore, the cinnabar moth (*Tyria jacobaea*). This study was motivated by

incidental observations of predation of cinnabar moth larvae by carpenter ants in the field (K. Crider, personal observation). This study serves to determine the potential influence of carpenter ants on cinnabar moth larvae and ultimately on tansy ragwort fecundity. The experiments were designed to answer three questions: (1) how do soil moisture and site structural attributes affect carpenter ant nest density? (2) does ant exclusion affect the predation of cinnabar moth larvae ? (3) do carpenter ants influence the efficacy of cinnabar moths on their host plants?

Tansy ragwort is a noxious invasive species producing pyrrolizidine hepatotoxins which are sequestered in its tissues. These compounds pose severe toxicity risks to livestock and wildlife (Mattocks 1986). Ragwort is capable of displacing native forage and infesting large areas of nonirrigated pasture, range, and forest land (McEvoy et al. 1993). The two prominent herbivores released in North America to control tansy ragwort are cinnabar moth (*Tyria jacobaea*), a folivore and seed predator, and ragwort flea beetle (*Longitarsus jacobaea*), a root-borer and folivore. The combined action of the flea beetle and cinnabar moth has led to a reasonable degree of control with continued persistence of the moth, the beetle, and tansy ragwort at desirable, low densities in pastures in Oregon regardless of precipitation, elevation, and landuse history (McEvoy et al. 1991). However, other studies suggest that summer moisture stress can significantly reduce the strength of the interaction between the agents and the host plant (Hawkes and Johnson 1978, Cox and McEvoy 1983). Abiotic conditions that support increases in ant predation could undermine the efficacy of cinnabar moths as biocontrol agents.

## **METHODS**

### *Study system*

Tansy ragwort's native range extends from Norway, south through Asia Minor, and from Great Britain East to Siberia. It was first recorded in North America in 1913 from Vancouver Island (Harris et al. 1971). It is a biennial or short-lived perennial herb that grows as a basal rosette during the first growing season and reproduces via dimorphic achenes borne on inflorescences of a bolting shoot produced during the second growing season. A specialist flower and seed predator, the cinnabar moth was first introduced to North America in California in 1959, and subsequently into Montana in 1997.

The cinnabar moth is a univoltine, host-specific moth in the family Lepidoptera. Pupae overwinter and adults emerge in late spring as adults when juvenile plants begin to grow and flower. Female moths lay eggs on the underside of the leaves of the basal rosettes, or on the underside of leaves on the bolting stems in mid-summer. The first (of five) larval instars feed on the leaves on which they hatched from their eggs. (Dempster 1971). As the larvae grow and exhaust their immediate food resources, they make their way up the bolting stalk to feed, usually in synchrony with the host plant's developing inflorescences. Larvae can remain on the same plant during their entire development, or if food resources are depleted they can move to an adjacent rosette or bolting stem. Larvae can develop to full maturity by ingesting leaf or stem tissue, but most commonly consume flowers or flower buds. Development from egg to adult takes approximately four weeks and larvae are capable of stripping the flowering stalk to a bare stem during

this time. Upon maturation, the larvae pupate on or just below the soil surface where they overwinter (Dempster 1971).

Carpenter ants (*Camponotus* spp.) are widely distributed throughout North America. These ants are among the largest and most abundant of the ants (Wheeler 1910). Carpenter ants are omnivorous with a high diversity of documented food items, including a variety of herbivorous arthropods and aphid nectar exudates. The ants nest in colonies founded in woody material such as tree stumps as well as in dead portions of living trees. Nesting sites are chosen based on availability of nesting substrate, temperature, humidity, and competition pressure from other ant colonies or species (Chen et al. 2002).

#### *Experimental design*

The Kootenai National Forest is located approximately 50 km west of Kalispell, Montana. I chose two study areas within the forest with differing site conditions: the Little Wolf site consisted of a large southwest-facing slope. This site was burned in 1994 by the Little Wolf wildfire, and many areas were salvage-logged after the fire creating more extensive soil disturbance than in areas that were burned in the same wildfire but were not salvage logged (i.e., dead trees were left standing). Vegetation at the Little Wolf area was characterized by a groundcover of forbs and bunchgrasses under a canopy of ~10 year-old lodgepole pines (*Pinus contorta*). The Island Lake site was located adjacent to the site but did not burn in 1994. It consisted of moister forest characterized by open, grassy understory in most areas with late successional pine on east- and northeast-facing gentle slopes.

This study was conducted within the framework of a previously established plant demographic study taking place in the Island Lake and Little Wolf area. We used four previously established macroplots in the Island Lake and Little Wolf site. In the Island Lake site, the macroplots were 30-40 m x 30-40 m and surrounded by barbed wire fencing to exclude grazing cattle. In the xeric site, the four macroplots were similar in size but not fenced because the site is closed to cattle grazing.

I also collected data from a third site in Flathead National Forest (Flathead National Forest) to compare densities of tansy ragwort, cinnabar moth, and carpenter ants. This site also burned in the Little Wolf Wildfire and is located on the opposite side of the ridge from the Little Wolf site. Flathead National Forest was not logged following the wildfire, and as a result has a high abundance of standing, dead timber. Cinnabar moths were released in this site earlier (1997) than in the other study sites (2001) and are thought to be responsible for the drastic reduction of tansy ragwort that has been observed in this site (G. Markin, personal communication). As a result, it is valuable to determine similarities or differences between the two sites with high densities of tansy ragwort (i.e., Island Lake, Little Wolf) and low densities of cinnabar moth, to the Flathead National Forest site that has low densities of tansy ragwort (K. Crider, unpublished data) and historically high densities of cinnabar moth.

*Observational study: Site characteristics and ant colony density*

I quantified differences in soil moisture, ant nesting substrate, and ant colony density at four locations in three sites: Little Wolf, Island Lake, and Flathead National Forest. At the approximate center of each macroplot, I chose a random direction from 360° and a random distance from 0 to 100 m to locate a starting point for a 100 m x 2 m

belt transect. The transects ran parallel to any existing slope (generally east to west). I established two transects at each location; the second transect was chosen to run parallel to the first and was located at a random distance up to 100 m and at least 10 m away from the first transect. Along the transect I searched for suitable nesting substrate and active carpenter ant colonies. Downed wood equal to or larger than 10 cm wide x 10 cm long or a stump with a diameter of at least 10 cm was considered suitable ant nesting substrate. Live trees were also searched although no active colonies were found in live trees over the course of the study. To quantify active colonies, I scanned any suitable substrate for actively foraging ants and signs of active nest construction (i.e., sawdust). Carpenter ants are known to build satellite colonies in materials surrounding primary nests (Gibson 1989). I did not account for satellite colonies but rather counted each separate colonized substrate object as a single active colony, as the overall goal was to estimate ant nest density in different habitat types. The existence of more colonies simply implied habitat that was suitable to support more individuals regardless of whether the ants were members of the same colony or of independent colonies.

Previous work has shown that Carpenter ant density is negatively related to soil moisture (Chen et al. 2002). In order to determine how ant abundance varied with soil moisture between sites, I measured soil moisture at each location within each site during July 2007 (the time of cinnabar moth larval feeding). I chose three random points at each location to sample soil by making a grid with points at each meter (approx. 30 x 30 m) and choosing coordinates within the grid at random. I used a cylindrical aluminum bulb digger to extract a soil core 10 cm long and 5cm diameter and placed these in brown paper bags, which were placed in plastic resealable bags that were placed in a cooler for

transport back to the lab for weighing. I weighed the soil for wet weight within 24 h of collection and subtracted the weight of the paper bag from this total weight. Samples were then placed in a drying oven at 48° C for 48 h and reweighed to determine dry weight. The ratio of dry to wet weight was used to determine the proportion of total weight of the soil sample that could be attributed to water.

Active carpenter ant colony counts were originally compared between the three sites by using a Poisson regression. However, the values were overdispersed (i.e., variance  $\neq$  expected value) and a negative binomial model was ultimately used to correct for the overdispersion (SAS GENMOD; SAS Institute, Inc. 2003). Ant colony density comparisons between site pairs were conducted using Wald tests based on a chi-squared distribution. Soil moisture values were compared using the General Linear Model option in SPSS (SPSS, Inc. 2003) with soil moisture values (moist soil weight (g) - dry soil weight (g)/dry soil weight (g)) as the dependent variable and site as the independent fixed variable. Post hoc analysis was conducted using Tukey's test for honestly significant differences of soil moisture values between each pair of sites.

I used two experiments involving ant exclusion to test for potential effects of ant presence on cinnabar moth disappearance. The first experiment, conducted in 2006, focused on comparing effects of ant exclusion on larval density at the Island Lake and Little Wolf sites. I observed greater ant predation in the Little Wolf site and focused attention on the ant-larva interaction in this site for the second experiment in 2007. The second experiment tested the direct relationship between ant exclusion, cinnabar moth survival, and tansy ragwort fecundity at Little Wolf, the dry burned site with high ant density.

*Ant exclusion experiment 1: Site specific larvae predation*

The first experiment was conducted 14 July through 17 July 2006 in the Little Wolf site, and from 20 July to 23 July 2006 in the Island Lake site. In the first experiment, I located two ant colonies at two locations within both the Little Wolf and Island Lake sites. At each ant colony, I located five pairs of flowering tansy ragwort plants spaced at least 10 cm apart at distances of 1, 3, 5, 10, and 15 m from each of the two different ant colonies within each site (2 sites x 2 locations x 2 colonies x 10 plants/colony= 80 total plants). I quantified the number of flowers or buds (not yet flowered) for each stem both before the experiment began, and 4 weeks after it was completed (15 August 2006). I removed nearby vegetation from around each of the plants, and added a small amount of Tanglefoot™ to the lower stem of one plant within each pair. To exclude ants from the plant, I placed a metal, wire, circular tomato cage around each plant to reduce loss of larvae from accidental bumping by researchers or wildlife. I added ten third or fourth instar larvae to each plant for a total of 100 larvae per colony (200 per location), one half of which were available to ants and one half of which were protected with Tanglefoot. I observed each plant pair for 15 min increments for at least 3 d to obtain at least 10 consecutive observations per plant pair per site. During each observation period, I counted the number of larvae on each plant and noted any insect activity including predation events, presence of other species, and abnormal larval behavior. I conducted one observation period after dark, using a headlamp, on one pair of plants at each site and did not observe ant activity at this time. Statistical analysis of data was conducted using a paired mixed model (SAS PROC MIXED; SAS Institute, Inc. 2003) with site and individual plant stems as random factors and ant exclusion treatment

as a fixed factor. The dependent variable was number of larvae at each observation time point.

*Ant exclusion experiment 2: Effects of ant predation on plant damage*

In the second experiment, I chose four carpenter ant colonies that were at least 20 m apart, but were present at locations that shared the same aspect, elevation and general vegetation characteristics. Twenty bolting, adult tansy ragwort plants at each of the four colonies were selected (10 stems per treatment per colony). All stems occurred within a 5 m radius of the colony. I counted buds and flowers for each stem at the onset of the experiment, and the number remaining at the end (8 days later). I made sleeves from bridal veil netting to exclude aerial predators, while favoring crawling predators. The sleeve also provided some security to the larvae, which tend to fall as a behavioral defense if a plant is bumped, blown by the wind, or bitten by a predator. To control ant access, I cut away surrounding vegetation and placed a small amount of Tanglefoot™ on the lower stems of half of the plants at each site (10 plants). I placed a sleeve on each plant made of bridal veil netting (1 mm x 1 mm mesh) that was long enough to surround the inflorescences (~20 cm long x 15 cm wide). The top and bottom of each sleeve was secured tightly to the stem of each plant with a small (1/8 in) clear plastic cable tie. I placed 10 third or fourth instar larvae directly onto buds or flowers of each plant. I then secured each sleeve at the top with a cable tie. The top of each sleeve was secured without touching the plant; the weight of the cable tie and the sleeve itself were not substantial enough to pull down the sleeve or prevent the plant from standing erect. With scissors I cut 10 holes approximately 3-5 cm diameter through the sleeves on the ant accessible plants so that ants could access the larvae. Holes were cut small to provide as

much structural support as possible to prevent the possibility of larvae falling through the holes, but large enough to enable carpenter ant access to the inside of the sleeve. I tested this method by observing two plants with the ant accessible sleeves to determine whether ants could access and maneuver within the sleeves and that falling larvae were not immediately lost from the plant when disturbed. I observed at least two occasions where ants entered a hole and pulled single larva from an inflorescence and successfully maneuvered it outside of the netting and down the plant stem. Each plant was visited every other day to ensure that they were upright. Statistical analyses were conducted using ANOVA (SPSS Inc., 2003) with mean number of flowers or buds remaining after the experiment as the dependent variable, and treatment (ants excluded, or not excluded) as the fixed independent variable with ant colony number and plant within ant colony as random factors.

## **RESULTS**

Carpenter ant nesting substrate density (logs and stumps combined) did not vary significantly among sites ( $F_{(2,23)}=1.33$ ,  $P=0.285$ ; Figure 1A). There were fewer logs and stumps for colonization at Island Lake (145/ha; unburned) compared to Flathead National Forest (250/ha; burned in 1994, Tukey hsd:  $P=0.26$ ), while Little Wolf had intermediate values (185/ha) and did not differ significantly from Flathead National Forest (Tukey hsd:  $P=0.59$ ) or Island Lake (Tukey hsd:  $P=0.81$ ). Percent soil moisture differed significantly among sites ( $F_{(2,35)}=7.36$ ,  $P=0.004$ ). Soil was driest at Little Wolf (7.0%), followed by Island Lake (16.4%) and Flathead National Forest (21.9%), differences were significant between Little Wolf and Flathead National Forest (CI of difference (4%-25%),  $P=0.01$ ), while Island Lake was not significantly drier or more moist than Flathead

National Forest (CI of difference -15%, +4%,  $P=0.32$ ) or Little Wolf (CI of difference -1%, +20%,  $P=0.09$ ) (Figure 1C). Little Wolf, the driest site with relatively high amounts of nesting substrate, had a significantly higher number of active carpenter ant colonies (21.3 colonies/ ha) than the wettest site (Flathead National Forest), where no active carpenter ant colonies were observed (0.0 colonies/ha;  $\chi^2=16.89$ ,  $P<0.00$ ,  $df=22$  Figure 1B), and Island Lake (3.8 colonies/ha;  $\chi^2=9.97$ ,  $P<0.002$ ;  $df=22$  Figure 1B) which was intermediate in moisture and nesting substrate.

#### *Ant exclusion experiment 1: Site specific larvae predation*

There was no significant effect of ant exclusion treatment on number of larvae remaining when both sites were combined ( $F_{(1,220)}=2.99$ ,  $P=0.0864$ ; Figure 2). Within Little Wolf, after five observations, more larvae remained on protected plants (6.4) compared to unprotected plants (4.6) but this effect was not statistically significant ( $F_{(1,111)}=2.99$ ,  $P=0.09$ ; Figure 2). There was no detectable treatment effect within Island Lake (protected plants 7.8, unprotected plants 7.2;  $F_{(1,111)}=0.56$ ,  $P=0.45$ ; Figure 2). At the commencement of the experiment, percentage of remaining, undamaged buds or flowers per plant was 20% higher on plants protected from ants (94%) compared to unprotected plants (74%) at Little Wolf ( $F_{(1,111)}=3.799$ ,  $P=0.07$ ; Figure 3). There was no effect of treatment within Island Lake, 87% of buds were damaged on protected plants vs. 84% on plants not protected from ants ( $F_{(1,111)}=0.13$ ,  $P=0.75$ ; Figure 3).

#### *Ant exclusion experiment 2: Effects of ant predation on plant damage*

In the second experiment, conducted at the driest site only (Little Wolf), initial numbers of buds and flowers were similar before treatment application ( $F_{(1,78)}=0.414$ ,  $P=0.522$ ). When the experiment commenced, plant damage, in terms of buds and flowers

damaged or completely consumed, differed significantly between protected and unprotected plants ( $F_{(1,78)}=91.57$ ,  $P<0.0001$ ; Figure 4). When plants were protected from ants, larvae consumed 81% of the original flowers or buds, while larvae consumed only 14% of the original number of flowers or buds on plants that were not protected from ants.

## **DISCUSSION**

Predation of cinnabar moth by generalist carpenter ants has the potential to interfere with the efficacy of cinnabar moth larvae as biological control agents of tansy ragwort. This interaction appears to be influenced by carpenter ant colony abundance that varies with site conditions primarily related to soil moisture. The opportunistic predation of moth larvae where carpenter ant density is high could play a role in the ability of cinnabar moths to achieve the abundance required to impact tansy ragwort population control.

I found higher densities of ant colonies at Little Wolf, the driest site and the only site in this study that was salvage-logged within the past 15 years (Figure 1A & 1B). These findings support the general knowledge that wood ants (*Formica* spp.) and carpenter ants (*Camponotus* spp.) are particularly sensitive to forest structural components, using such elements as dry stumps and logs as nesting substrate. However, in this case, even though the Flathead National Forest site had the highest levels of nesting substrate, carpenter ants were absent from this site (Figure 1B). Soil moisture is the most plausible factor explaining this difference (of the two variables measured) because carpenter ants are sensitive to moisture and are generally more abundant at dry sites (Chen et al. 2002). The difference in ant abundance is important, especially at the

local level, because it provides some support to the anecdotal claims that cinnabar moths played a major role in reducing tansy ragwort abundance in Flathead National Forest (G. Markin, personal communication). Notably, cinnabar moths are still abundant in Flathead National Forest whereas larvae are difficult to find in Little Wolf and Island Lake despite numerous releases since 2001.

Carpenter ants disturbed and consumed cinnabar moth larvae (Figures 2, 3), corresponding with their opportunistic, omnivorous feeding strategy. Work in both the native (van der Meijden 1979) and invaded (Myers and Campbell 1976) ranges of tansy ragwort has shown that the presence of wood ants or carpenter ants, respectively, leads to reductions in numbers of cinnabar moth larvae. Indeed, carpenter ants, have been cited as potential biological control agents of native and invasive Lepidopteran forest pests they such as spruce budworm pupae (*Choristoneura occidentalis* Clemens) (Youngs and Campbell 1984) and gypsy moth pupae (*Lymantria dispar* L.) (Weseloh 1988). Carpenter ants show the potential to affect cinnabar moth abundance because they can readily switch prey items in response to prey abundance and may also exhibit food storage behavior similar to *Cerapachys* ants and fire ants (*Solenopsis invicta*) (Hölldobler and Wilson 1990, Gayahan and Tschinkel 2008) allowing for collection of more larvae than needed at a single point in time. Future work could explore the functional response of ants to larvae abundance in order to quantify population level consequences on cinnabar moth. In one of few field studies that quantifies functional response of a generalist insect predator to prey densities, Schenk and Bacher (2002) demonstrated prey switching in paper wasp (*Polistes dominulus*) with temporary increases in density of the shield beetle (*Cassida rubiginosa*), a biocontrol agent of the invasive creeping thistle (*Cirsium*

*arvensis*), showing the potential to lead to serious reductions in local densities or even cause local extinction of beetle populations (Schenk and Bacher 2002), implying a reduction in the impact of beetle larvae on its host plant (Bacher and Schwab 2000).

This study provides some evidence that variation in herbivore abundance influenced by ant predation may ultimately affect the population dynamics of tansy ragwort. While our experiments did not allow for larvae to move to and from plants freely, still, we might not have expected less herbivory if larvae were not restricted to single plants. Complete defoliation of tansy ragwort by cinnabar moths is common under natural conditions in both the native (Dempster and Lakhani 1979) and introduced range (Isaacson 1973). Furthermore, previous work has shown that movement (Marston et al. 1978, Bergelson and Lawton 1988,) and feeding (Bernays 1997) generally increase the risk of predation of caterpillars by predators. Therefore, the large differences in number of intact buds and flowers on plants from which ants were excluded (Figure 4) are likely real. Data from experiments using uncaged larvae in larger plots indicates that defoliation was generally high in terms of reduced seed production even when larvae were free to move off of plants and outside of plots (See Chapter 2, this dissertation). Future work that incorporates the consequences of plant damage on tansy ragwort populations coupled with carpenter ant exclusion, if possible, could clarify the direct link between ant predation, herbivory by the cinnabar moth, and the population dynamics of tansy ragwort.

This study adds to a growing body of evidence for interactions of introduced biological control agents with native species (Louda et al. 2003). For example, Louda et al. (1997) demonstrated reductions in fitness of rare, native thistles from weevils introduced to control a related invasive thistle. Pearson et al. (2000) discovered that deer

mouse diet and habitat selection was altered by the presence of introduced gall flies for invasive plant control. But how do these examples work to influence or change the paths that managers might take in adopting biological control programs for weed species? One recommendation from this work might be to try to meticulously predict the ecological outcomes of all proposed agent within its proposed new range. However, this approach is hardly realistic. Pre-release screening in a laboratory setting is mandatory to prevent accidental introduction of pathogens associated with insect biological control agents as well as determining the degree of host-specificity to prevent non-target effects on native species. In the past few decades, selection of biological control agents has focused more on host specificity, while less resources are devoted to measuring or predicting their efficacy (McClay and Balciunas 2005). Despite the lack of efficacy testing, biocontrol agents of invasive plants are continually released, but rarely monitored post hoc, despite a consistent call for increased and improved monitoring for over a decade (e.g., Simberloff and Stiling 1996; Thomas and Willis 1998). Post-release monitoring could serve as an important check on actual efficacy under natural conditions. The development of thorough monitoring programs, post-release, can be a practical and cost-effective means to inform the theory behind biological control while also serving to help focus management on the most economic and effective handling of biological control agents for the control of invasive plant populations.

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## FIGURE LEGEND

Figure 1. Summary of abiotic factors measured in each study area. Estimated means for: (A) nesting substrate per hectare, (B) carpenter ant colonies per hectare, and (C) Mean percent soil moisture content per site (calculated as  $\text{wet soil (g)} - \text{dry soil (g)} / \text{dry soil (g)}$ ). Bars =  $\pm 1$  SE of the mean. Site history: Flathead National Forest (burned in 1994 and not salvage logged), Island Lake (unburned, unlogged), Little Wolf (burned in 1994, salvage logged). Means with different letters indicate statistically significant differences at  $P < 0.05$  between sites within each variable in (A) Wald test:  $P < 0.05$ , (B) and (C) Tukey hsd  $P < 0.05$ .

Figure 2. Number of larvae remaining over time by observation period. Solid lines (—) indicate the Little Wolf (dry) site, dashed lines (– –) indicate the Island Lake (moist) site. Circles (○) indicate ant accessibility to stems; triangles (▲) indicate ant exclusion from stems.

Figure 3. Proportion of buds or flowers consumed per adult plant in ant access and ant exclusion treatments, at the Little Wolf (dry) and Island Lake (moist) sites. Bars =  $\pm 1$  SE of the mean.

Figure 4. Mean number of buds or flowers on flowering stalks before and after ant exclusion treatments at the Little Wolf site. Bars =  $\pm 1$  SE of the mean. Means with different letters are significantly different at  $0.00 < P < 0.05$ .

FIGURE 1

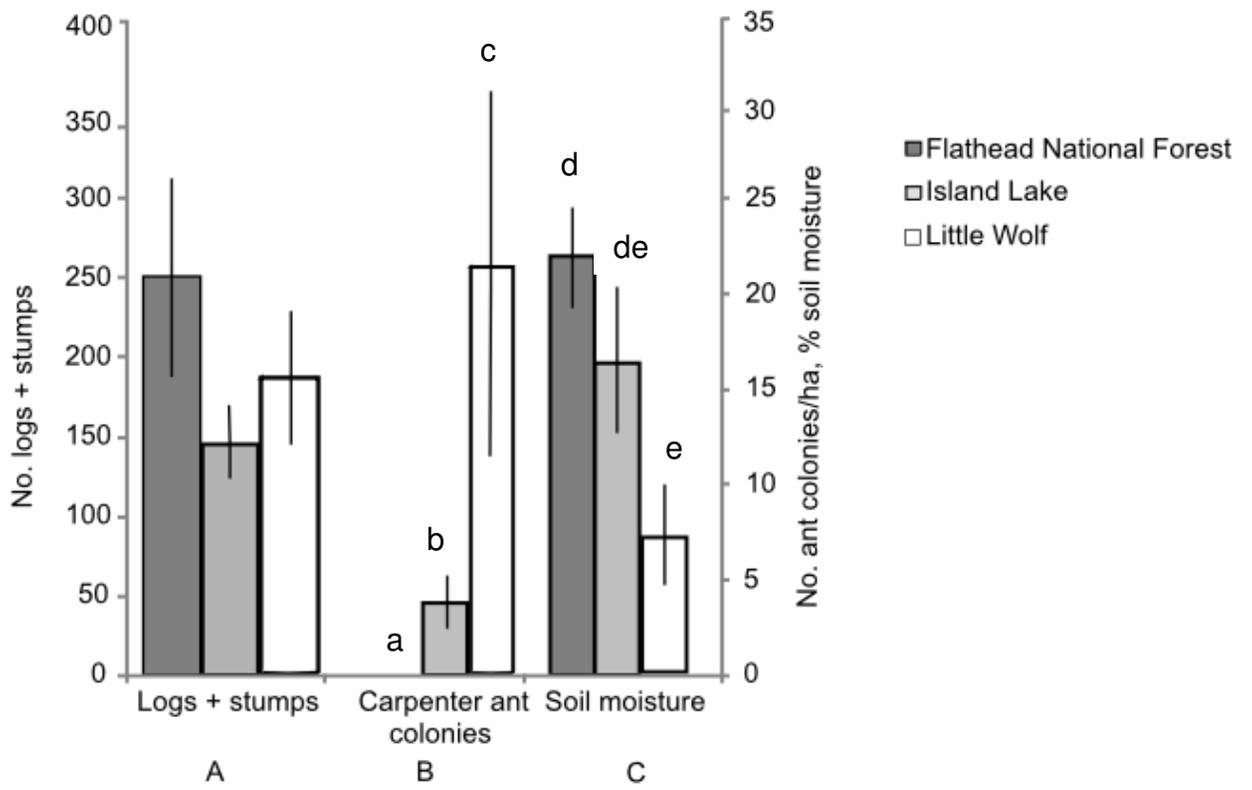


FIGURE 2

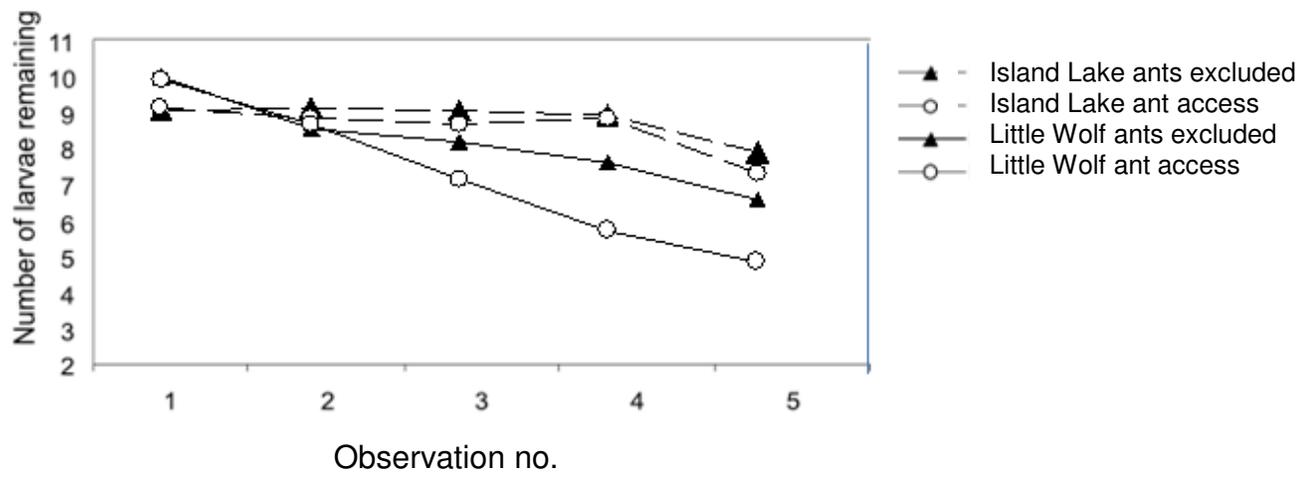


FIGURE 3

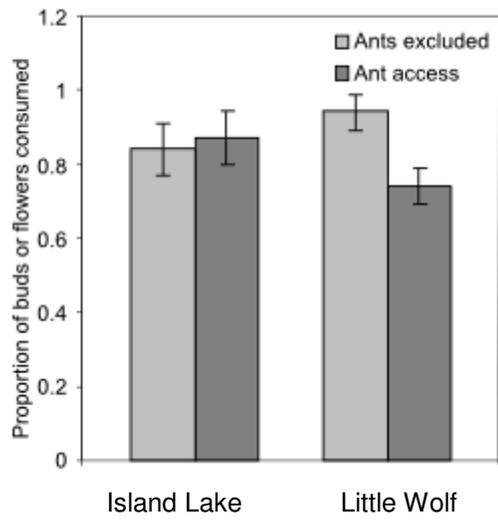
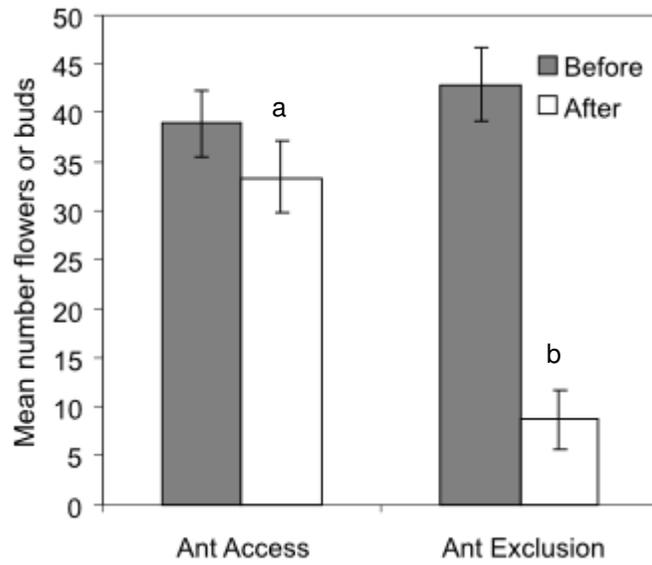


FIGURE 4



## **CHAPTER 4**

LIFE HISTORY PLASTICITY AS A MECHANISM OF HERBIVORE TOLERANCE?

DELAYED EFFECTS OF DAMAGE ON DEMOGRAPHY OF TANSY RAGWORT

## ABSTRACT

Plant consumers are one of the greatest stressors that plants face. Plants exhibit a variety of tolerance mechanisms to compensate for losses from herbivores. While it is well documented that herbivores affect individual plant performance, much less is understood about how herbivory affects plant populations. Here, we quantify the demographic effects of herbivory by the cinnabar moth larvae (*Tyria jacobaea*) on its biennial host plant, tansy ragwort (*Senecio jacobaea*). We added and excluded cinnabar moth larvae from plots with natural densities of tansy ragwort in 2005 and recorded the amount of damage to juvenile rosettes and adult flowering plants. We continued to monitor these individuals in 2006 and 2007. For vital rates (survival, fecundity, and growth) in each transition year (2005-06, 2006-07), we tested three possible models: two levels that reflected individual effects of damage (damage amount or presence of damage) and a model that reflected only treatment differences. Herbivore treatments, specifically amount of damage to individual plants, had positive effects on adult plant survival from 2005-06 and negative effects on fecundity in 2005, suggesting a life history tradeoff between these two processes. Persistent, negative effects on fecundity in the following year (2006) were strongly related only to the presence of herbivory in the previous year. Juvenile rosettes were less likely to transition to flowering adults with increasing amounts of herbivore damage. Using matrix models, we found that effects of herbivore presence on individual vital rates resulted in strong reductions in total fitness ( $\lambda$ ) with the exception of slightly positive effects of adult survival in 2005-06. Sensitivity and elasticity values demonstrated that, in matrices with herbivores,  $\lambda$  was less sensitive to fecundity and seedling survival, while more sensitive to vital rates associated with

rosette and adult survival. Together, these results suggest that tansy ragwort might actively re-allocate resources away from reproduction in exchange for increased survival especially in response to the amount of damage incurred and, potentially, in response to the presence of herbivory alone.

## **INTRODUCTION**

Plant consumers are one of the greatest stressors that plants face. Mechanisms of tolerance work to offset fitness losses from herbivore damage (Tiffin 2000). Increased photosynthetic ability (McNaughton 1979) and compensatory growth after leaf defoliation (Inouye 1982) are two of the most commonly observed mechanisms of tolerance. In addition to physiological responses to herbivory, plants can also change their phenology by delaying flowering, seed or fruit maturation, or growth, to avoid or minimize overlap with herbivore life cycles in an effort to avoid or reduce incidence of herbivory (e.g., Harnett and Abrahamson 1979, Islam and Crawley 1983, Marquis 1988, Bergelson and Crawley 1992, Juenger and Bergelson 1997, Mabry and Wayne 1997, Lennartsson et al. 1998). Patterns of resource allocation are themselves a mechanism of tolerance (Stowe et al. 2000) and likely influence the avoidance or regrowth strategies. The timing of allocation to growth, storage, and reproduction, prior to damage can affect the amount of damage experienced (Krupnick and Weis 1999) and the degree and type of tolerance expressed. The ability to change resource allocation following damage can also act as a mechanism of tolerance, such as in mobilization of carbon reserves after grazing (e.g., van der Heyden and Stock 1996), or where root-shoot ratios are positively correlated with regrowth following damage (van der Meijden et al. 1988).

In addition to these well-studied within-season mechanisms, plants can increase tolerance to herbivores by changing life histories. In other words, plants can shift relative allocation of resources to vegetative growth, survival, and reproduction in the presence of herbivory, e.g., by shifting the age of first reproduction and relative amount of semelparity vs. iteroparity. Many studies have shown that plant life histories vary within species (e.g., Law et al. 1977, Johnson 2007), and some have shown differences in life histories among populations with different histories of herbivory (e.g., Daehler and Strong 1995). In this paper, we show data that suggest that individual plants shift life histories in one year, after being exposed to herbivores in the previous year. We then use demographic models to compare the relative impacts of direct and delayed effects of herbivory on plant fitness, and to explore whether these shifts would allow individual plants to tolerate higher levels of herbivory.

In 2005-06, we conducted an experimental demographic study of the effects of an introduced biological control agent, the cinnabar moth (*Tyria jacobaea* Arctiidae), on an invasive plant, tansy ragwort (*Senecio jacobaea* L.) (Chapter 2, this dissertation). We continued monitoring in 2006-07 and noticed, surprisingly, that plants displayed delayed effects of herbivore damage even after cinnabar moths had disappeared from the system (see Chapter 3, this dissertation for potential causes). In this chapter, we investigate potential sources of these delayed effects, by comparing relationships between plant performance in 2006-07, and damage in 2005, quantified at three different scales: (1) treatment effects, i.e. whether plants were in herbivore addition plots in 2005, (2) presence of damage at the individual level, i.e., whether individual plants were damaged by herbivores in 2005 (regardless of treatment) and (3) amount of damage received by

individual plants. If delayed effects reflected direct resource costs of herbivory, we expected that the amount of damage received by individual plants in 2005 would be the best of these three predictors of performance in 2005-06 and 2006-07. We also expected that delayed effects would generally be in the form of reduced survival and fecundity, with the possible exception that florivory in 2005 could increase survival of mature plants, by removing the costs of reproduction. Alternatively, delayed responses could reflect phenotypic plasticity, the reallocation of resources to life history traits that increase fitness in the presence of herbivory. If this were the case, we would expect plants to respond simply to the presence of herbivory, either at the individual or – possibly – plot level if undamaged plants can detect volatile compounds released from neighboring damaged individuals, regardless of actual damage amount (see, e.g., Karban et al. 1999, Thaler 1999). We would also expect vital rates to increase and decrease in concordance with their relative contributions to fitness in the presence and absence of herbivores.

In addition to testing for shifts in life histories, we interpret their net consequences using matrix transition models. Total fitness effects of damage by herbivores depend on how strongly damage affects different components of fitness, and on how strongly each fitness component affects total fitness (Ehrlén 2003). Following standard methods from population ecology and life history theory (Caswell 2000, Silvertown and Charlesworth 2001), we use the leading eigenvalue of matrix transition models,  $\lambda$ , as our measure of total fitness. This technique is notable because many other studies of herbivore tolerance use flower or seed production alone as a fitness surrogate. Life history shifts imply the

possibility of trading current for future reproductive success, which means changing the relationship between seed production in one year and total lifetime fitness.

## **METHODS**

### *Study system*

Tansy ragwort is an invasive weed, whose native range extends from Norway south through Asia Minor and from Great Britain East to Siberia. It was first recorded in North America in 1913 from Vancouver Island (Harris et al. 1971). It is a biennial or short-lived perennial herb that grows as a basal rosette during the first growing season and reproduces via dimorphic achenes borne on inflorescences of a bolting shoot produced during or after the second growing season. In northwest Montana, plants emerge in spring, and inflorescences begin to bolt in July, flowering occurs in August, and seeds are mature by the beginning of September.

Cinnabar moth, a *Senecio*-specific lepidopteran species, was introduced as a larval-stage flower, seed, and leaf consumer of tansy ragwort first to northern California in 1959, and specifically in Montana in 1997. Pupae overwinter and adults emerge in late spring (May-June) as adult and juvenile plants begin to grow and flower. Female moths lay eggs on the underside of basal rosette leaves, or on the underside of leaves on the adult bolting stems. Early larval instars mainly feed on the leaves from which they emerge. As the larvae grow and exhaust immediate food resources, they make their way up the bolting stalk usually in synchrony with the host plant's developing inflorescences. Larvae can remain on the same plant during their entire development, or if food resources are depleted they will move to an adjacent rosette or adult stem.

### *Study area/experimental design*

The demographic analysis was conducted in Kootenai National Forest, 40 km east of Libby, Montana in Lincoln County. We monitored plants annually from 2005 to 2007 in four large macroplots in each of two broad areas representing mesic and xeric habitat conditions. In the mesic site, we used four 30-40m x 30-40 m macroplots; macroplots varied in size based on existing barbed wire fence to exclude cattle (Trainor 2003). In the xeric site we randomly selected 4 locations, based on random selection from 5 potential dead-end logging roads (with replacement), and a random distance based on the length of the chosen road. Next, we randomly selected a side of the road (north or south) on which to place a macroplot. We chose four similar-sized macroplots by finding the nearest populations with  $> 5$  mature plants /  $m^2$  at four random locations. This area had been closed to motor vehicle and cattle use since 1994, so fencing was not necessary. At each of the 8 macroplot locations we established 12 randomly located 1 m x 1 m plots. Nine plots had wood borders on all sides (25 cm high x 2.5 cm thick) around their perimeters resting on the ground to minimize soil disturbance. We randomly assigned 4 plots to each of 4 treatments: High density herbivore (cinnabar moth larvae) addition (H), Low density herbivore addition (L), Cage with wood borders, herbivore exclusion, no herbivore addition (C), and an ambient control with no borders and no herbivore exclusion or addition (N). In 2005, high-density plots received 250 larvae per plot, and low density plots received 150 larvae per plot. We chose a low density (150 per  $m^2$ ) and a higher density of larvae (250 per  $m^2$ ) that corresponded roughly, but were slightly lower than, median densities that McEvoy and colleagues (1993, their Figure 9) found at study sites in for the biological control of tansy ragwort in Oregon. Our densities appear higher

than those reported from the native range, but densities of moths and eggs are highly variable (<1 egg to 114 eggs per m<sup>2</sup>; Dempster 1971). More importantly, the amount of damage that we documented from experimental larval additions were analogous to instances of large areas of ‘complete defoliation’ of the host plant (see Results, Figure 2) commonly documented in both the native and invaded range (Dempster 1971, Crawley and Gillman 1989, van der Meijden et al. 1991, McEvoy et al. 1991). No larvae were added to plots in 2006, and we did not observe any caterpillar damage in 2006. As in Chapter 2 of this dissertation, we recorded stage (seedling, juvenile, rosette or reproductive adult) of each plant in August in 2005, 2006, and 2007 (see Figure 1). We also recorded damage in 2005 (Chapter 2, this dissertation) and fecundity (capitula per plant) in 2005 and 2006. We estimated the relationship between capitula production and seedling recruitment using a seed addition experiment to rule out the potential influence of density dependence in this study (Chapter 2, Figure 4, this dissertation)

We analyzed individual growth, survival, and fecundity in 2006-07 as a function of plant damage in 2005, using generalized linear mixed models (lmer procedure in R; R Foundation for Statistical Computing 2008) with macroplot and plot within macroplot as random factors, and site (xeric vs. mesic), and damage as fixed factors. As noted above (see *Introduction*), we compared three ways of coding plant damage: treatment groups (H, L, and C), presence of damage at the individual level, and amount of damage at the individual level. In each analysis we tested statistical significance of factors using likelihood ratio tests of models with the appropriate factor, relative to reduced models without that factor (analogous to Type III hypothesis tests in ANOVA). We tested binomial and Poisson-distributed variables for overdispersion. Capitula production per

plant was overdispersed with a high mean, so we approximated this variable with a log-normal distribution. No other variables were overdispersed (scale parameter < 1.5 for all other variables). Our analyses revealed large magnitude effects that were marginally statistically significant ( $0.10 < P < 0.15$ ), so we explored the consequences of these effects as well as those we detected at a threshold of  $P < 0.10$ .

We used matrix transition models to explore the significance of direct and delayed responses to damage. We used two-year transition matrices to integrate the direct and delayed effects of herbivory, i.e.,

$$M_{05-07} = M_{06-07} \times M_{05-06}$$

where  $M_{x-y}$  is the transition matrix between years  $x$  and  $y$ . Matrices separated herbivore effects by treatment groups, because plot-level variables were the strongest predictors of plant vital rates (see Results). All matrices used the estimate of seed germination from our seed addition experiment in 2005-06 (Chapter 2), and estimates of seed bank vital rates from Bauer (2006) and Trainor (2003). All matrices used the seedling survival estimates from 2005-06, as few seedlings germinated in 2007, due to a combination of dry conditions and low seed set in herbivore addition plots. For herbivore addition plots, we included direct effects of treatment, measured in 2005-06 (Chapter 2), as well as treatment effects for vital rates in 2006-07 (i.e., delayed effects). We compared the relative impacts of direct (2005-06) and delayed (2006-07) effects by substituting each vital rate into the two-year transition matrix from control plots, and calculating the effect of this vital rate on the annual rate of increase  $\lambda$  (the square root of the leading eigenvalue of the two-year transition matrix; c.f., Crone et al. 2009), relative to control plots. Each matrix contained estimated values for vital rates in each treatment (L or H) and habitat

combination (mesic or xeric), for a total of four matrices for each significant or marginally significant vital rate, and two matrices for controls (one in each habitat).

In addition, we used sensitivity and elasticity analyses of the 2005-06 vital rates (Chapter 2) to calculate the relative importance of different vital rates in the presence and absence of herbivory. In brief, vital rates with higher sensitivities in the presence of herbivory are relatively more important for population growth in the presence of herbivores, and, if delayed effects represent adaptive phenotypic plasticity, plants should allocate more resources to these vital rates in herbivore addition plots (Caswell 2000).

## **RESULTS**

### *Direct effects of herbivores*

Both juvenile rosettes and flowering adult plants were damaged by cinnabar moth larvae. Amount of damage per plant was greater for adult, flowering plants than juvenile rosettes (Figure 2). The influence of herbivore damage on vital rates is illustrated in significance tests conducted at the treatment level. Seed set was strongly influenced by herbivore treatments in 2005, the year in which herbivores were present on plants (Table 1, Table 2; also see Chapter 2, this dissertation). Rosettes in plots with added herbivores (L and H) in 2005 were less likely to transition to adult flowering plants in 2006 compared to controls (C) (Table 1, Table 2). Survival of adult flowering plants was positively affected by herbivore treatments (Table 1, Table 2). Plants that were flowering in 2005 were more likely to survive and revert back to the rosette stage in treatment plots (L, H) compared to flowering plants in control plots that were more likely to die after flowering. Remaining vital rates did not differ significantly among treatments (Table 1).

We compared three models for each significant vital rate above to determine the level at which herbivores affected plant performance: treatment, presence of damage, or amount of damage (Table 1). Only flower production was strongly related to individual amount of damage (Table 1); flowering plants that experienced more damage produced fewer flowers than less or undamaged plants. Although amount of damage was the best predictive model for adult survival, in terms of AIC score, survival differed more significantly among treatment groups, than as a logistic function of individual amount of damage. Although this discrepancy means we cannot determine which level of damage best predicts survival, results were broadly consistent across the two analyses ( $\Delta AIC < 2$ ,  $P = 0.05$  vs.  $P = 0.13$ , and both analyses indicated increased survival with higher damage; see Tables 1 and 2). Finally, the presence of damage was the best predictor of rosette-adult transitions; plants that were damaged as rosettes in 2005 were less likely to flower in 2006, regardless of the actual amount of damage they experienced (Table 1).

#### *Delayed effects of herbivores*

Herbivore treatments in 2005 significantly affected plant performance in 2006-07. Plants in treatment plots set fewer capitula in 2006, the season following the addition of herbivores (L and H), yielding lower flower (and ultimately, seed) estimates compared to controls (Table 1, 2). Note that plants that were adults in 2006 were non-flowering rosettes when herbivores were added in 2005. Rosettes in herbivore treatments were less likely to transition to reproductive adults ( $0.10 \leq P \leq 0.15$ , Table 1) and these transition rates decreased with increased herbivore density (Table 2). Herbivore treatments in 2005 also affected the survival of reproductive plants in 2006-07, but rates were not consistent

among treatments within either site (Table 1, 2). We did not detect any treatment effects for remaining vital rates in 2006-07 (Table 1).

Amount of damage to individuals in 2005 was a weaker predictor of 2006-07 than 2005-06 vital rates. The treatment model was the best predictor of flower production in 2006 (Table 1). Flower production differed among treatment groups (Table 2), despite the fact that flower production was not significantly related to the presence or the amount of damage at the individual level (Table 1). Adult survival from 2006-07 was significantly and positively related to both the presence of damage and the amount of damage the individuals incurred as juvenile rosettes in 2005 (Table 1), but these effects were only slightly stronger at the individual level than at the treatment level ( $\Delta$  AIC < 3, Table 1). Only rosette survival was noticeably more affected by amount of damage at the individual level rather than at the treatment level (Table 1).

#### *Demographic analysis*

Direct effects of the 2005 herbivore additions on fecundity had negative effects on fitness ( $\lambda$ ), and effects were especially large in the mesic habitat (Figure 3). Direct effects of adult survival on  $\lambda$  were very weakly positive, but not nearly as large as effects on fecundity (Figure 3). Reduced rosette to adult transition rates during the first year had negative effects on fitness that were intermediate in magnitude (Figure 3). In L and H treatments, delayed effects of herbivores on fecundity were negative with the largest differences at the mesic sites (Figure 3). Marginally statistically significant delayed effects of herbivores on rosette to adult transitions (Table 1, Table 2) had relatively large negative effects on  $\lambda$  (Figure 3). Finally, delayed effects on adult survival increased  $\lambda$  compared to controls at both mesic and xeric sites, with the exception of H in mesic

habitats where adult survival values were slightly higher in controls (Table 2, Figure 3). When considered together, direct effects reduced  $\lambda$  considerably from control values while combined delayed effects were negative, but had a weaker effect on  $\lambda$  (Figure 3). When all effects were considered together in the two-year projection matrix, as expected, the effects reduced  $\lambda$  considerably in herbivore treatments compared to non-herbivore controls (Figure 3).

The sensitivity of  $\lambda$  to rosette and adult survival rates increased in where herbivores were added ( $S_r$  and  $S_a$ , Table 3), based on both sensitivity (which measures the effects of absolute changes in this vital rate) and elasticity (which measures proportional changes in this vital rate) analyses, and matrix models for both site types. Herbivory generally decreased the importance of vital rates associated with fecundity and seedling survival (Table 3), including flowering probability (conditioned on survival,  $T_{ra}$  and  $T_{aa}$ ), seed germination ( $G$ ), and seed bank and seedling survival ( $S_b$  and  $S_s$ ). Notably, the sensitivity and elasticity of flowering probability was negative in the presence of herbivores, implying that increased survival in the presence of herbivory was not sufficient to outweigh reduced seed set (Chapter 2, this dissertation). Successful flower production ( $F_s$ ) was much lower in the presence of herbivory and this rate had slightly higher sensitivity and noticeably lower elasticity in the presence of herbivory (Table 3,  $F_s$ ).

## **DISCUSSION**

This study demonstrates that herbivory has both direct and delayed effects on plant performance. Direct effects on fecundity were strongly related to individual plant damage by cinnabar moth larvae. However, delayed effects on fecundity, realized the

following season, although evident, were primarily related to the presence of herbivory in the preceding season and less to direct, physical damage. In biennials where herbivores affect adult survival, plants are predicted to respond by shifting to a monocarpic, perennial life history (e.g., Klinkhamer et al. 1997) where survival is generally favored over reproduction. We showed that herbivores that affect fecundity have the opposite effect, and shift tansy ragwort life history towards iteroparity. Delayed flowering and facultative iteroparity are common in so-called biennials (van der Meijden and van der Waals-Kooi 1979, Klinkhamer and de Jong 1983, Reinartz 1984). Such ‘facultative’ biennials (sensu Kelly 1985) occur commonly in fertile, open, disturbed or early successional sites (van der Meijden and van der Waals-Kooi 1979). Our results suggest that life history shifts might be a mechanism of tolerance to damage in this and other short-lived species. Few studies have looked at demographic effects of herbivores in general (Maron and Crone 2006), so it is likely that this phenomenon might occur often but is not noticed.

Responses of plants that were reproductive during herbivore additions could easily reflect simple resource consequences of florivory. These plants had higher survival in the year of herbivore treatment, and did not appear to experience strong delayed effects. In both herbivore treatments, the plants that transitioned from adults to rosettes in 2005-06 had slightly lower survival in 2006-07 than other rosettes in the treatments (K. Crider, unpubl.), which partly explains the strong predictive power of individual damage, but not treatment groups, on this vital rate (Table 1). However, damage in 2005 did not affect rosette transition probabilities, regardless of individual plant histories. Gillman and Crawley (1990) demonstrated that defloration of tansy ragwort reduced the resource costs

of reproduction leading to the increased the survival of flowering plants, and similar patterns have been observed in response to flower removal in other systems (Bastrenta 1995, Auestad 2009, Crone et al. 2009). Our results corroborate this pattern, particularly because these responses were best predicted by the amount of damage received by individual plants (Table 1).

However, responses of plants that were damaged as immature rosettes in 2005 seem more consistent with adaptive plasticity. These plants were less likely to flower in 2006, and this effect was more tightly associated with the presence of damage at the individual and plot level than with the amount of damage received by individual plants (Table 1). Transitions from rosette to flowering adults had a negative sensitivity and elasticity in the presence of herbivory (Table 3), which means that delayed reproduction would increase fitness in the presence of herbivory. Second, if these plants did flower in 2006, they tended to produce fewer flowers and have higher survival. It could be that plants exposed to herbivory in 2005 produced fewer flowers because they had fewer resources. However, the presence and amount of damage to individual rosettes were both weak predictors of flower production in 2006; these effects were only detectable at the treatment level (Table 1). This pattern suggests a plastic response to the presence of herbivores or the presence of damage to neighboring plants. In addition, if reduced seed set were due to lower resource stores, it is puzzling that these plants had higher survival than reproductive plants in control plots, at least in the mesic habitat.

By definition, tolerance to damage implies the ability of individuals to withstand higher levels of damage than plants that do not exhibit mechanisms of tolerance. Our conclusion that resource reallocation is a mechanism of tolerance is based on sensitivity

analysis of 2005-06 vital rates, which implied that plants allocated relatively more resources to vital rates that were more important for fitness in the presence of herbivory. However, our 2-year matrix projections implied that these delayed effects still reduced fitness (Figure 3). This apparent discrepancy is because these two analyses are based on different ecological assumptions. The 2-year model implies an environment in which plants alternate between years with high herbivory and no herbivory. Our 1-year sensitivity analysis included only the matrix for the year with high herbivory. Thus, the fitness consequences of resource reallocation in the year after herbivory depend on whether herbivores are likely to be more abundant in that year. Other work in this system suggests that populations of moths and tansy ragwort can be cyclic in some locations, but on longer timescales than our study (~5 yrs; Bonsall et al. 2003). Therefore, we conclude that, in natural environments, shifting allocation from fecundity for some years after exposure to herbivory would increase plant fitness in this species. Similarly, it seems reasonable to conclude that life histories should be phenotypically plastic in tansy ragwort, since herbivore pressure varies widely in space and time.

We were initially surprised that plants seem to actively reallocate resources in response to herbivores. In retrospect, two bodies of literature support this unanticipated possibility. First, the effects leaf removal on fitness components in other systems have been mixed (Ågren 1989, Lehtila and Syrjanen 1995, Niesenbaum 1996, Mothershead and Marquis 2000), suggesting that many plants have the capacity to tolerate relatively large amounts of leaf damage. Tansy ragwort is able to partially compensate for herbivory through regrowth (Cox and McEvoy 1983, Crawley and Gillman 1989, Chapter 2, this dissertation). Van der Meijden et al. (2000) reported that tansy ragwort

increased allocation to storage in sites with a history of herbivory, environmental stress, or competition. Their comparative results support our experimental conclusion that individual plants might shift resource allocation in the presence of herbivores or herbivory. Second, there is growing evidence that herbivore damage to plants can activate plant responses to herbivory (Reinbothe et al. 1994, Wasternack and Parthier 1997), including emitting volatile cues from both induced (produced after damage) defensive chemicals (Karban and Baldwin 1997, Karban 2000) and constitutive (already present in plant tissue) defensive chemicals (Degenhardt and Lincoln 2006). We know of one laboratory example where plants were shown to reallocate biomass from shoots to roots when exposed to volatiles of a damaged cultivar (Ninkovic 2003). Tansy ragwort produces a complex and variable profile of pyrrolizidine alkaloids (PAs) that act as constitutive defenses against herbivory (Witte et al. 1992, Macel et al. 2002). In light of general evidence, it may not be unreasonable to speculate that similar cues can stimulate life history shifts in the presence of herbivory by cinnabar moth larvae.

Our original goal in this study was to quantify the demographic consequences of cinnabar moth larvae as biological control agents. To what extent do these delayed effects change conclusions based on traditional matrix models, without delayed effects (Chapter 2, this dissertation)? When cinnabar moths were present in this system (2005), they consumed ~ 98% of tansy ragwort flowers (Chapter 2, this dissertation). We explored this question using the 2006-07 projection matrices from herbivore addition plots. In the absence of any herbivory, this matrix indicates that tansy ragwort populations would tend to increase ( $\lambda > 1$ ); however, ~ 75% seed predation would be enough to cause these populations to decline ( $\lambda < 1$ ). In contrast, projection matrices

from control plots in this year require > 80% seed predation to achieve population declines. Furthermore, plants in herbivore addition plots would only have higher fitness than plants in control plots if > 98% of seeds were consumed. Therefore, we conclude that life history shifts are a form of tolerance in the sense of making the best of a low-resource situation. In other words, they would allow populations to persist longer in the presence of extreme herbivory, as opposed to converting declining to growing populations. The net effects are negative, and do not change the overall conclusion that cinnabar moths have the potential to control tansy ragwort in this area.

A final caveat to our study is that 2007 was an unusually dry year in our study area, with noticeably less fecund plants than previous years and almost no seedling recruitment. There is some possibility that the responses we observed reflect interactions of herbivory and environmental stress, rather than direct effects of herbivory alone. This issue is beyond the scope of our study, but raises intriguing possibilities for future research investigating the abilities of plants to shift life histories in response to biotic and abiotic environmental stress.

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Table 1. Summary of maximum likelihood analysis results testing vital rates for direct (2005-06) and delayed (2006-07) treatment effects and individual effects (presence and Amount of damage). \* = significant effect  $P \leq 0.10$ ; ‡ = marginally significant effect ( $0.10 \leq P \leq 0.15$ ); † = model with highest predictive potential (lowest AIC value). Dmg= mean damage measured per individual per plot

Vital rate	Effect	Direct effects (2005-06)									Delayed effects (2006-07)								
		Treatment			Presence of damage			Amount of damage			Treatment			Presence of damage			Amount of damage		
		$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P
Rosette survival, Sr (N = 1833, 1741)	Dmg	0.8	2	0.68	0.8	1	0.39	1.1	1	0.30	0.1	2	0.95	0.6	1	0.44	8.5	1	0.00
	Site	0.2	1	0.66	-0.2	1	0.19	0.2	1	0.63	0.5	1	0.95	0.0	1	0.86	0.11	1	0.74
	Sitex Dmg	0.2	2	0.91	1.2	1	0.28	0.0	1	0.95	1.7	2	0.42	0.6	1	0.44	0.3	1	0.60
	AIC	696.0			691.7			692.5			1682.0			1652.0			1646.0†		
Adult survival, Sa N = (294, 212)	Dmg	3.8	2	0.05*	0.4	1	0.50	2.3	1	0.13‡	1.3	2	0.51	0.0	1	0.83	1.7	1	0.20
	Site	1.53	1	0.21	1.60	1	0.21	1.4	1	0.24	0.1	1	0.81	0.0	1	0.99	0.18	1	0.67
	Site x Dmg	1.5	1	0.21	0.3	1	0.57	0.0	1	0.94	6.1	2	0.05*	5.8	1	0.03*	4.9	1	0.03*
	AIC	389.3			390.4			388.9 †			287.2			285.8			284.3†		
Rosette to Adult, Tra N = 1741, 1256	Dmg	0.2	2	0.90	1.5	1	0.22	1.3	1	0.25	4.5	2	0.11‡	3.0	1	0.09*	2.6	1	0.11‡
	Site	0.5	1	0.47	0.4	1	0.52	0.8	1	0.39	1.27	1	0.26	1.5	1	0.22	1.6	1	0.20
	Sitex Dmg	4.9	2	0.09*	4.5	1	0.03*	0.7	1	0.39	3.8	2	0.15	0.2	1	0.68	0.12	1	0.73
	AIC	1284			1280 †			1284			713.6 †			714.7			715.1		
Seeds per plant, Fs N = (296, 212)	Dmg	61.2	2	0.00*	49.4	1	0.00	96.2	1	0.00	5.4	2	0.07*	0.5	1	0.49	1.3	1	0.25
	Site	0.7	1	1.00	0.0	1	1.00	0.0	1	1.00	0.9	1	0.33	0.8	1	0.38	0.5	1	0.48
	Sitex Dmg	2.4	2	0.31	5.8	1	0.02*	7.8	1	0.01*	1.1	2	0.59	0.3	1	0.59	0.1	1	0.71
	AIC	1238.0			1245.0			1196.0 †			988.8 †			992.0			988.8		

Table 2. Estimated vital rates for significant and marginally significant treatment effects. C= control; L= low herbivore density; H= high herbivore density.

Vital Rate	Treatment	2005-06		2006-07	
		Mesic	Xeric	Mesic	Xeric
Fecundity (Fs)	C	1156.63	1156.63	896.79	896.79
	L	13.85	13.85	544.65	544.65
	H	3.31	3.31	266.64	266.64
Adult survival (Sa)	C	0.41	0.41	0.35	0.26
	L	0.61	0.61	0.50	0.32
	H	0.58	0.58	0.29	0.59
Rosette survival (Sr)	C	0.96	0.96	0.74	0.74
	L	0.96	0.96	0.75	0.75
	H	0.96	0.96	0.73	0.73
RA transitions (Tra)	C	0.14	0.14	0.09	0.09
	L	0.09	0.09	0.05	0.05
	H	0.09	0.09	0.06	0.06

Table 3. Sensitivity and elasticity values for estimated vital rates by treatment.

Vital rate	Sensitivity			Elasticity		
	Control	Low	High	Control	Low	High
A. mesic sites						
Ss, seedling survival	0.53	0.04	0.01	0.18	0.02	0.01
Sr, rosette survival	0.73	0.85	0.88	0.49	0.87	0.92
Tra, transition from rosette to adult (conditioned on survival)	2.09	-0.18	-0.33	0.16	-0.02	-0.04
Sa, adult survival	0.04	0.10	0.11	0.01	0.06	0.06
G, seed germination	26.29	1.98	0.53	0.18	0.02	0.01
Fs, Flowers per adult plant	0.00	0.00	0.00	0.18	0.02	0.01
Sb, seed bank survival	0.34	0.06	0.02	0.17	0.05	0.01
Taa, transition from adult to adult (conditioned on survival; very rare)	0.09	-0.01	-0.02	0.00	0.00	0.00
B. xeric sites						
Ss, seedling survival	0.35	0.04	0.01	0.21	0.04	0.01
Sr, rosette survival	0.77	0.82	0.87	0.46	0.83	0.90
Tra, transition from rosette to adult (conditioned on survival)	2.77	-0.04	-0.28	0.19	0.00	-0.03
Sa, adult survival	0.03	0.09	0.10	0.01	0.05	0.06
G, seed germination	33.70	3.42	0.99	0.21	0.04	0.01
Fs, Flowers per adult plant	0.0003	0.0025	0.0030	0.21	0.04	0.01
Sb, seed bank survival	0.36	0.10	0.03	0.16	0.08	0.02
Taa, transition from adult to adult (conditioned on survival; very rare)	0.10	0.00	-0.02	0.00	0.00	0.00

## FIGURE LEGEND

Figure 1. Life cycle diagram for tansy ragwort that corresponds to the transition matrix model. Arrows indicate all possible transitions in the model.  $F_s$  = fecundity,  $S_a$ =Adult survival (includes  $T_{ar}$ ),  $S_r$ = rosette survival,  $T_{ra}$ = rosette to adult transitions (conditioned on  $S_r$ ),  $T_{aa}$ =adult stasis (conditioned on  $S_a$ ),  $T_{ar}$ = adult reversion to rosette (conditioned on  $S_a$ ).

Figure 2. Cinnabar moth larval damage amount (proportion) per adult and rosette plants in 2005.

Figure 3. Differences between population growth rates of control matrices (product of 2006-07 and 2005-06) and matrices where rates were replaced with vital rates affected by herbivore treatments. Rates were substituted in separate matrix scenarios for direct (2005-06) and delayed (2006-07) effects in high and low treatments by habitat (mesic or xeric): A= Low density herbivore treatment, mesic sites, B=High density herbivore treatment, mesic sites, C=Low density herbivore treatment, xeric sites, D=High density herbivore treatment, xeric sites.  $F_s$  = fecundity,  $S_a$ =Adult survival,  $T_{ra}$ = rosette to adult transitions (conditioned on survival),  $S_r$ = rosette survival, all= all effects combined.

Figure 1

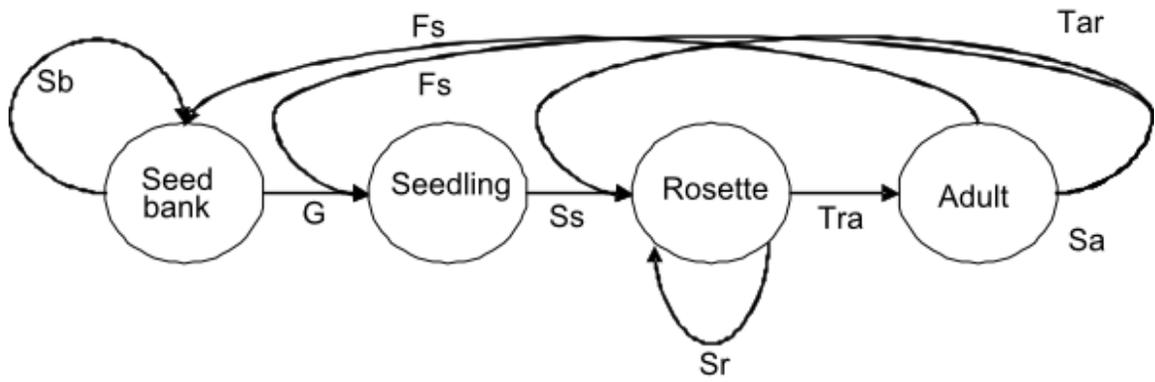


Figure 2

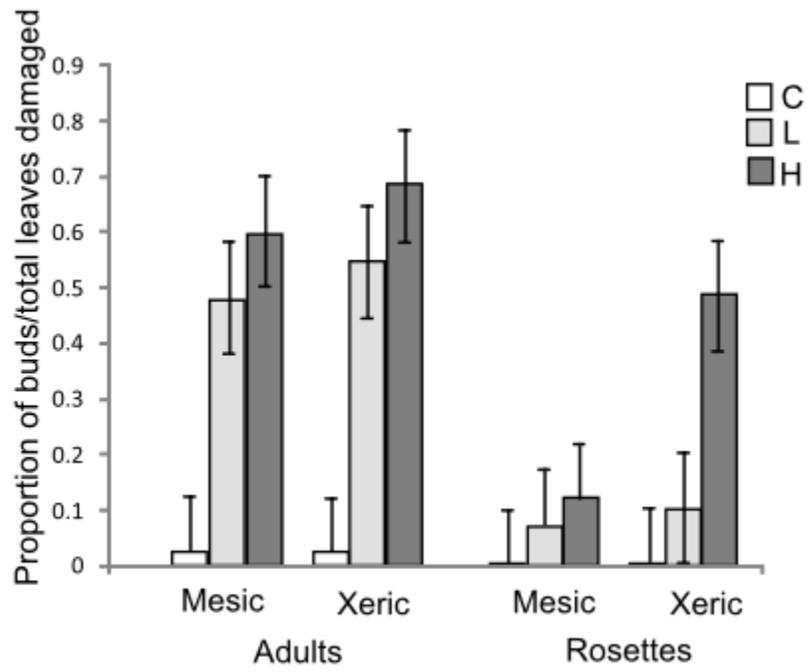


Figure 3

