

NON-NATIVE PLANT SPECIES IN MOUNTAINOUS AREAS: A CASE STUDY  
OF *LINARIA DALMATICA* IN THE GREATER YELLOWSTONE ECOSYSTEM

by

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## ABSTRACT

Non-native plant species are increasingly being viewed as a threat to sub-alpine and alpine ecosystems, and the need to determine the causes and mechanisms of non-native plant invasions in mountain systems has been recognized. This study was initiated to provide: 1) useful information for managers in the local area and, 2) information that can be used in concert with data from similar studies to help elucidate the causes and mechanisms of non-native plant species invasions in mountain systems at the global scale. Eighteen populations a non-native species (*Linaria dalmatica*) and 14 populations of a closely related native species (*Castilleja miniata*) were surveyed along an elevation gradient in the Greater Yellowstone Ecosystem. Climate, environmental, and species demographic data were collected from each site from 2008-2011. Climate and environmental predictors varied along the elevation gradient, with stem density of the two test species being explained by different sets of predictors. Vital rates of *L. dalmatica* were found to be more variable and more highly associated with climate and environmental predictor variables than those of *C. miniata*. The population growth rate of *L. dalmatica* did not show any consistent trend with elevation, but did appear to be influenced by extremely cold temperatures and predictors related to the vegetative community. Probability of occurrence of *L. dalmatica* was related to elevation. Percent cover of *L. dalmatica* was not associated with elevation, instead being strongly associated with vegetative community characteristics such as percent perennial cover. The current range of *L. dalmatica* was broader than the majority of native species in the study area, and the non-native plant community in the study area was significantly more nested with increased elevation than the native plant community. These results suggest that *L. dalmatica* is a broadly adapted species. Overall, our data fail to provide conclusive evidence of climatic limits for this species, but suggest that it may be limited from upward expansion by extremely cold winter temperatures. Until conclusive evidence of climatic limitation is provided, the upper populations of this species should be monitored and managed to prevent further spread into sub-alpine/alpine environments.



## CHAPTER 1: INTRODUCTION AND OBJECTIVES

### Introduction

Non-native plant species have been reported to cause a number of negative impacts (Collier et al. 2002; Martin and Marks 2006; Galbraith-Kent and Handel 2008). As a result of these perceived impacts, many state and national agencies have undertaken efforts to limit the spread of non-native plant species. The efficiency and effectiveness of these control efforts would seem to be proportional to the amount of species specific information related to the rate of spread and probability of occurrence. Although factors affecting the spread of non-native species have been reasonably well studied, there are still gaps in the current knowledge of this subject. One issue that is of particular concern within the Greater Yellowstone Ecosystem (GYE) is the phenomenon of non-native plant species invasions into mountainous areas, and the effects of elevation on the potential of non-native plant species to spread and colonize new areas.

Mountain systems, because of their high elevation and subsequently more severe climatic conditions, have been claimed to be relatively unthreatened by non-native plant invasions (MEA 2003). However, several studies have shown that non-native plants are indeed present within mountainous areas of the world (Arevalo et al. 2005; Becker et al. 2005; McDougall et al. 2005; Pickering and Hill 2007; Liang et al. 2008; Ross et al. 2008; Alexander et al. 2009; Kosaka et al. 2010; McDougall et al. 2011; Paiaro et al. 2011; Siniscalco et al. 2011). A recent study has found that there are 972 non-native plant species noted from 13 mountain regions around the world (McDougall et al. 2011).

It is obvious then, that mountain systems are not unaffected by the problems of non-native plant introductions and invasions/naturalizations.

The motivation behind the current interest in non-native species invasions in mountain systems is highly related to the fact that these systems are presently relatively un-invaded (Becker et al. 2005, Pauchard et al. 2009). Concerns about the potential effects of climate change and increased use by humans have added a level of urgency, as both of these factors are seen to have the potential to increase the presence of non-native species in higher elevation areas (McDougall et al. 2005; Pauchard et al. 2009). Perhaps the greatest motivation behind the current interest in this area of research is the idea that it is not too late to do something to limit non-native species invasions into these areas (Pauchard et al. 2009)

Previous investigations have revealed that, in general, non-native plant species richness tends to decrease with increasing elevation (Pauchard et al. 2009; Alexander et al. 2011). However, it is clear that there are several other factors besides elevation which could influence non-native plant species in mountain systems. Arguably, many of these factors, such as temperature, soil moisture, and precipitation, change as a result of elevation, but not all of these change in consistent ways from one geographic area to the next (Körner 2004).

Alexander et al. (2011) have suggested that the decrease in non-native plant species richness as elevation increases results from a filtering of the lowland species pool, whereby species with narrow climatic tolerances are eliminated as elevation increases. This process, called directional ecological filtering, provides a useful framework for

considering the dynamics of non-native plant invasions from a community assembly standpoint and serves as a valid explanation for the similarity in trends of non-native species richness along elevation gradients throughout the world (Alexander et al. 2011). However, the generalities of the process of invasion itself, whereby a species spreads outward from its point of introduction towards the limits of its potential range, are still relatively unknown in the context of mountain systems. Since at least some of the current interest in this area of research is driven by the idea of biodiversity conservation, it seems as though factors at the species level also need to be considered, since this is the level at which most management decisions are made in the realm of non-native plant management. Thus, while concepts like directional ecological filtering potentially allow one to determine which species may be future invaders into mountain systems (Alexander et al. 2011), species specific information is also needed to inform management decisions and practices.

Species specific studies will help to elucidate which environmental and climatic factors may be responsible for the general trend of declining non-native plant species richness as elevation increases. While studies of non-native plant frequency or abundance along elevation gradients in relation to these factors will be informative, there may also be a need for more in depth examinations. For example, the effects of climatic and or environmental factors on any given species could manifest themselves in subtle ways such that if only a survey of density was conducted, a large part of the story could be missed. It follows that if questions related to the future fate of a non-native plant

species in a mountainous area are to be addressed, the demographic details of populations of the species throughout its current range can offer many insights.

Given the current concerns about non-native plant species invasions in mountain systems throughout the world, and the relatively small quantity of species specific studies in this area of research, we endeavored to undertake a case study of one particular non-native plant species which is of concern within the GYE. *Linaria dalmatica* (L.) Mill is a perennial plant in the Scrophulariaceae family. For management purposes, this species is listed as a state noxious weed in both Montana and Wyoming, and thus represents a management demand within the study area.

*L. dalmatica* reproduces via seeds and rhizomes, and each plant commonly produces several stems from a common root crown. It is native in a region from Yugoslavia to Northern Iran, where it is generally found in open and/or rocky habitats from sea level up to 2800 m (Alex 1962). Large individuals of this species have been reported to produce up to ½ million seeds (Robocker 1970). In a study of seed germination for this species, Robocker (1970) found that pre-treatment of seeds, including cold treatment and acid scarification, were unnecessary to achieve maximum germination, suggesting that there is very little seed dormancy in this species. The primary dispersal agent of *L. dalmatica* seeds is wind (Robocker 1970). Floral stalks of the species remain upright for approximately two years, but nearly all seed is dispersed within the first year (Robocker 1970). Maximum depth below the soil surface for germination was reported to be 3 cm, and seeds may remain viable in soil for up to ten

years (Robocker 1970). The seeds are also known to remain viable after passing through the gut of a cow (Robocker 1970).

*L. dalmatica* is reported to have been introduced into the United States in Massachusetts as an ornamental plant in 1894 (Alex 1962). It was introduced into the study area for the same purpose in the 1950's (Roy Rankin, *pers. comm.*). In North America, *L. dalmatica* persists as a short-lived perennial adapted to cool, semi-arid climates and coarse textured soils (Robocker 1974). Although mature *L. dalmatica* is reported to be competitive with winter annuals and shallow rooted perennials, it is not thought to be competitive with established perennial communities (Gates and Robocker 1960, Robocker 1974), and seed recruitment is thought to be affected by interspecific competition for suitable microsites (Grieshop and Nowierski 2002) and reliant on disturbance (Gates and Robocker 1960). Thus, *L. dalmatica* is primarily a concern in areas where there is bare ground or where the soil is subject to disturbance.

### Project Objectives

The general goal of this study was to gather information relating to how non-native plants are affected by their relative position along elevation gradients in mountain systems at the species level. To that aim, we chose *L. dalmatica* as our test species due to its presence along a broad range of elevations in the study area and its status as a noxious weed within the study area. We were also interested in how a related native species would respond along the same gradients, and therefore had a second test species for this study, *Castilleja miniata* (Douglas ex Hook.). Our specific objectives were as follows:

Objective 1. Determine if *L. dalmatica* growth/reproductive variables were associated with environmental/climate variables along elevation gradients within the study area.

Objective 2. Determine if *C. miniata* growth/reproductive variables were associated with environmental/climate variables along elevation gradients within the study area, and compare responses to those of *L. dalmatica*.

Objective 3. Examine the population dynamics of *L. dalmatica* along an elevation gradient within the study area and determine: 1) if population growth and vital rates varied with environmental/climate variables, 2) which vital rates were most sensitive to perturbation at various points along the gradient, and 3) if population growth rates differed between marginal (at range limits) and interior populations of the species.

Objective 4. Examine the response of *L. dalmatica* abundance to characteristics of the vegetative community along elevation gradients within the study area to determine if *L. dalmatica* abundance was associated with biotic habitat factors.

Objective 5. Compare the elevational ranges of *L. dalmatica* and other non-native species within its range to those of native species found within its range as a test of the theory of directional ecological filtering.

Objectives 1 and 2 are addressed in chapter 3, objective 3 is addressed in chapter 4, and objectives 4 and 5 are addressed in chapter 5. Chapter 2 is intended to give adequate background information with which to frame the research project.

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## CHAPTER 2: LITERATURE REVIEW

### Impacts of Non-Native Plant Species

#### Relationship Between Native and Non-Native Plant Species Richness

It is often assumed that non-native plant species have negative effects on the ecosystems into which they are introduced. While the potential monetary costs of non-native plants have been evaluated (Pimentel et al. 2000; Pimentel et al. 2005), the effects of non-native plants on plant biodiversity still remain somewhat unclear. Many studies have investigated the relationship between non-native and native plants in natural systems. These studies have investigated the relationships between native plant richness and the abundance of either a single non-native plant species (Knight and Reich 2005; Ortega and Pearson 2005) or general non-native species richness (Morgan 1998; Stohlgren et al. 1999; Deutschewitz et al. 2003; Davies et al. 2005; Maskell et al. 2006; Belote et al. 2008; Powell et al. 2011). A general phenomenon that has been recognized as a result of these studies is that the shape of the relationship between native and non-native species richness, diversity, or abundance is often scale dependent (Lonsdale 1999; Davies et al. 2005; Knight and Reich 2005; Fridley et al. 2007; Powell et al. 2011). The studies that examined this relationship at multiple spatial scales found the relationship to be negative for small spatial scales (i.e. fine resolution, plot level) and positive (Davies et al. 2005; Knight and Reich 2005) for larger spatial scales (i.e. coarse resolution landscape or county level). This finding does not necessarily end the debate about whether or not non-native plant species could potentially have negative effects on native plant species

(or vice versa), but it does highlight the importance of also considering the scale at which any observed phenomena may be occurring.

Most explanations for the differences in the relationship between native and non-native plant richness between large and small scale studies typically follow the logic of Lonsdale (1999). He suggested that both native and non-native richness increase with increasing habitat heterogeneity at large scales, such that there is a positive relationship between native and non-native richness with no direct causal link (Lonsdale 1999). He goes on to point out that at much smaller scales, competition between plants would begin to influence the relationship between native and non-native richness, making it more complicated (Lonsdale 1999). Davies et al. (2005) expanded upon this idea, stating that spatial heterogeneity can explain the scale dependence of the relationship. They state that at small scales, competitive exclusion drives the relationship between native and non-native plant species richness (Davies et al. 2005). However, as the spatial scale increases, coexistence mechanisms that are driven by spatial heterogeneity override competitive exclusion, such that large areas which support more native plant species can also support more non-native plant species (Davies et al. 2005). Powell et al. (2011) have carried this idea a step further, noting that there is a negative relationship between the effect of non-native plant species and spatial scale, such that non-native plants have a greater effect on biodiversity at smaller scales of study.

#### Direct Impacts on Native Plant Species

While it has been relatively easy to examine relationships between non-native and native plant species richness, elucidating exactly what the mechanism is which allows

non-native plants to influence native diversity has proven to be much more of a challenge. There have been many studies which cite allelopathy as a potential mechanism whereby non-native plant species can have negative effects on native plant species (Chen et al. 2007; Ens et al. 2009; Jarchow and Cook 2009; Tassin et al. 2009; Thorpe et al. 2009; Small et al. 2010; Bossdorf et al. 2011; MacDougall et al. 2011). The differential use of resources by native and non-native plants is another possible mechanism. For example, several studies have shown that non-native plants are able to use nitrogen more effectively than their native counterparts, thereby causing some negative competitive interactions (Badgery et al. 2005; Jose and Daneshgar 2009; Esque et al. 2010; Everard et al. 2010; Littschwager et al. 2010; Mangla et al. 2011). In terms of water use, a meta-analysis revealed that non-native plants leaves tended to have higher stomatal conductance, and that ecosystems dominated by non-natives tended to have higher sap flow per unit of ground area than those dominated by natives (Cavaleri and Sack 2010). However, this same study also found that natives and non-natives were relatively equivalent in sap flow at the plant scale, and that evapotranspiration did not differ between ecosystems dominated by natives or non-natives (Cavaleri and Sack 2010). These results suggest that the idea that non-native plants use more water and thereby negatively affect native plants is plausible, but perhaps not universal. It further suggests that non-native plant density could play a large role in the presence of the effects noted above.

## Factors Contributing to Non-native Plant Species Invasions

### Human Movement of Plant Propagules

The seeds of plants have been the travelling companions of humans and their livestock throughout history (Crosby 1986). As such, many plants have been introduced to areas in which they are not native, either intentionally or unintentionally. However, it appears as though a majority of non-native plant introductions have been intentional. In North America, it has been noted that most of the species used in agriculture, forestry, and horticulture are non-native species (Reichard and White 2001). A recent article by Martin et al. (2009) cites Weber's book (2003) on invasive species as saying that 81% of the invasive plant species described in the book were intentionally introduced. Another study found that 82% of the non-native woody species that were identified as colonizing habitats outside of cultivation were intentionally introduced (Reichard and Hamilton 1997). This phenomenon is not confined to North America. In other areas where non-native plants have become problematic, such as Australia and the Pacific Islands, the introduction of many of these plants has been intentional (Sherley 2000; Reichard and White 2001). As such, it appears that our current problems with non-native plant species are mostly self-made. However, there have been instances in which non-native plants have been introduced unintentionally to new continents in contaminated grain seed, ship ballast, or even attached to livestock (Mack 2003).

Within North America, one of the most active pathways of intentional introductions of non-native plant species is the horticultural industry (Reichard and White 2001). Within this pathway, plants are intentionally brought to areas where they are not

indigenous and introduced via botanical gardens, garden clubs, the seed trade industry, or other types of commerce (i.e. medicinal plant trade) (Reichard and White 2001).

Historically, many species were introduced for strictly agricultural purposes (as crops), but as civilizations grew and developed, a large number of plants began, and continue to be introduced for ornamental purposes (Reichard and White 2001). Within the

horticultural industry, there are objections to the limitation of trade as a means to reduce the possibility of importing potentially invasive species (Reichard and White 2001).

However, several efforts have been undertaken to create voluntary initiatives for self-regulation within the horticultural industry in order to prevent the introduction of new

invasive species (Burt et al. 2007). In addition, Reichard and White (2001) outline

several strategies for collaboration between horticulturalists and conservation scientists

so that they can work together on addressing the issue of invasive plant introductions via

horticultural pathways. Regardless, the fact remains that many of the plant species which

are considered invasive in wild-land systems have been introduced intentionally through

horticultural trade, and this area remains in need of stronger regulatory measures

(D'Antonio et al. 2004).

Within agriculture, many species have been introduced unintentionally via contaminated crop seed (Baker 1986; Thill and MallorySmith 1997; Hobbs 2000).

Several recent studies on the subject demonstrate the fact that this is a continuing problem (Shimono and Konuma 2008; Norsworthy et al. 2009; Michael et al. 2010;

Shimono et al. 2010; Tamis et al. 2010). Once these species are introduced to an area,

their dispersal is augmented further by tillage (Mayer et al. 1998; Barroso et al. 2006) and

combine harvesting (Ballare et al. 1987; Mccanny et al. 1988) within and between crop fields. Seed cleaning is the primary preventative measure used to limit new weed species introductions in agricultural systems (Thill and MallorySmith 1997). It has been recognized that agricultural activities and the seed trade can result in the introduction of non-native plant species, and that the greatest risk of new species introductions comes from the commercial seed trade (Benvenuti 2007). Several characteristics of weed seeds, such as small size and similarity to crop seeds, make it extremely difficult to ensure that crop seed is not contaminated with weed seeds (Benvenuti 2007). As such, it is likely that this pathway of introduction will also continue to be responsible for the arrival of new weed species in the future.

Outside of the realms of horticulture and agriculture, other human activities also result in the introduction of non-native plant species to new areas. With our current ability to travel long distances, the simple act of going from one point to another can result in the introduction of non-native plant species to new areas if seeds become attached to our mode of transport or to ourselves. Although research in this area is still rather scant, the area that has received the most attention deals with motor vehicles. Several studies have shown that motor vehicles are capable of moving seed material unintentionally (Clifford 1959; Schmidt 1989; Hodkinson and Thompson 1997; Zwaenepoel et al. 2006; Von der Lippe and Kowarik 2007; Jorgenson and Elsner 2009; Veldman and Putz 2010). In addition, a recent review of seed transport by tourists noted 11 and 13 studies that had found seeds attached to humans or pack animals respectively (Pickering and Mount 2010). Therefore, it is evident that human activities, even those

that do not directly deal with the intentional movement of plants or plant propagules across long distances (e.g. agriculture and horticulture), can easily result in the introduction of non-native plant species into new environments. In addition to humans and their machines, animals such as horses (Campbell and Gibson 2001; Lauenroth and Wells 2007; Pickering and Mount 2010), deer (Vickery et al. 1986; Myers et al. 2004; Williams and Ward 2006), sheep (Manzano and Malo 2006), and cattle (Tews et al. 2004; Bartuszevige and Endress 2008) are all capable of moving seed on non-native plants, either in their dung or on their coats. While things such as motor vehicles, tourists, and animals contribute to the unintentional movement of non-native plants at more local scales, any of them could contribute to global movement if an adequate vector of transport were provided (i.e. a contaminated motor vehicle, horse, human, cow etc. was put on a ship and moved to another continent).

#### Factors Which Increase the Suitability of Habitat for Non-Native Species

Among all of the factors which potentially contribute to non-native species invasions, beyond the introduction of the species themselves, disturbance is one of the most cited. Although the intermediate disturbance hypothesis (Fox 1979) puts forth that some level of disturbance is necessary to maintain peak biological diversity, disturbance can facilitate invasions by non-native species and thus may also act as a negative force (Hobbs and Huenneke 1992). Within the realm of non-native plant invasions, disturbance is an obvious catalyst since it creates empty space in which seedlings can establish (Thompson et al. 1995). If these seedlings happen to be those of non-native

plants, then a non-native plant invasion is possible. The types of disturbance which humans create on the landscape are many. Agricultural activities, construction of buildings and roads, creation of trails and campsites, and controlled burns are just a few of the ways in which humans create spaces devoid of vegetation on the landscape. There are also several ways in which this type of destruction of vegetation can occur naturally, such as landslides, fires, and destruction by burrowing or wallowing animals. Regardless of how disturbance occurs, it is often cited in the literature as being linked to non-native plant invasions (Parker et al. 1993; Duggin and Gentle 1998; Jutila and Grace 2002; Bellingham et al. 2005; Hendrickson et al. 2005; Hierro et al. 2006). However, at least one study which tested for a link between success of invasive plants and disturbance found no relationship (Larson et al. 2001).

Disturbance is not the only factor believed to facilitate non-native species invasions. Fluctuations or changes in the availability of resources, such as light, water, and nutrients, are also believed to be important to this process (Davis et al. 2000). This theory is consistent with Grime's (2002) model of plant strategies, which puts forth that competition is less intense in recently disturbed areas where the resident plant community is not using all of the available resources (Davis et al. 2000). Davis et al. (2000) point out that resource levels can fluctuate in a positive direction due to a decline in resource use by resident vegetation, or an increase in overall resource availability can occur. These fluctuations in resources are not completely unrelated to disturbance, since disturbances are certainly capable of causing fluctuations in any of those three resources.



However, it is possible that resources such as nutrients and water could fluctuate independent of disturbance.

Several studies have shown positive associations between increased nitrogen and the success of non-native plant species (Brooks 2003; Rickey and Anderson 2004; Sharma et al. 2010), or that invasive species accumulate more nitrogen than natives (Durand and Goldstein 2001; McDowell 2002; Feng et al. 2007). Whether fluctuations in such resources always contribute to plant invasions is still unclear. One study which specifically tested the relationship between fluctuating resource availability and invasibility found no relationship between invader success and resource fluctuations (Walker et al. 2005). As such, it appears that generalizations cannot be made, and that all invasive species do not respond identically to fluctuations in resources. Regardless of the fact that few generalizations exist related to the phenomenon of non-native plant invasions, the combination of disturbance and increased resource availability seems to make the event more likely. When these two factors are combined with a vector of seed/propagule movement, it would seem that this would represent an ideal habitat for non-native species invasions and expansion. The primary habitat in which these factors are combined is that of roadsides.

#### Roads as Vectors of Non-Native Species Invasions

Non-native plant species are often more common along primary roadways than in nearby habitat (Tyser and Worley 1992; Arevalo et al. 2010), more natural areas (Timmins and Williams 1989; Parendes and Jones 2000), or lesser used roads/trails

(Parendes and Jones 2000; Gelbard and Belnap 2003). Findings like these have led to the idea that roadways are a large source of non-native plant introductions via vehicular transport (Von der Lippe and Kowarik 2007; Veldman and Putz 2010). There are several reasons why roadside habitats may be ideal for non-native plant establishment. First, roadsides favor the establishment of non-native plants by virtue of the disturbances created there (Greenberg et al. 1997; Trombulak and Frissell 2000). It is also possible that roads create micro-environmental changes which favor the establishment of plants in general, such as less diurnal temperature variation (Trombulak and Frissell 2000), greater moisture availability (Hillel and Tadmor 1962), and altered pH and nutrient availability (Greenberg et al. 1997; Trombulak and Frissell 2000). However, Trombulak and Frissell (2000) note in their review that the accumulation of dust on plants and the presence of heavy metals in soils could have negative effects on plant growth in roadside environments.

As mentioned previously, several studies have shown that seeds can become attached to vehicles (Hodkinson and Thompson 1997; Zwaenepoel et al. 2006; Von der Lippe and Kowarik 2007; Veldman and Putz 2010). Combining this vector of transport with suitable conditions for establishment makes roadways ideal sites of establishment and spread of non-native species (Davis et al. 2000; Parendes and Jones 2000; Coffin 2007). Several biotic and abiotic factors affect the ability of non-native plant species to spread into the surrounding habitat. These include, but are not limited to, poor soil conditions (Williamson 2002), large amounts of plant litter (Fowler 1988), shading (Parendes and Jones 2000), and more general stressful climatic conditions (Baker 1986;

Lambdon et al. 2008; Ross et al. 2008; Hautier et al. 2009). While several studies have shown that non-native plants are less common farther away from roads (Timmins and Williams 1989; Tyser and Worley 1992; Parendes and Jones 2000; Arevalo et al. 2010; Seipel et al. 2012), few experimental studies exist which delve into the possible mechanisms of this phenomenon. One study has shown that, under the conditions of identical propagule pressure, a surrogate non-native plant species showed a decrease in germination with increased distance from a road (Pollnac et al. 2012). These results lend some support to the idea that certain habitats may be less prone to invasion than others. In the case of the study, it would seem that perhaps habitats away from the roadside are less invasible than those closer to the roadside (Pollnac et al. 2012). However, these results are far from conclusive, and similar research needs to be carried out for a variety of species in a variety of geographical contexts before any generalizations can be made.

### The Concepts of Invasibility and Invasion Resistance

Invasibility, in the context of plant communities, is defined as the tendency for a given community to be invaded by new plant species (Lonsdale 1999). Many studies have explored the concept of invasibility in the context of plant communities (Rejmánek 1989; Lonsdale 1999; Davis et al. 2000; Naeem et al. 2000; Prieur-Richard et al. 2000; Wardle 2001; Brown and Peet 2003; van Ruijven et al. 2003; Walker et al. 2005; Maron and Marler 2007; Belote et al. 2008). Hand in hand with invasibility goes the concept of invasion resistance, defined as the resistance of a community to invasion (Williamson

and Fitter 1996). In this section, the two will be discussed somewhat interchangeably, as they are the two opposite sides of the same issue.

In his coverage of invasibility, Rejmánek (1989) stated that the probability of successful plant invasions is dependent on the extent and type of disturbance, the rate of propagule deposition, and the length of time over which propagules are introduced to the area. He went on to say that the amount of cover or biomass in the area may be an efficient measure of resistance to invasion in some situations (Rejmánek 1989). One of the key observations from Rejmánek's treatment of the subject is that it is inherently difficult to separate resistance to invasion based on properties of the biotic community from resistance based on abiotic conditions (Rejmánek 1989). Recognition of this fact led to Lonsdale's (1999) proposal that invasibility is an emergent property of ecosystems, not just plant communities. He states that it is "...manifested in the rate of mortality of exotic species, but at the same time potentially affected by the climate, the properties of native species, the level of disturbance, and the ecosystem's resistance to invasion." (Lonsdale 1999).

As interesting and well-studied as the related concepts of invasibility and invasion resistance are, it has been extremely difficult to quantify either one of these properties in terms of mechanisms. Several studies have related invasibility to ecosystem properties, where invasibility is measured as the abundance of non-native species, or of a single non-native species. Of these studies, several have directly examined the relationship between invasibility and 1) properties of the plant community (number of natives, plant density, etc.) (Lonsdale 1999; Stohlgren et al. 1999; Naeem et al. 2000; Prieur-Richard et al.

2000; Stadler et al. 2000; Larson et al. 2001; Brown and Peet 2003; van Ruijven et al. 2003; Knight and Reich 2005; Von Holle and Simberloff 2005; Maron and Marler 2007; Eschtruth and Battles 2009), 2) disturbance (Larson et al. 2001; Hendrickson et al. 2005; Von Holle and Simberloff 2005; Hierro et al. 2006; Belote et al. 2008; Eschtruth and Battles 2009) 3) propagule pressure (Rouget and Richardson 2003; Von Holle and Simberloff 2005; Eschtruth and Battles 2009), and 4) resource availability (Walker et al. 2005; Maron and Marler 2007). While these references are not exhaustive, they provide a good overview of the subject.

Studies examining the relationship between plant community characteristics and invasibility largely agreed with the previous discussion of the scale dependence of the relationship between native and exotic species. The studies which examined the relationship at multiple scales found a positive relationship between invasibility and native species diversity at larger scales, but a negative relationship at smaller scales (Brown and Peet 2003; Knight and Reich 2005). The experimental or observational studies conducted only at smaller scales all found a negative relationship (Naeem et al. 2000; Prieur-Richard et al. 2000; van Ruijven et al. 2003; Von Holle and Simberloff 2005; Maron and Marler 2007), whereas those conducted only at larger regional scales found a positive relationship (Stohlgren et al. 1999; Stadler et al. 2000). The studies that did not explicitly quantify native species diversity found that invasibility differed with vegetation type (Larson et al. 2001) and biome (Lonsdale 1999). One study found that native diversity did not explain a significant amount of the variation in invasibility

(Eschtruth and Battles 2009). Interestingly, this study was also examining propagule pressure.

Although propagule pressure does not necessarily contribute to the invasibility or invasion resistance of a habitat since it is not a quality of that habitat, it is related to the process of invasion. The studies that examined propagule pressure all found that it was an important determinant of invasion success (Rouget and Richardson 2003; Von Holle and Simberloff 2005; Eschtruth and Battles 2009), and two of the studies suggest that a large amount of propagule pressure may be able to negate any invasion resistance conferred by native plant diversity (Von Holle and Simberloff 2005; Eschtruth and Battles 2009).

Studies which examined the relationship between disturbance and invasibility found a positive relationship between increased disturbance and invasibility at both large (Belote et al. 2008) and small (Larson et al. 2001; Hendrickson et al. 2005; Von Holle and Simberloff 2005; Hierro et al. 2006; Eschtruth and Battles 2009) spatial scales. The studies which examined resources had varying results. One study found that the addition of water to plots increased invasibility as measured by the abundance of a non-native plant (Maron and Marler 2007), whereas the other found no increase in the abundance of a non-native plant following pulses of water or nutrients (Walker et al. 2005). These were both small scale plot level studies.

Other attributes of the resident plant community have also been tied to the concepts of invasibility and invasion resistance. These deal mainly with how the plant community alters the growing environment. For example, the shade created by the

existing plant community has been suggested as a means by which the plant community can resist invasions by non-natives (Martin and Marks 2006; Martin et al. 2009; McDaniel and Ostertag 2010). Other studies have suggested that excess plant litter can suppress the establishment of non-native plants (Hager 2004; Bartuszevige et al. 2007). However, there are also cases where litter has been shown to increase the survival and growth of a non-native plant (Schramm and Ehrenfeld 2010). Finally, environmental conditions themselves may influence the invasibility or invasion resistance of a community or ecosystem. The stressfulness of the environment has been suggested as a mechanism whereby certain habitats can resist invasions by non-native plants (Rejmánek 1989; Alpert et al. 2000; Pauchard and Alaback 2004; Gerhardt and Collinge 2007; Ross et al. 2008; Pauchard et al. 2009; Alexander et al. 2011).

Despite all of the interest in the concept of invasibility, there still are no unifying theories which would allow one to predict the invasibility of a plant community or ecosystem based on its attributes. However, there is enough observational and experimental data available to at least allow one to assess a plant community or ecosystem and derive some general conclusions about its invasibility. Furthermore, the abundance of data should also allow for more refined hypothesis testing in the future, and hopefully will inspire more experimental studies which can examine the effects of various plant community or environmental attributes on invasibility and invasion resistance in the absence of so many confounding factors. Davis et al. (2000) state that “...it is unlikely that any single theory will be able to account for all differences in invasibility among all environments.” Nonetheless, this concept will undoubtedly remain

of interest to scientists as long as non-native plant species are considered problematic. Currently, the concepts of invasibility and invasion resistance are of particular interest in habitats which are not yet as heavily invaded. This is due to the fact that management of non-natives in these more pristine areas depends on knowledge of whether or not it is likely that the current non-native species will continue to spread, and if new non-native species are likely to establish if they are introduced. One area in which such questions are of critical importance is in mountain systems.

### Plant Communities in Mountain Systems

#### General Climatic Trends and Conditions in Mountain Systems

There are several climatic and environmental conditions which change as one proceeds from lower elevations to higher elevations. Within mountain systems, the progression from low to high elevations can be quite sudden, and it is for this reason that mountain systems and the elevation gradients therein are often used to study the effects of the environment on organisms (Körner 2003; Körner 2004; Körner 2007). Among the conditions which have been noted to change with elevation above sea level, some are directly tied to elevation in the same way all over the world, and others are related to elevation in different ways depending on the geographic context (Körner 2007).

Temperature and atmospheric pressure both decrease at the same rates with increasing elevation, regardless of geographical context (Körner 2007). In addition, solar radiation under cloudless conditions, and the proportion of UV-B radiation for any given amount



of solar radiation, both increase with elevation regardless of geographical context (Körner 2007).

Other climatic factors have varying relationships with elevation depending on geographical context. For example, precipitation can increase with elevation, decrease with elevation, or have mid elevation peaks, depending on location (Körner 2007). The relationships between average wind velocity and elevation, and length of the growing season and elevation also change based on geographical context (Körner 2007). Certain mountain ranges are windier than others, and the length of the growing season has been seen to decrease (as in humid high latitude areas) stay the same (as in the tropics) or increase (as in regions with dry low latitude climates) based on geographical context (Körner 2007). As such, there are no general altitudinal trends for any of these factors (Körner 2007).

#### Unique Characteristics of Alpine Plant Communities

As elevation above sea level increases, plant communities change. One of the most noticeable changes in plant communities occurs above tree line, in the alpine zone. This area often has a unique assemblage of plants, characterized by low stature shrubs, tussock forming grasses and sedges, rosette forming herbaceous perennials, and cushion plants (Körner 2003). There are several limitations that the alpine environment imposes which affect the plants which grow there. Time under snow, temperature stress, and solar radiation can all potentially affect the growth of alpine plants (Körner 2003)

Snow cover does not necessarily limit plant growth, as long as the snow is not too thick, solar radiation is high, and plants are not dormant (Körner 2003). However, to survive for prolonged periods under snow cover plants must: 1) be resistant to the physiological stresses imposed by snow cover, 2) have a phenology which is coordinated with the duration of snow cover, and 3) be able to accumulate enough carbon annually to complete their lifecycle and persist via reserve formation and clonal or reproductive propagation (Körner 2003).

In order to survive in an alpine environment, plants must be able to cope with freezing temperatures without sustaining fatal injuries (Körner 2003). The two main ways in which this is accomplished are tolerance or avoidance (Körner 2003). Plants can avoid exposure to low temperatures, avoid freezing of exposed tissues, tolerate freezing, or replace damaged tissue (Körner 2003). Plants can avoid exposure to low temperatures phenologically or morphologically (Körner 2003). In terms of phenology, if the plant is dormant during times of low temperatures, then the risk of damage is minimal (Körner 2003). Small stature and the location of meristematic tissue close to or below the ground surface are two ways in which the morphology of the plant leads to avoidance of exposure to low temperature extremes (Körner 2003).

Plants can also avoid freezing in tissues in a variety of ways. The first is through osmotic adjustments in solute concentration at the cellular level which prevent the formation of ice crystals and subsequent damage to the cells (Körner 2003). The second is through a process called super cooling, in which nucleation of ice crystals is prevented such that plants can experience temperatures below freezing without the formation of ice

crystals in cells (Körner 2003). The third mechanism is called freezing tolerance, in which water is moved out of the living part of the plant cells and freezes there, instead of freezing within and subsequently damaging the protoplast (Körner 2003). In the event that plants become damaged and lose tissue due to freezing, repair and replacement of damaged tissue is necessary to ensure survival (Körner 2003).

Alpine plants also experience levels of heat stress similar to lowland plants, and must therefore possess similar heat tolerance (Körner 2003). Körner (2003) notes in his book, that this causes a dilemma in alpine plant growth. Tall plants cannot accumulate enough heat to survive low temperatures, but low plants are more subject to heat stress due to excess heat accumulation. He suggests that high biodiversity in the alpine flora, with a variety of morphotypes which distribute climatic risks from freezing or heat stress, is the best way in which alpine plant communities can persist (Körner 2003). Alpine plants are also exposed to more UV-B radiation than lowland plants, but direct effects of UV-B radiation on alpine plants in terms of growth inhibition appears unlikely (Körner 2003).

From the brief discussion of climatic stresses above, it is apparent that alpine plant communities are structured primarily based on their tolerance to these stresses. Water and nutrient stress appear not to be issues, since ample moisture is available in alpine environments and leaf concentration of nutrients does not appear to differ between lowland and alpine plants (Körner 2003). Although nitrogen supply in the alpine zone is less than in lowland areas due to less nitrogen fixation, alpine plants are seen to cope with this by more efficient recycling of nutrient resources (Körner 2003). In Grime's (2002)

framework of plant strategies, alpine plants fit well into the category of stress tolerators, given their exposure to low temperatures, potentially desiccating heat extremes, and low nutrient availability. They are seen to cope with this by their low stature (Körner 2003) and efficient use of resources (Grime 2002). However, it is unclear exactly how these alpine species would cope if their climatic or resource conditions were to change or if new species were introduced into alpine areas.

#### Threats to Native Plant Communities in Mountain Systems

Mountain systems contain many unique habitats and plant communities.

Mountains cover approximately 12% of the land surface of the earth (Körner et al. 2011), and house roughly one quarter to one third of the world's terrestrial plant diversity (Barthlott et al. 1996, Körner 2004 ). As such, these areas are important targets for the conservation of biodiversity. It should be noted here that while the previous section dealt with alpine plant communities, this section also deals with plant communities found in mountain systems at and below tree-line. While alpine plant communities may represent some of the most unique communities present in mountain systems, the other transitional communities at and below the tree-line are also unique and shaped by the same stresses, albeit at a lesser intensity, as the truly alpine communities.

Mountain systems often have the reputation of being pristine natural areas which are relatively untouched by humans. However, the situation which has fostered that reputation is rapidly changing. Mountain systems are no longer as inaccessible to humans as they once were, which presents a number of opportunities for the degradation

of native mountain plant communities. The first threat to native plant communities in mountain systems that will be discussed here is that of non-native plant invasions.

Mountain systems have been claimed to be relatively unthreatened by non-native plant invasions (MEA 2003). However, several studies have shown that non-native plants are indeed present within mountainous areas of the world (Arevalo et al. 2005; Becker et al. 2005; McDougall et al. 2005; Pickering and Hill 2007; Liang et al. 2008; Ross et al. 2008; Alexander et al. 2009; Kosaka et al. 2010; McDougall et al. 2011; Paiaro et al. 2011; Siniscalco et al. 2011). A recent study has found that there are 972 non-native plant species noted from 13 mountain regions around the world (McDougall et al. 2011). It is obvious then, that mountain systems are not unaffected by the problems of non-native plant introductions and invasions/naturalizations. Although the effects of non-native plants in mountain systems have not been well studied, it is possible that they could have some of the same effects discussed earlier in the context of more lowland environments, and thus represent a potential threat to the plant communities of mountain systems.

Another potential problem for native plant communities in mountain systems is altered forms of land use. Mountainous areas have been used for pasture and for hunting historically (GarciaRuiz et al. 1996; Olsson et al. 2000; Tasser and Tappeiner 2002; Körner 2003). However, the use of such areas is generally increasing in both diversity and intensity for both agricultural and recreational purposes (Price 2006). This increase in human use is thought to pose a risk for native plant communities in that it could result in the introduction of more non-native species (Pauchard et al. 2009). While this seems

likely, the issue of land use in mountainous areas is not entirely straightforward. Some studies have shown a decrease in land use in mountainous areas and noted that this has actually resulted in a decrease in plant diversity due to successional processes (Olsson et al. 2000; Agnoletti 2007). Thus, it appears that no real generalizations can be made about trends in land use in mountainous areas. However, where land use is seen to be increasing, it is likely that the introduction and establishment of new non-native species will also increase, based on the previous discussion of the links between non-native species and disturbance.

The final major threats for the plant communities of mountain systems are those of climate change and altered atmospheric chemistry. Climate change has the potential to change the distribution of plants in mountain systems, since it is thought that it will generally increase temperatures and eliminate some of the coolest climate zones in mountain systems (Beniston 2003). It is thought that this will result in a loss of plant species at the highest altitudes, and a linear shift of the remaining species upslope (Beniston 2003). In terms of non-native plants, it has been suggested that warming of the high elevation areas might make it easier for non-native plant species to colonize those areas (McDougall et al. 2005). If this is the case, then it is possible that native mountain plant communities could be replaced by new communities of plants from lower elevations consisting of both natives and non-natives (Körner 2003; McDougall et al. 2005). However, this operates on a number of critical assumptions that may not necessarily be met (Gaston 2003). Gaston (2003) states that, in order for this to be correct, we must assume that current species have no physiological capacity to withstand

the changing climate and that current correlations between climate and the occurrence of species are causal. If these (and a number of other assumptions not mentioned here, see Gaston (2003)) are true, then it seems likely that current plant species ranges would shift in the face of climate change.

It has been suggested that many of the climate change scenarios which are currently accepted could result in a loss of biodiversity by selecting for the more mobile species which could track the relatively fast movement of climatic conditions (Malcolm et al. 2002). However, in a simulation model examining plant species extinctions in a mountainous area under different climate change scenarios, the number of species going extinct was shown to be relatively equivalent whether dispersal was assumed to be unlimited or short distance only (Engler et al. 2009). It should be noted that the authors of this study also found that migration index had a negative association with potential distribution decreases, such that the potential distributions of those species with higher migration rates were less affected by climate change (Engler et al. 2009). Thus, while the number of predicted extinctions did not appear to be reliant on dispersal ability, the potential range of species was dependent on dispersal ability (Engler et al. 2009). This is in agreement with the suggestion of Malcolm et al. (2002) above, and has implications for changes in the composition of plant communities in mountain systems. Most non-native plants in mountain systems are introduced into lowlands and then migrate into the mountains (Alexander et al. 2011). This suggests that, in general, those species which make it into the mountains have good dispersal capabilities. If non-native species have better ability to disperse than native species in mountainous areas, then it is possible that

they could be selected for under the scenario of rapid climate change given the findings above.

Changes in atmospheric chemistry also have the capacity to affect plant communities in mountain systems. Mountainous areas, like the rest of the globe, are receiving increased amounts of carbon dioxide and atmospheric nitrogen deposition, which increase plant growth (Körner 2003). It has been hypothesized that the combination of changing temperatures along with the changes in atmospheric chemistry will reduce many of the constraints which restrict the development of alpine plants, although the overall effects of these changes on the diversity of plant communities in mountain systems are unknown (Körner 2003).

Given the potential changes in land use, climate, and nutrient dynamics in mountainous areas discussed above, the potential for changes in the plant community that could result in a loss of diversity are a valid concern. However, the fact remains that the future trajectories of any of the changes discussed above are uncertain. As a result, no definite statements can be made about what will or will not happen to the diversity and composition of plant communities in mountain systems as a result of such changes. The possibility that these changes will have negative effects on plant diversity or community composition in mountainous areas is the primary motivation for the current research in this area. One way that these changes are seen to be a threat is through their potential to increase the future presence and abundance of non-native plant species in mountain systems. Although the future ecological impacts of non-native plant species in mountain systems is unknown, the current trends of abundance and population dynamics of non-



native plant species which are currently found in these areas may yield some helpful insights for the future.

### Non-native Plants in Mountain Systems

#### Trends in Richness and Abundance Along Elevation Gradients

Several studies have examined the patterns of non-native plant species richness and abundance along elevation gradients. In general, it has been found that non-native plant species richness tends to decrease at higher elevations, and that this trend is a global phenomenon (Alexander et al. 2011). This response has been observed in some cases to be somewhat linear (Becker et al. 2005; McDougall et al. 2005), and to be hump shaped in other cases (Tassin and Riviere 2003; Arevalo et al. 2005). One recent exception to this generality was found by Paiaro et al. (2011), who observed that non-native species richness increased at both ends of an elevation gradient in central Argentina.

Numerous reasons are given for the shapes of these trends. For the linear trend, increasingly harsh climatic conditions and decreasing human influence with increased elevation are cited as potential causes for the linear decline (Becker et al. 2005; McDougall et al. 2005). In relation to the hump shaped trend, environmental conditions (Tassin and Riviere 2003; Arevalo et al. 2005), anthropogenic factors such as disturbance (Tassin and Riviere 2003) and distance to the nearest urban center (Arevalo et al. 2005), and geometric effects which increase the probability of occurrence of plants in the center of a gradient (Tassin and Riviere 2003) are cited as potential causes. For the concave pattern, no real explanation was given, other than that perhaps the non-native species had

not had enough time to reach their potential altitudinal range limits (Paiaro et al. 2011). Thus far, the observed trends seem to be consistent within general geographical context, with temperate region mountain systems exhibiting linear trends and subtropical oceanic mountain systems exhibiting hump shaped trends (Pauchard et al. 2009; Seipel et al. 2012).

When considering individual non-native species, several studies have noted decreases in population size and/or fitness with elevation (Trtikova et al. 2010; Liang et al. 2008; Alexander et al. 2009; Monty and Mahy 2009), and at least one has noted increased success at higher elevations (Ansari and Daehler 2010). It is clear that both the trends in non-native species richness and in individual non-native species seem to be general, with a few exceptions. As stated by Alexander et al. (2011), non-native richness tends to decrease with elevation, even at the global scale. The other studies mentioned above suggest that this phenomenon is also apparent at the individual species level. As a result, a general theory of non-native plant community assembly, called directional ecological filtering, has been developed for mountain systems.

#### Directional Ecological Filtering as a Model for Non-Native Plant Community Assembly in Mountain Systems

The concept of ecological filtering has been put forth as an explanation for the assembly of both native (George and Bazzaz 1999; Mayfield et al. 2005; Lawes et al. 2010) and non-native (Godfree et al. 2004; Becker et al. 2005) plant communities. In general, the concept of ecological filtering implies that plant communities are structured by biotic or abiotic ecosystem “filters”, which exclude some species while allowing

others to establish (Myers and Harms 2009). Expanding upon this model, and applying it to the specific case of mountain systems, Alexander et al. (2011) outlined the concept of directional ecological filtering of non-native plants in mountain systems.

The model of directional ecological filtering as the driver of non-native plant community assembly in mountain systems operates based on one critical assumption. This assumption is that, in general, the non-native plant species which invade mountain systems are first introduced into lowland areas, and then migrate up-slope (Alexander et al. 2011). As such, these introduced species are not specifically pre-adapted to the alpine environment, but are perhaps broadly adapted enough to survive there (Alexander et al. 2011). Thus, Alexander et al. (2011) note that the resistance of high-elevation environments to invasion might not be due strictly to environmental factors, but perhaps also to the separation of these environments from lowland sources of introduced species by steep environmental gradients.

The upshot of this theory is that non-native plant communities in mountain systems are composed of nested sets of introduced species from the lowland pool (Alexander et al. 2011). As elevation increases, these nested sets become smaller and smaller, and the climatic tolerance of the species therein increases (Alexander et al. 2011). Thus, the filters operating under this theory are primarily abiotic, and as elevation increases, harsh climatic and environmental conditions filter out all but the most broadly tolerant species (Alexander et al. 2011). One testable hypothesis from this theory is that the most successful mountain invaders will tend to be climatic generalists, and will be found to have broad distributions along elevation gradients (Alexander et al. 2011).

### The Future of Non-Native Plant Species in Mountain Systems

The plant communities in mountainous areas of the world are facing an uncertain future. Climate change has the potential to alter the range of both native (Crimmins et al. 2009; Engler et al. 2009), and non-native (Becker et al. 2005; McDougall et al. 2005; Marini et al. 2009; Pauchard et al. 2009) plant species. In terms of non-native plants, it has been recognized that broad geographic ranges and climatic tolerances as well as characteristics which may facilitate rapid range shifts may lead to responses to climate change that differ from those of native plants (Hellmann et al. 2008). Hellmann et al. (2008) note that climate change may also cause some taxa that were previously invasive to diminish in impact while other formerly non-invasive species may become invasive. In addition, they state that the spread of currently invasive species is likely to follow changes in temperature or hydrologic constraints that may occur with climate change (Hellmann et al. 2008). Thus, in the context of mountain systems, there is some concern that changes in climate could potentially result in increased success of non-natives plants at higher elevations (McDougall et al. 2005; Crimmins et al. 2009).

In addition to climate change, the fate of non-native plants in mountain systems is also tied closely to patterns of intensifying human use and potential dispersal in these areas (Pauchard et al. 2009). It has been recognized that human land use in these areas is often correlated with the presence of non-native plant species (Tassin and Riviere 2003; Arevalo et al. 2005; Becker et al. 2005; McDougall et al. 2005; Pickering and Hill 2007; Liang et al. 2008; Arteaga et al. 2009). The increased use of mountainous areas by

humans is seen to have the potential to lead to increased dispersal and establishment of non-native species in mountainous areas (Pauchard et al. 2009; McDougall et al. 2011). Additionally, if humans begin to deliberately introduce species which are pre-adapted to the climatic conditions present in mountain ranges, this could drastically change the dynamics of plant species invasions in mountain systems (Alexander et al. 2011).

The exact nature, and thus the future consequences, of climate change are unclear. As a result, it will be difficult to determine exactly what the consequences of climate change will be for non-native plant species, and how managers will need to deal with these consequences (Hellmann et al. 2008). This is true especially for mountain systems, where areas previously not invaded by non-native plant species may become so. One way in which the consequences of climate change for non-native species may be examined is through the study of population dynamics of individual non-native species at their current elevation range limits. Investigations of the response of population demographic rates to environmental and climate variables can provide some insight into what might happen if these climatic or environmental conditions were to change. Additionally, observing seed production rates at range limits in conjunction with responses of the species to climatic variables can provide insight into whether or not the species is primarily dispersal limited as opposed to being limited by climate. Thus, it is important to know the exact nature of the limitation of a species within its current range in order to elucidate how that range may shift due to changes in climate and/or human mediated dispersal and establishment.

### Range Limits of Species

#### Factors That Limit the Range of Plant Species

There are three main areas of consideration used to assess exactly which factors limit the geographic range of a species (Gaston 2003). These are: 1) abiotic and biotic factors, 2), population dynamics, and 3) genetics (Gaston 2003). The abiotic and biotic factors are largely seen to be physical barriers, climatic conditions, or interactions with other species (Gaston 2003). These abiotic and biotic factors act upon populations of the species, thereby influencing the population dynamics of the species (Gaston 2003). Finally, as these populations are acted upon and population dynamics are influenced by these factors, the genetics of the population are responsible for the rate and magnitude of adaptation of the population, and thus also have an effect on the range limits of the species (Gaston 2003). While these factors operate on all species, plant species experience them in particular ways.

Since plants are not mobile and depend upon dispersal to expand in range, the only meaningful physical barriers are those that prevent the dispersal of seeds across the landscape. Since the dispersal adaptations of individual species vary, then the status of any given impediment as an actual barrier to dispersal varies depending on which species one is considering (Cousens et al. 2008). Thus, dispersal limitation is also seen as an important factor controlling plant community composition and structure (Primack and Miao 1992; Ehrlen and Eriksson 2000; Verheyen and Hermy 2001; Satterthwaite 2007; French et al. 2011).

Climatic conditions limit the range of a species when the conditions at range edges either kill individuals directly or limit their reproduction (Gaston 2003). Studies have been conducted modeling potential species distributions under climate change scenarios based on how the current climate relates to species distribution data (Iverson and Prasad 1998; Malcolm et al. 2002; Kriticos et al. 2003; Thomas et al. 2004; Thuiller 2004; Hannah et al. 2005; Thuiller et al. 2005; Gritti et al. 2006; Engler et al. 2009). While these studies are informative, they assume that species are set within a distinct climate envelope and will be unable to exist anywhere other than that same envelope in the future. Thus, as climate changes, these species will still be restricted to those envelopes, and ranges will need to change accordingly. In order to get a better idea of how climate affects the range of plant species, studies must seek to elucidate the associations between plant growth/reproductive parameters and climate variables (Gaston 2003). Studies of this type have been conducted, and associations have been found between various measures of plant growth and temperature (Grace and Norton 1990; Despland and Houle 1997; Chambers et al. 2007; Jakalaniemi 2011), precipitation levels (Mack and Pyke 1984; Tardif et al. 2006), soil water (Chambers et al. 2007), and duration (Ross et al. 2008) and depth (Griffith and Loik 2010) of snow cover.

Interactions with other plants may also limit the range of a plant species. The forms of negative interference which typically limit plant growth are competition, parasitism, and allelopathy (Radosevich et al. 1997). It is possible that the presence of one or any number of plant species at the range edges of the species in question could be interfering with the growth of that species in such a way as to limit its range. Plants, like

other types of organisms, may also be limited in their range by the presence of a necessary resource or the presence of organisms which consume them to the point where reproduction and/or growth is impossible (Gaston 2003)

The range of a plant species may also be limited through genetics. If there is a large source of propagules at some intermediate part of the range, where individuals are not adapted to conditions present at the edge of the range, a phenomenon known as genetic swamping may occur (Garcia-Ramos and Kirkpatrick 1997). When this occurs, the abundance of propagules from the poorly adapted part of the range will hamper the ability of peripheral populations to adapt to conditions present there (Garcia-Ramos and Kirkpatrick 1997), thereby limiting the range of the species (Gaston 2003; Becker et al. 2005). Another genetic problem at range margins is that populations are often small, and hence comprise less genetic variability (Gaston 2003). Studies have shown that genetic diversity tends to be lower in plant populations which are at the periphery of the range for the species (Jump et al. 2003; Arnaud-Haond et al. 2006; Eckstein et al. 2006; Liang et al. 2008). However, at least one study found no difference in genetic variation between peripheral and core populations (Mandak et al. 2005). No studies specifically testing for the presence of genetic swamping from core to peripheral plant populations were found.

#### Population Demographics at Range Limits

As stated previously, the ultimate manifestation of abiotic/biotic factors and genetic factors on plant populations at range margins will be evident in the population dynamics of that species (Gaston 2003). Ultimately, the growth rate of the population is



affected by such factors, and this is generally why the species experiences a limit to its range (Gaston 2003).

Small changes in population demographic rates are enough to cause abrupt range limits for species (Gaston 2003). In a review on the topic of range limits, Sexton et al. (2009) found that out of 321 empirical studies comparing populations at range centers to those at range limits, 64 examined vital rates such as fecundity, recruitment, or survival. A further 17 studies examined the population growth rate, or lambda, based on position within the range (Sexton et al. 2009). The results were mixed, with roughly half of the studies supporting the hypotheses that these parameters decline at range limits (Sexton et al. 2009). In a study of two species of Monkey flowers (*Mimulus cardinalis* and *Mimulus lewisii*), range limit populations were found to have decreased values of lambda as compared to core populations for *M. lewisii*, and increased values of lambda as compared to core populations for *M. cardinalis* (Angert 2006). Another study focusing on an endangered orchid found no difference in demographic rates between central and marginal populations of the species (Garcia et al. 2010). These findings suggest that the ways in which population demographic parameters change, and whether or not they change, in response to position within a species' range are not necessarily consistent between species. However, since the demographic rates of populations are closely tied to their future fate on the landscape, examining these rates at varying points in a species' range can yield insights about whether or not the current range of the species is likely to expand in the near future, or what factors may be most instrumental in population expansion. For example, a recent study examining demographic rates of *Artemisia*

*ordosica* found that populations of this species expand the fastest in the earliest stages of sand dune formation (Yu et al. 2011). Another study has found that a long-lived high mountain plant, *Silene ciliata*, may become endangered at the lower end of its current altitudinal range, based on the decrease in demographic rates observed for these marginal populations (Gimenez-Benavides et al. 2011). Thus, examining the demographic rates of a species across its range can provide valuable information relating to its future presence and abundance on the landscape.

### Examining the Population Dynamics of a Plant Species

#### Types of Models Used to Examine Population Dynamics of Plant Species

Demographic models are fundamental to the understanding of how populations of plants change over time based on rates of birth and death, and potentially dispersal (Radosevich et al. 1997). The two primary ways in which the fate of plant populations are modeled are through difference equations or matrix models (Radosevich et al. 1997; Watkinson 1997; Caswell 2001; Soetaert and Herman 2009). Difference equations project the growth of populations by relating the number of individuals in one time step to the number of individuals in the next time step via an equation which incorporates, at the minimum, reproductive rates and death rates (Watkinson 1997). These models can be made to accommodate plants with and without vegetative reproduction, and can also accommodate age or stage structure within the population (Radosevich et al. 1997). A more streamlined alternative to difference equations is the use of matrix models (Radosevich et al. 1997, Caswell 2001). This type of model calculates the number of

individuals in each distinct age group or stage based reproductive rates and on the probabilities that an individual will survive and remain in its current group or survive and transition to the next group (Watkinson 1997). These probabilities and rates are defined within a transition matrix, which is then multiplied by an age or stage vector (Watkinson 1997). The result is an age or stage vector representing the structure of the population at the next time step (Watkinson 1997). Both difference equations and matrix models are classified as discrete time models, where time is considered to jump from one generation to the next, and the process of population growth is not considered to be a continuous process (Soetaert and Herman 2009). Another type of population model which can be used for estimating population growth is called an integral projection model. A criticism of stage based models has been that if the stages are based on some continuous trait, such as size, arbitrarily grouping heterogeneous individuals into the same stage class can create error in the model, and that elasticities and sensitivities are affected by stage duration, which affects comparisons within and between species (Ellner and Rees 2006). This type of model replaces the population vector with a distribution function, and replaces the transition or projection matrix with a projection kernel (Ellner and Rees 2006). It should be noted that this type of model is only useful if there is evidence that demographic parameters such as survival and reproduction are dependent upon some continuous variable, such as size or weight, and if data related to that continuous variable are collected.

### Population Models and the Process of Invasion

One of the pieces of information that a population dynamics model yields is an estimate of lambda, or the growth rate of the population (Watkinson 1997). Lambda is often used to approximate the invasiveness of a species because positive population growth rates are necessary for establishment, and those species which have very high rates of population growth may be more likely to become invasive (Burns 2008).

Although few studies have compared the population growth rates of invasive and non-invasive congeners (Burns 2008), at least one study has found that lambda is higher for invasive than for non-invasive members of the same genus (Burns 2008). A review of several published matrix model studies of invasive and native species, Ramula et al.

(2008) found that, in general, non-native species tended to have higher rates of lambda than native species. Lambda has also been used in recent studies of invasive species to gauge the rate of population growth in different habitats (Meekins and McCarthy 2001; Koop and Horvitz 2005), areas of differing light intensity (Decocq et al. 2007), burned versus unburned areas (Jacquemyn et al. 2005), and urban versus prairie environments (Parker 2000). Thus, it is a useful tool for comparing the relative invasiveness of different populations of the same species in different environments (Ramula et al. 2008).

Population dynamics models are also useful for examining the process of invasion in that population demographic rates can be varied by a systematic proportion to determine which of those rates have the greatest proportional impact on overall population growth, or lambda, of the population (Dekroon et al. 1986). This is referred to as an elasticity analysis (Dekroon et al. 1986). Elasticity analyses have been employed

for comparisons between populations of a single species under different conditions (Parker 2000; Buckley et al. 2003; Emery and Gross 2005; Jacquemyn et al. 2005), and for comparisons between native and non-native congeners (Lambrecht-McDowell and Radosevich 2005).

In their review of several matrix model studies for both native and non-native species, Ramula et al. (2008) found that as overall lifespan increased, sensitivity of  $\lambda$  due to differences in survival rates increased while sensitivity of  $\lambda$  due to differences in growth and fecundity decreased. Ramula et al. (2008) found that simulated reductions in either survival, growth, or fecundity transitions for long-lived non-native plants generally did not produce population declines, whereas reductions in survival and growth combined or in survival and fecundity combined were more effective. For short-lived invaders, simulated reductions in growth or fecundity and all pairwise multiple reductions were sufficient to reduce population levels (Ramula et al. 2008). These findings lead to the conclusion that the control of short-lived invaders should focus on reducing growth or fecundity rather than survival, and that simultaneous reductions in growth and fecundity are required to reduce populations of long-lived invaders (Ramula et al. 2008).

The landscape across which non-native plant species spread is often not a homogenous one. As such, the response of population growth rates to those differences in the landscape is of interest. The comparative studies listed above often compared population growth rates between distinctly different areas (Parker 2000; Meekins and McCarthy 2001; Jacquemyn et al. 2005; Koop and Horvitz 2005; Decocq et al. 2007).

When considering how a particular species may advance within a particular area, the response of population demographic rates to some environmental gradient may be more useful. Studies of this type have been conducted for native plant species, and it has been found that positions along gradients across sand dune habitats (Keddy 1982), soil moisture levels (Diez 2007), and riparian areas (Yuko et al. 1999) affect demographic rates for the species studied. Consequently, knowledge of population dynamics along the gradient would be more broadly useful for management of the species than specific habitat information.

Studies have also been conducted for non-native species. For the non-native species *Bromus tectorum* in the United States, it has been found that gradients in growing season length (Pierson and Mack 1990), snow cover (Griffith and Loik 2010), and temperature and water availability (Chambers et al. 2007) all influence the demographic rates of this species. In addition, survival of the non-native species *Cenchrus ciliaris* was found to be related to a gradient of soil conditions in the United States (Ibarraf et al. 1995). These studies all deal with specific aspects of the demography of the species, but fail to use the data to produce models of population growth across these gradients. Studies have been successfully conducted which have used demographic data to create models and estimate lambda for species within a variety of habitats. For example, (Menges and Dolan 1998) estimated rates of population growth for the species *Silene regia* across a range of fire management strategies in an effort to determine how to manage and conserve this species in the United States. For the species *Silene ciliata* in Spain, estimates of lambda across the elevation range of this high mountain plant

indicated that it may be headed towards extinction at the lower elevation limit of its current range (Gimenez-Benavides et al. 2011). In addition, a recent study on the non-native plant *Syzygium jambos* in Puerto Rico used demographic models of the species to project rates of growth ( $\lambda$ ) of the species across a heterogeneous landscape in an effort to determine where this particular species was likely to be problematic for managers (Brown et al. 2008). Thus, population demographic models can be useful for determining the fate of a species, be it a native or a non-native, across a heterogeneous landscape.

Population growth rate studies can be useful in evaluating the fate of a species under future climate change scenarios. Evidence from several studies looking at the changes in plant species ranges over the past several decades have related these shifts to changes in climate (Klanderud and Birks 2003; Wilson et al. 2005; Kelly and Goulden 2008; Lenoir et al. 2008; Kimball et al. 2010; Kullman 2010; Lenoir et al. 2010). Experimental studies examining the potential effects of climate change on population growth rates as a way to determine the future fate of individual plant species have found that population growth may increase as a result of global warming (Carlsson and Callaghan 1994; Dullinger et al. 2004). These studies used models which were based on demographic data gathered for the species in question. Another approach that is often used is one in which the current distribution of species are matched to current climate conditions and then the future potential distributions of those species are projected based on predicted changes in climate, assuming that the species can only persist in their current climate envelope (Pearson and Dawson 2003). Several studies have used this

approach to examine the potential distribution of species under various climate change scenarios (Iverson and Prasad 1998; Malcolm et al. 2002; Kriticos et al. 2003; Thomas et al. 2004; Thuiller 2004; Hannah et al. 2005; Thuiller et al. 2005; Gritti et al. 2006; Engler et al. 2009). However, these types of models have met with criticism because other factors such as biotic interactions, adaptation, and dispersal which were not included in the studies also influence species ranges (Pearson and Dawson 2003). In response to these criticisms, studies have been conducted which have found that biotic interactions (Araujo and Luoto 2007; Brooker et al. 2007) and dispersal (Brooker et al. 2007; Engler et al. 2009) are influential in the predictions of these models. No studies on the effects of adding adaptive capacity to these models were found, perhaps because the influence of a plant species' ability to adapt to changing climate on its potential distribution is obvious. Regardless, it is clear that models based on current distributions alone may be insufficient to predict the future distributional changes of species as a result of climate change (Araujo and Luoto 2007). It has been suggested that species level studies are necessary to adequately determine the effects of climate change on plant species distributions, as demographic rates at range edges may not behave consistently among all species in the face of climate change (Doak and Morris 2010). Thus, studies which examine the demographic rates of individual species across a range of environmental conditions are valuable not only for describing what factors may be currently limiting the range of that species, but how the range of that species may shift in the future as a result of climate change.



Despite the large amount of interest in non-native plant species invasions, the preceding literature review should have conveyed the idea that there are still gaps in our knowledge of the subject. As mentioned in chapter 1, one such knowledge gap is present in the processes driving non-native plant invasions in mountain systems, and it is the goal of the subsequent chapters in this thesis to begin to fill in that gap.

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CHAPTER 3: THE INFLUENCE OF CLIMATIC AND ENVIRONMENTAL  
FACTORS ON THE DISTRIBUTION OF A NATIVE AND A NON-NATIVE  
PLANT SPECIES ALONG AN ELEVATION GRADIENT IN THE GREATER  
YELLOWSTONE ECOSYSTEM

Introduction

Non-native plant species have been the travelling companions of man-kind since we began to move across the landscape (Crosby 1986). However, one area where the introduction of non-native plant species is seen to be a recent phenomenon is in the mountainous areas of the world. Although, in some parts of the world, mountainous areas have been used for agricultural purposes for thousands of years (Körner 2004), the large scale influence of man in such areas has only recently become a concern (McDougall et al. 2009).

Recent interest in non-native species invasions in mountain systems is related to the fact that these systems currently have comparably low rates of invasion (Becker et al. 2005; Pauchard et al. 2009). Concerns about the potential effects of climate change and increased use by humans at higher elevations have added a level of urgency, as both of these factors are seen to have the potential to further increase the presence of non-native species in higher elevation areas (McDougall et al. 2005; Pauchard et al. 2009). Perhaps the greatest motivation behind the current interest is that it may be possible to prevent future invasions in these areas (Pauchard et al. 2009; Alexander et al. 2011).

Non-native plant species richness has been found to decrease with increasing elevation (Tassin and Riviere 2003; Arevalo et al. 2005; Becker et al. 2005; McDougall et al. 2005; Pauchard et al. 2009; Alexander et al. 2011; Siniscalco et al. 2011; Seipel et al. 2012). Alexander et al. (2011) have suggested that the decrease in non-native plant species richness results from a filtering of the lowland species pool, whereby species with narrow climatic tolerances are eliminated as elevation increases. This process, called directional ecological filtering, provides a useful framework for considering the dynamics of non-native plant invasions from a community assembly standpoint and serves as a valid explanation for the similarity in trends of non-native species richness along elevation gradients throughout the world (Alexander et al. 2011). However, the generalities of the process of invasion itself, whereby an individual species spreads outward from its point of introduction towards the limits of its potential range, are still relatively unknown in the context of mountain systems. Since biodiversity conservation is of interest in these areas, understanding factors affecting invasion at the individual species level is important, as this is the level at which most non-native plant management decisions are made. Thus, while concepts like directional ecological filtering potentially allow one to determine which species may be future invaders into mountain systems (Alexander et al. 2011), species specific information is also needed to fully understand the process of invasion from both scientific and management perspectives.

Knowledge of the factors currently limiting the range of an individual non-native plant species are of great importance when considering if and how to apply management to prevent further spread of the species. Climate may have a direct influence on range

limits through mortality and growth of individuals, or it could be affecting other vital rates such as seed production or viability (Gaston 2003). Additionally, a species may not be able to respond adaptively to differences in environmental variables along an elevation gradient due to genetic swamping (Gaston 2003; Becker et al. 2005). Dispersal may be limited due to lack of a dispersal vector, some physical barrier, or a general lack of seeds (propagule pressure) (Cousens et al. 2008). Thus, determining what limits the current range of a species is a complex endeavor. However, in order to gauge the potential present and future impacts of climate and dispersal on the management of the species, detailed investigations may be necessary.

Some studies of individual non-native species along elevation gradients have been conducted previously, and have varied in focus. While several of these studies have found trends in target species density (Trtikova et al. 2010; Liang et al. 2008; Alexander et al. 2009; Monty and Mahy 2009), and genetic composition (Liang et al. 2008), few have included fine scale climate data or information on survival from outside of the current introduced range. In order to improve our understanding of how climate affects the range of plant species, studies must seek to elucidate the associations between plant growth/reproductive parameters and climate variables (Gaston 2003). In addition, such studies could also help to address context specific management concerns.

The main objective of this study was to provide a detailed investigation of potential factors affecting the range limits for the species *Linaria dalmatica* (L.) Mill along an elevation gradient within the Greater Yellowstone Ecosystem (GYE). *L. dalmatica* is a relative newcomer to this area, having been introduced around 1947 (Roy

Rankin, *pers comm*). At present, this large meta-population seems to be isolated from other sources of the plant, such that the current distribution of *L. dalmatica* in the area is a result of spread from one known site of introduction. A closely related native species, *Castilleja miniata* (Douglas ex Hook.), was also selected for observation along the same elevation gradient so that a qualitative comparison for a native/non-native pair of species could be made. These two species only overlap slightly on the elevation gradient within the study area: *L. dalmatica* populations occur up to ~2,300 m, and *C. miniata* occurs from ~2,200 m up to 2,800 m. Our general hypothesis was that the current upper range limits of both species are limited by climate and/or environmental (including biotic and abiotic components) factors, and not propagule pressure. As such, we hypothesized that: 1) the stem density of both species would decrease at the upper range limits 2) models including climate and environmental variables would perform better than models containing only elevation when describing trends in the stem density of each species, and 3) overall reproductive output of each species per plot would not decrease with elevation. We only tested seedling survival rates outside of current range limits for the non-native *L. dalmatica*, and hypothesized that 4) seedling survival would decrease outside of the current elevation range limits for this species.

## Materials and Methods

### Study Area and Site Selection

This study was conducted along an elevation gradient within the GYE in the vicinity of Gardiner, MT, 45°01'60" N, 110°42'33" W, 1,598 m elevation. Three

networks of linked roads were chosen as transects in the area, and will henceforth be referred to as elevation transects. In general, each of these transects proceeded from elevations near the bottom of the Yellowstone River Valley in Gardiner, MT to elevations just short of the highest elevation extent for the specific peak, but represent the highest point of road access (2,900 m for transect 1, 2400 m for transect 2, and 2200 m for transect 3). See figure E-1 for map of study area.

During July and August of 2008, the three elevation transects were surveyed for the presence of *L. dalmatica* and *C. miniata*, both hereafter referred to collectively as the test species. During initial surveys, an effort was made to identify every distinct population of the test species present within 5 to ~200 m of the elevation transects (roads) from their lowest elevations up to the highest extent that was navigable in a vehicle. Each population's center was marked with a Global Positioning System (GPS, Trimble GeoXT 2008 Series), and if multiple discrete patches were present at a site, the boundaries of these patches were also mapped by walking the perimeter. Study sites were selected from the pool of sites to represent a relatively even spread of elevations along each elevation transect.

For *L. dalmatica*, six sites were established on each one of the three elevation transects. For *C. miniata*, five sites were selected on elevation transects one and three, and four on elevation transects two. Fewer sites per elevation transect were possible for *C. miniata* due to lower frequency of occurrence along the elevation transects. During August of 2008, ten 1 m<sup>2</sup> monitoring plots were established at each one of the study sites.



Each plot was marked and its position recorded with a GPS. At each site, plots were placed randomly in areas where the test species was present.

### Test Species Measurements

Stem density of the test species was measured within each 1 m<sup>2</sup> plot at every site. These measurements were taken during mid to late August each season from 2008-2011. At each set of plot markers, a 1 m<sup>2</sup> frame was placed on the ground and the number of stems within the frame was counted. Stems were counted as flowering, vegetative, or grazed. For *L. dalmatica* and *C. miniata*, stems were counted as separate stems if they diverged from a common point at the ground (root crown) or were truly isolated stems. Stems which branched off of a main stem above the ground were not counted as separate.

To estimate the reproductive output of *L. dalmatica*, the number of seed capsules present within each plot at each site was counted during late August of each field season. For more precise information on the amount of seed produced per seed capsule, additional sampling took place from July through September 2009 at four sites along each elevation transect. Forty-five capsules were collected from plants outside of the monitoring plots at each site. Since capsule size appeared to be variable based on stem position, fifteen seed capsules were collected from each of the lowest, middle, and highest regions of the stems, with no more than one capsule being collected from a given stem. Capsules were then dried at constant temperature (43° C) and seeds within were counted. To test for germination, extra seeds were collected from each of the sites in 2008. Four batches of 50 seeds per site were placed into plastic containers containing blotting paper which was wetted with distilled water. These containers were placed in a

germination chamber at 15° C alternating 12 hours light/12 hours dark and germination was monitored weekly for 5 weeks. These conditions were chosen based on the work of Robocker (1970) which noted that the highest level of germination occurred under temperature conditions of 15-20° C.

In order to account for the fact that not all of the capsules counted in late August may have contained viable seeds, a late season survey of seed capsules was conducted to determine what proportion of seed capsules were mature and contained viable seeds at the end of the growing season in late September of 2010. At the same sites from which seed was collected in 2009, ten stems were randomly selected for surveying. On each stem, the number of capsules which were open and the number that were closed were recorded. Additionally, 20 closed capsules were collected from outside the study plots at each site. The closed capsules were put in cold dry storage for 3 months. Each capsule was then opened and the contents were rated as either immature or mature based on color (black = mature, and brown, tan, green, or grey = immature).

Reproductive output for *C. miniata* was estimated more coarsely based on the number of flowering heads present within plots at each site, as measured during stem density counts. Individual seed capsules were not counted because it was extremely difficult to count the number of capsules on any given flowering head without causing extensive damage to it. An estimate of actual seed production was achieved by randomly harvesting 10 flowering heads from outside of the monitoring plots at each of the *C. miniata* sites in the late summer of 2009. These flowering heads were dried at constant temperature (43° C) for several weeks and then dissected such that for each seed capsule,

the number of seeds could be counted. Seed production for both species was estimated for 2010 and 2011 based on data collected from 2009. Thus, the results for the germinable and raw seed production should be treated with caution for 2010 and 2011, as it is conceivable that seed production and initial germination rates could vary from year to year.

Since few seedlings of *L. dalmatica* were observed during the initial years of the study, a study was conducted for this species to assess 1) seedling survival as it would result from natural events, and 2) the ability of seedlings grown from seed from the lowest elevation sites to survive at higher elevations along the elevation gradient. During the spring and summer of 2011, seedlings were placed at five sites along each of the two elevation transects outside of Yellowstone National Park. Three of these sites were within the current range of *L. dalmatica*, with the remaining two sites being above and below the current elevation range of the species. Seedlings used for each site were grown from seeds collected at the same site during fall 2010 which were then stored in cold, dry storage at 4° C. Seeds for the sites outside of the current range were from the nearest site along the gradient. To assess survival of seedlings from the lowest sites at higher elevations, seedlings grown from seeds from the lowest site were also planted at the highest sites (within and just above the current range of *L. dalmatica*) along the elevation gradient. Seedlings were transplanted in 8 cm round pots filled with potting soil (equal parts sand, loam, and peat). From our data and Robocker (1970), it was determined that 55 growing degree days using 10° C as the base temperature were sufficient for the germination of *L. dalmatica*. Five pots of five seedlings were thus placed at a given site

on the date at which that site had accumulated 55 growing degree days the previous year, as we did not have access to site specific current season temperatures. Seedlings were started in a greenhouse (18° C) at staggered dates such that seedlings were all in the cotyledon stage when they were planted at each of the different sites. Seedlings were subjected to rapid acclimatization to ambient conditions over a period of 24 hours. Seedlings were monitored weekly after planting until early September to quantify seedling survival rates along the elevation transects. All pots were protected with a wire mesh cage (0.63 cm grid size) to prevent larger herbivores from eating seedlings and were removed after the final survey to prevent new populations from establishing.

#### Measurement of Climate and Environmental Variables

Temperature was measured hourly at each site using one Lascar EL-USB 1 temperature data logger (temperature logger). Temperature loggers were placed within protective wire mesh cages (0.63 cm grid size) prior to placement. These cages were then secured to the North side of existing vegetation at a height of approximately 0.5 m from the ground surface to capture the hourly air temperature at the average height of the herbaceous/shrubby vegetation, and to avoid the influence of radiant heat from the ground during the summer months. To avoid the loss of any temperature probes, the cages were also secured to a metal anchor in the ground via a metal cable. Temperature probes were placed in the field in late June of 2009 and removed in early September of 2011. Thus, growing season (early June to early September) temperature data was collected for 2010 and 2011, and winter data for 2009 and 2010.

Soil moisture was measured at each site using three randomly placed Delmhorst gypsum blocks. Gypsum blocks were placed at a depth of 15 cm in the ground following the procedure described in Aho and Weaver (2008). Gypsum blocks were monitored weekly and the moisture level was recorded with a Delmhorst KS-D1 meter from June to late September of 2010 and 2011. The gypsum blocks were left in the ground over the winter of 2010/2011. The readings taken from the gypsum blocks were converted to water potential (MPa) following (Aho and Weaver 2008).

Rain gauges (Taylor Pro-Gauge) were placed at each site in early June of 2010 and again in early June of 2011. Rain gauges were removed in mid-September to avoid damage caused by freezing. Each gauge was placed within a bracket and mounted to a 1 m wooden stake which had been pounded into the ground in an area with open canopy. Upon placement, 3 ml of machine oil was placed in each rain gauge to prevent evaporation of precipitation between survey times. Throughout the growing seasons of 2010 and 2011, rain gauges were monitored weekly and the amount of precipitation was recorded.

Canopy cover was measured at each site using a spherical densiometer at four random locations at each site. Percent of bare ground, litter, and vegetation cover were estimated by randomly selecting six out of the ten 1 m<sup>2</sup> vegetation monitoring plots at each site. A ¼ m<sup>2</sup> frame was centered within each plot and the percent of bare ground (including rock cover), litter (including moss and lichens), and vegetation cover were estimated by a single observer. Ten soil samples were taken to a depth of 10cm (approximately 285 cm<sup>3</sup>) from random locations at each site. These ten samples were

then thoroughly mixed together. Sub-samples were stored 4° C until the time that they were analyzed for pH, organic matter, nitrogen, and phosphorous content.

### Data Analysis

#### Climate Variables along the Elevation Gradient

All analyses were performed in R version 2.14.1 (R-Development-Core-Team 2011). The relationship of each of the measured climate variables (number of weeks until the permanent wilting point was reached [weeks to wilt], growing season mean minimum temperature, growing season absolute minimum temperature [lowest measured temperature], number of growing season frost free days, growing degree days[base 10° C], growing season precipitation, winter mean minimum temperature, winter absolute minimum temperature, number of winter days at or below zero) to elevation was examined for the entire length of the surveyed elevation gradient. Although the elevation gradient contained plots which were purposefully placed in areas where there was either *L. dalmatica* or *C. miniata*, neither the temperature related variables nor precipitation should have been locally influenced by any characteristics of the site related to whether it was occupied by *L. dalmatica* or *C. miniata*. Initial models regressed each climate variable against elevation, year (pooled), type of site (containing *L. dalmatica* or *C. miniata*) and the interaction between elevation and year. When interactions between elevation and year were found, data were analyzed for each year separately. If type of site was significant, the climate variable was only analyzed within the different species' elevation ranges. All climate data were then also analyzed strictly within the elevation

ranges of each test species. For all models, residuals were assessed for normality. The only variables for which model residuals were found to be non-normal were growing season frost free days and weeks to wilt. Poisson generalized linear models (GLMs) were used to address this issue.

#### Environmental Variables along the Elevation gradient

Environmental variables included biotic (percent canopy closure, percent bare ground, percent litter cover, and percent vegetation cover) and abiotic (soil nitrogen, soil pH, soil phosphorous, and soil organic matter) components. As these variables were suspected to be closely related to the type of site, they were only analyzed within the different species' elevation ranges. Environmental variables were only measured once, so there were not multiple years of data. Initial models for all environmental variables regressed the variable against elevation and its second order polynomial. If no polynomial relationship was detected, the final model was a linear regression with elevation as the sole predictor variable. The residuals of all models were assessed for normality. The only variable for which the residuals were non-normal was soil nitrogen. Soil nitrogen was natural log transformed to successfully address this issue.

#### Density of Test Species in Response to Elevation, Climate, and Environment

Observations of stem density were made for all four years of the study. Preliminary analyses indicated that year had significant effects on the shape of the relationship between stem density and elevation for both species, so years were analyzed

separately. Patterns of stem density with elevation were analyzed for each year using generalized linear mixed effects models (GLMERs) with elevation as a fixed effect and site and patch (if multiple patches were present) as random effects due to the nested structure of the data. Elevation transect was investigated as another potential random effect, but was found to be insignificant. For each year, two candidate models were compared using a chi square test: one with elevation as the only predictor and one with elevation and its second order polynomial as predictors.

Preliminary analyses of *L. dalmatica* data indicated that for the last two years of the stem density data collection (the only two years for which there was corresponding climate data), only the 2011 data showed a significant trend in stem density (Appendix B, tables 1-8). As the primary interest was in how the potential predictor variables related to the current patterns of density for *L. dalmatica*, only data from the last survey of the study (2011) was used. For the analysis of the effects of climate and environmental variables on stem density of both species, a model selection procedure was employed. Analysis of the climate variables along the elevation gradient suggested that snow cover may have been influential. This variable was not measured, and was thus not included in the previous analyses. However, although it was not measured, we estimated days of deep snow cover ( $\geq 0.5$  m) for the purposes of this analysis from September 1 to June 1 (pre-season) by totaling the number of days where the minimum and maximum temperatures were both within  $1^\circ$  C of zero. We also estimated days of snow cover from June 2 to August 31 (growing season) the same way. There was no growing season snow cover for *L. dalmatica*, but two *C. miniata* sites had growing season snow days. To



define a framework for the initial full model, the main hypothesis was that pre-season snow cover, abiotic environmental variables (soil nutrient levels), and growing season climate variables would account for variation in stem density, such that models including these variables (collectively referred to as primary variables) would perform better than the null model containing only elevation as a predictor variable, using Bayesian Information Criterion values (BIC) as a measure of model performance. The BIC was chosen due to its tendency to reject models that over-fit in favor of more simple models (Burnham and Anderson 2004; Sullivan and Joyce 2005). A secondary hypothesis was that adding winter climate variables, season snow cover (for the native species *C. miniata*), and biotic environmental variables to the model would not improve BIC values. This was based on the concept that insulating pre-season snow cover, growing season climate, and resource levels would be the primary determinants of current season success for the test species, and that winter climate and biotic environmental factors might only have a secondary influence.

Initial correlations between and scatter plots for stem density and all of the potential soil, environmental, and climate variables were examined to determine 1) potential primary predictor variables to use in building a full model for each species and 2) the shape of their relationship with stem density. All primary variables with a correlation  $\geq 0.1$  with stem density were added to the full model. The number of GDD was not added to the full model as it was based on and thus highly correlated with other growing season temperature variables. The full model was then iteratively trimmed down manually. After the model had been trimmed, winter temperature variables, growing season snow

cover (for *C. miniata* only), and environmental variables were added individually if they had a correlation  $\geq 0.1$  in order of the magnitude of the correlation with stem density (largest first) to address the secondary hypothesis above. Highly correlated variables were tried individually. If any variable decreased the BIC, it was retained in the model and the addition of individual variables was continued.

#### Sexual Reproductive Output of the Test Species along the Elevation Gradient

For both *L. dalmatica* and *C. miniata*, the rate of seed production per seed capsule was analyzed using the mean rate from each site as the response variable. This was only regressed against elevation. Data on seed production per capsule for both species were only collected in 2009, and initial germination rate data for *L. dalmatica* were only collected for 2008 seed. Thus, for 2010 and 2011, the number of germinable seed for *L. dalmatica*, and raw seed data for both species were estimated using rates that were not from the current year. Since we did not have complete climate data from 2009, we did not model the relationship between climate and seed production for 2009. Models were attempted for 2010 and 2011 using estimated seed values. Results from these models were highly inconsistent and the BIC values (up to 100,000) indicated that the models were poor. As such, they are not included in the results. However, stem density is positively correlated with seed production for both species (data not shown), and one can infer that climatic factors have somewhat equivalent effects on stem density and overall seed production.

There was no evidence that the relationship between seed production and elevation required the addition of the second order polynomial term for elevation for either species. Estimates of total and germinable seed production were derived for *L. dalmatica* for each plot by multiplying the number of seed capsules by the average rate of seed production per capsule (to derive total seed production) and then by the germination rate for seeds from each site (to derive germinable seed production). It should be noted that for *L. dalmatica*, data on the maturity of seed capsules collected as described in the methods section were then used to adjust the seed capsule counts and account for the fact that not all capsules mature by the end of the growing season. For *C. miniata*, only total seed production was derived since no data were collected on germination rates. These response variables were then regressed against elevation (and its second order polynomial term for *L. dalmatica* germinable seed) separately for 2009, 2010, and 2011. Residuals from all models were assessed for normality and constant variance. Raw seed production for *C. miniata* was natural log transformed to meet the assumptions of the analysis.

#### Seedling Survival for *Linaria dalmatica*

Seedling survival data were analyzed using a binomial GLM with the number of seedlings out of the total planted which survived until the end of the trial (September) as the response variable. Since growing season climate data were collected during the same season as this experiment, these data were available as predictor variables in addition to elevation. Preliminary analysis indicated that the relationships between seedling survival and both elevation and growing season climate variables were linear, and did not require the addition of the 2<sup>nd</sup> order polynomial terms. For each site where seedlings survived,

an ANOVA was performed with the number of surviving seedlings as the response variable and the seed source (from the site or from the lowest site) as the predictor variable. This analysis was performed to determine if there was any difference in survival rate of seedlings based on the seed source.

## Results

### Climate Variables along the Elevation gradient

When examining the entire span of the surveyed elevation gradient, several of the climate variables were found to have significant trends. In initial models, type of plot (*C. miniata* or *L. dalmatica*) was not found to have a significant effect. Year was found to have significant interactions with elevation for growing season absolute minimum temperature and growing season precipitation. Thus, these two variables were modeled separately for each year, while all other variables were modeled with data from both years combined.

For the growing season climate variables, increased elevation was negatively associated with growing season mean minimum temperature ( $p < 0.01$ , Table 2-1, Figure B-1). Growing season absolute minimum temperature was negatively associated with increased elevation in 2010 ( $p < 0.01$ ) but had no association in 2011 (Table 2-1). Number of growing season frost free days and the number of growing degree days were found to be negatively associated with increased elevation ( $p < 0.01$ , Table 2-1). Growing season precipitation was positively associated with increased elevation in both 2010 and 2011 ( $p < 0.01$ ), but the slope of the model was lower in 2011 (Table 2-1,

Figure B-1). The number of winter frost days, where the temperature was found to be at or below zero, was positively associated with increased elevation ( $p < 0.01$ , Table 2-1).

Table 3-1. Results of individual regressions of climate variables against elevation for entire length of surveyed elevation gradient (Entire Range), and the *L. dalmatica* and *C. miniata* sections of the elevational ranges. NA= not applicable, \* = model fit as Poisson GLM. R<sup>2</sup> values only shown for significant models. Gs = growing season, Precip = precipitation, Abs. Min. = absolute minimum temperature, Mean Min. = mean minimum temperature, c = data from years combined.

Climate Variable	Entire Range				<i>L. dalmatica</i> Range				<i>C. miniata</i> Range			
	b <sub>1</sub> est.	n	p-value	r <sup>2</sup>	b <sub>1</sub> est.	n	p-value	r <sup>2</sup>	b <sub>1</sub> est.	n	p-value	r <sup>2</sup>
Gs Weeks to Wilt <sup>c</sup>	NA	NA	NA	NA	0.7e-3	36	0.08	*	-0.2e-3	26	0.44	*
Gs Mean Min <sup>c</sup>	-0.3e-2	57	<0.001	0.28	-0.5e-2	34	<0.001	0.35	0.1e-2	23	0.36	-
Gs Abs. Min. <sup>c</sup>	NA	NA	NA	NA	-0.4e-2	34	<0.01	0.24	NA	NA	NA	NA
Gs Abs. Min. 2010	-0.4e-2	27	<0.001	0.5	NA	NA	NA	NA	-0.2e-2	11	0.11	0.18
Gs Abs. Min. 2011	-0.8e-3	30	0.509	-	NA	NA	NA	NA	0.5e-2	12	0.03	0.37
Gs Precip. <sup>c</sup>	NA	NA	NA	NA	0.4e-2	34	0.14	-	NA	NA	NA	NA
Gs Precip. 2010	0.01	26	<0.001	0.37	NA	NA	NA	NA	0.6e-1	8	<0.001	0.89
Gs Precip. 2011	0.6e-2	25	<0.001	0.48	NA	NA	NA	NA	0.5e-2	9	0.29	-
Gs Frost Free Days <sup>c</sup>	-0.2e-3	57	<0.001	*	-0.1e-3	34	0.24	-	-0.2e-3	23	0.04	*
Growing Degree Days <sup>c</sup>	-0.76	48	<0.001	0.48	-0.6	28	<0.01	0.28	-0.30	20	0.18	-
Winter Mean Min. <sup>c</sup>	0.5e-3	54	0.701	-	NA	NA	NA	NA	0.4e-2	24	0.17	-
Winter Mean Min. 2009	NA	NA	NA	NA	-0.4e-2	16	<0.01	0.35	NA	NA	NA	NA
Winter Mean Min. 2010	NA	NA	NA	NA	0.4e-2	14	0.11	0.13	NA	NA	NA	NA
Winter Abs. Min. <sup>c</sup>	0.4e-2	54	0.273	-	NA	NA	NA	NA	0.5e-2	24	0.49	-
Winter Abs. Min. 2009	NA	NA	NA	NA	-0.4e-2	16	0.06	0.17	NA	NA	NA	NA
Winter Abs. Min. 2010	NA	NA	NA	NA	0.2e-1	14	0.03	0.27	NA	NA	NA	NA
Winter Frost Days <sup>c</sup>	0.4e-1	54	<0.001	0.28	0.6e-1	30	<0.001	0.44	0.3e-2	24	0.87	-

When examining the climate variables on the section of the elevation gradient where *L. dalmatica* was present, growing season mean minimum and absolute minimum temperatures, and number of growing degree days were all found to be negatively associated with increased elevation ( $p < 0.01$ , Table 2-11, Figure B-2), while weeks to wilt had a weak positive association with increased elevation ( $p = 0.076$ , Table 2-1, Figure B-2).

Winter mean minimum temperature was negatively associated with increased elevation in 2009 ( $p < 0.01$ ), but had a weak/insignificant positive association with increased elevation ( $p = 0.11$ ) in 2010 (Table 2-1, Figure 2-1). Similarly, absolute minimum temperature was found to be negatively associated with increased elevation in 2009 ( $p = 0.06$ ) and positively associated with increased elevation ( $p = 0.03$ ) in 2010 (Table 2-1, Figure 2-1). The number of winter frost days was positively associated with increased elevation ( $p < 0.01$ , Table 2-1, Figure 2-1).

When examining the climate variables on the section of the elevation gradient where *C. miniata* was present, growing season absolute minimum temperature had a weak positive association with increased elevation in 2010 ( $p = 0.11$ ) and a positive association ( $p = 0.03$ ) in 2011 (Table 2-1, Figure 2-2). Growing season precipitation was positively associated with increased elevation in 2010 ( $p < 0.01$ ), but showed no association with increased elevation in 2011 (Table 2-1, Figure 2-4). The number of growing season frost free days was negatively associated with increased elevation ( $p < 0.05$ , Table 2-1, Figure 2-2). None of the winter temperature variables had any association with elevation.

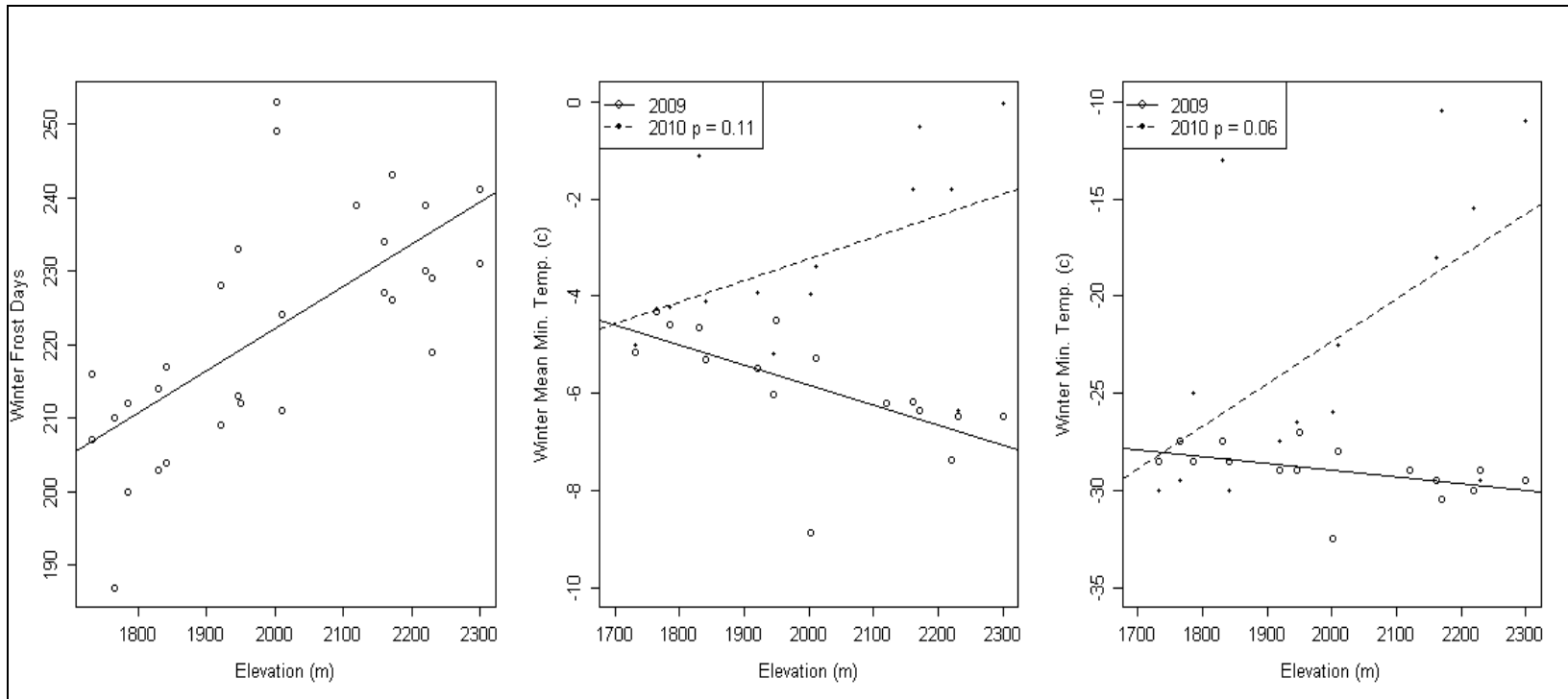


Figure 3-1. Significant relationships of winter response variables versus elevation for the *L. dalmatica* elevation gradient. All relationships significant at  $p \leq 0.05$  unless labeled otherwise.  $n = 54$  (winter frost days), 16 (winter mean and absolute minimum temperature 2009), and 14 (winter mean and absolute minimum temperature 2010).



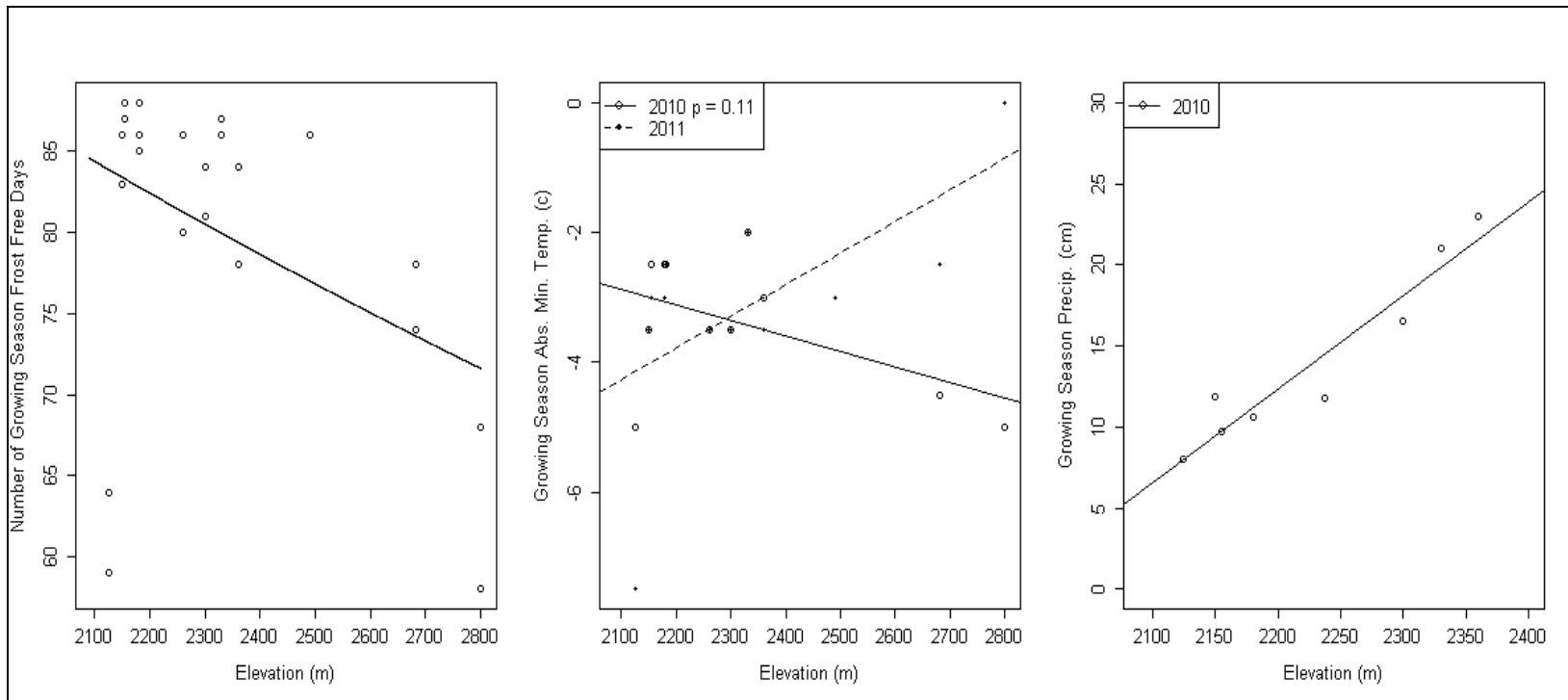


Figure 3-2. Significant relationships of growing season response variables versus elevation for the *C. miniata* elevation gradient. All relationships significant at  $p \leq 0.05$  unless labeled otherwise.  $n = 23$  (growing season frost free days), 11 (growing season absolute minimum temperature 2010), 12 (growing season absolute minimum temperature 2011), and 8 (growing season precipitation 2010).

### Environmental Variables along the Elevation Gradient

Environmental variables were only analyzed within each of the individual species' elevation gradients. For the *L. dalmatica* elevation gradient, percent litter cover showed a convex relationship with increased elevation ( $p < 0.05$ ), and percent canopy closure was positively associated ( $p = 0.05$ ) with increased elevation (Table 2-2, Figure B-3). Soil pH was negatively associated with increased elevation ( $p = 0.06$ , Table 2-2, Figure B-3). Soil Phosphorous was positively associated with increased elevation ( $p < 0.05$ , Table 2-2, Figure B-3).

For the *C. miniata* elevation gradient, Percent vegetation cover was negatively associated ( $p < 0.05$ ) with increased elevation, and soil phosphorous and percent bare ground were both positively associated with increased elevation ( $p < 0.01$ , Table 2-3, Figure B-4). Soil percent organic matter had a weak negative association with increased elevation ( $p = 0.1$ , Table 2-3, Figure B-4).

Table 3-2. Results of individual regressions of environmental variables against elevation for *L. dalmatica* elevation gradient.  $R^2$  values only shown for significant models.  $n = 18$  for all regressions. Std. err. = Standard error

Environmental Variable	Est. $b_1$	Std. err.	p-value	$r^2$
Soil pH	-0.00067	-2.031	0.0592	0.15
Soil % Organic Matter	5.37E-05	2.52E-03	0.983	-
log(Soil Nitrogen)	0.00015	0.000721	0.838	-
Soil Phosphorous	0.017091	0.007139	0.0293	0.22
% Bare Ground	-0.00928	0.022139	0.681	-
% Litter Cover	6.07E-01	2.19E-01	0.0143	-
+(% Litter Cover <sup>2</sup> )	-1.53E-04	5.44E-05	0.0131	0.3
% Vegetation Cover	0.02117	0.01744	0.242	-
% Canopy Closure	0.02595	0.0123	0.0511	0.17

Table 3-3 Results of individual regressions of environmental variables against elevation for *C. miniata* elevation gradient.  $R^2$  values only shown for significant models.  $n= 18$  for all regressions. Std. err. = Standard error

Environmental Variable	Est. $b_1$	Std. err.	p-value	$r^2$
Soil pH	-0.00048	-0.972	0.35	-
Soil % Organic Matter	-0.01676	-1.772	0.1018	0.14
log(Soil Nitrogen)	0.000332	0.211	0.836	-
Soil Phosphorous	0.02999	1.96	0.0736	0.18
% Bare Ground	0.038566	5.744	9.26E-05	0.71
% Litter Cover	0.0254	1.593	0.137	-
% Vegetation Cover	-0.081	-2.73	0.01825	0.33
% Canopy Closure	-0.02953	-0.965	0.354	-

Density of *L. dalmatica* in Response to Elevation, Climate, and Environmental Variables

For 2008 and 2009, the relationship between elevation and *L. dalmatica* stem density was better described by elevation and its second order polynomial term than by elevation alone (Figure 2-3, Table 2-4 and Tables B1-B4). In 2010, there was no significant relationship between stem density and either elevation alone or elevation and its 2<sup>nd</sup> order polynomial term (Figure 2-3, and Tables B-5 and B-6). In 2011, the polynomial term was not significant, so the relationship between stem density and elevation was better described by elevation alone (Figure 2-3, and Tables B-7 and B- 8).

For the 2011 data, the addition of growing season climate variables and abiotic environmental variables to the elevation only model improved the BIC Score, and this score was further improved by trimming down the models (Table B-15). Adding winter climate and biotic environmental variables to the model did not improve BIC scores (Table B-15). The model with the lowest BIC score contained elevation, the number of days of pre-season snow cover, the number of growing season frost free days, and

growing season precipitation as predictor variables of *L. dalmatica* stem density (Table 2-5).

Table 3-4. Results of comparisons between *L. dalmatica* stem density along the elevation gradient as a polynomial or linear predictor. Df = Degrees of freedom,  $\Delta$ BIC = Bayesian Information Criterion value compared to linear model, logLik=log likelihood, Chisq = chi-square value. n= 180 for all regressions except 2009 where n = 179.

Model/Year	Df	$\Delta$ BIC	logLik	Chisq	p-value
linear/2008	5	--	-470.77		
polynomial/2008	4	-1	-467.45	6.64	<0.01
linear/2009	5	--	-591.69		
polynomial/2009	4	-1	-589.47	4.45	0.04
linear/2010	5	--	-253.42		
polynomial/2010	4	5	-253.33	0.18	0.67
linear/2011	5	--	-657.09		
polynomial/2011	4	5	-656.99	0.22	0.64

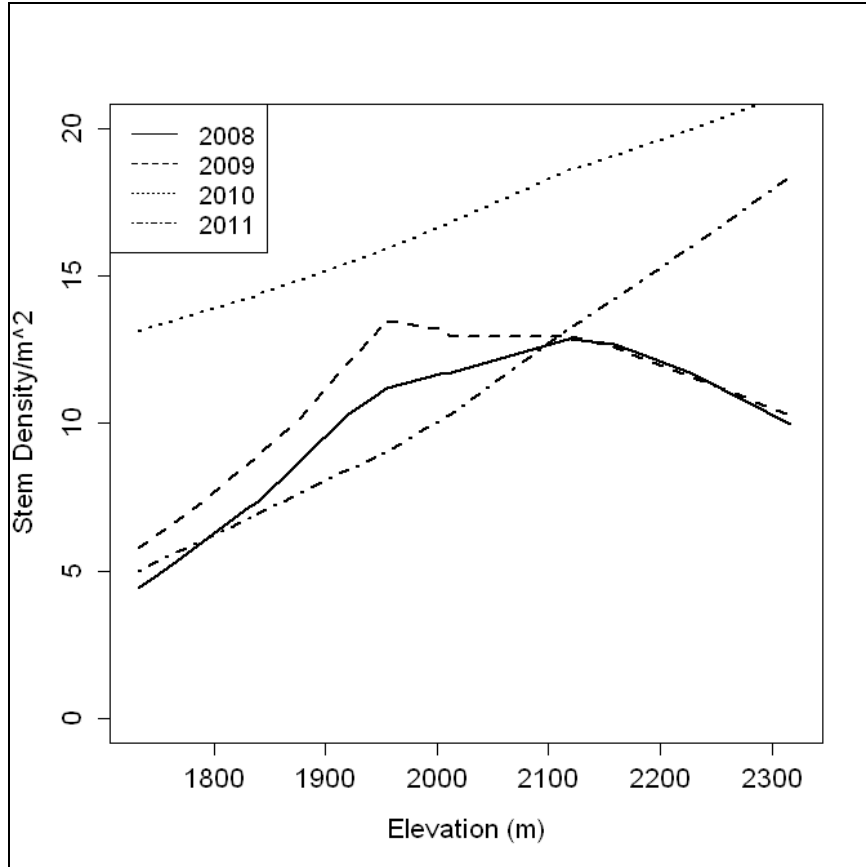


Figure 3-3 Relationship between stem density of *L. dalmatica* and elevation separated by year.

Table 3-5. Fixed effects output from best ranked generalized linear mixed effects model of the variation in *L. dalmatica* stem density in 2011. gs = growing season, frostfree = frost free days (minimum temperature >0° C), snow\_days = estimated number of days of snow cover from September to June, precip = precipitation. n = 110. Std. err. = Standard error, z = z-score.

	Estimate	Std. err.	z	p-value
(Intercept)	13.77	1.74	7.9	<0.001
poly(elevation,1)	7.07	2.96	2.4	0.02
snow_days	0.003	0.003	1.0	0.31
gs_frostfree	-0.12	0.02	-7.8	<0.001
gs_precip	-0.21	0.13	-1.6	0.10

#### Density of *C. miniata* in Response to Elevation, Climate, and Environmental Variables

For 2009, the relationship between elevation and *C. miniata* stem density was better described by elevation and its second order polynomial term than by elevation alone (Figure 2-5, Table 2-6 and Tables B-9 and B-10). In both 2010 and 2011, the relationship between elevation and *C. miniata* stem density was better described by elevation alone as a linear predictor (Fig 2-5, Table 2-6 and Tables B-11 – B-14).

The addition of growing season climate variables and abiotic environmental variables to the elevation only model for the 2011 data improved the BIC score, and this score was further improved by trimming down the models (Table B-16). Growing season snow cover had a correlation of 0.03 with stem density, and was not added to the model. Adding winter climate variables to the model resulted in a lower BIC score, but biotic environmental variables did not further improve the BIC score (Table B-16). The model with the lowest BIC score contained elevation, the number of days of pre-season snow cover, average growing season precipitation, soil nitrogen, soil pH, and minimum winter temperature as predictor variables of *C. miniata* stem density (Table 2-7).

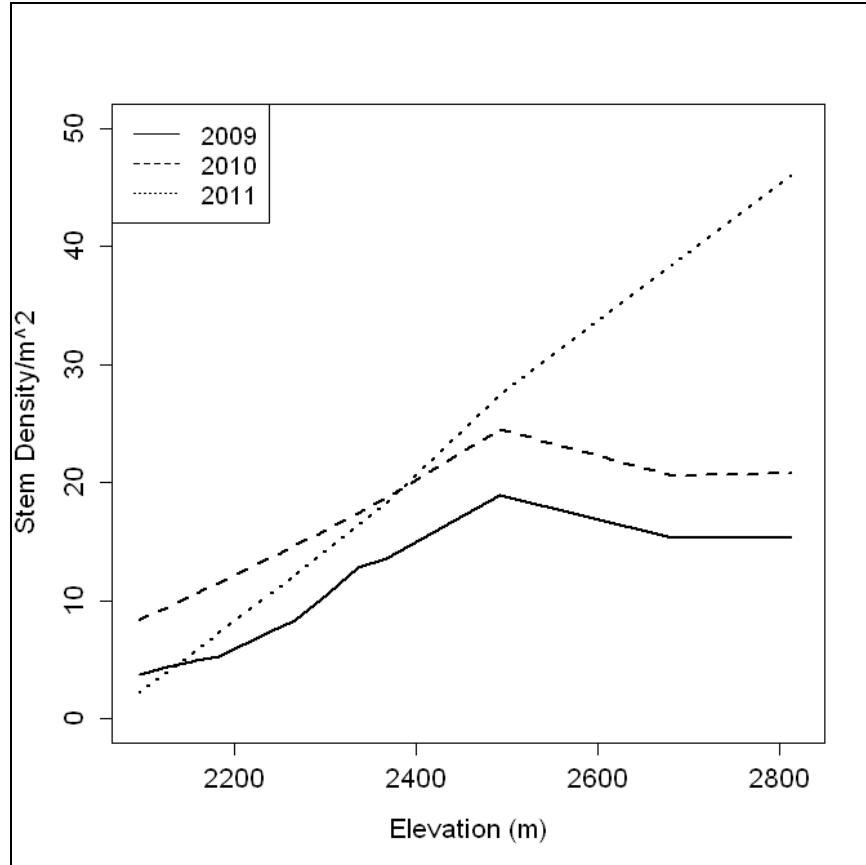


Figure 3-4. Relationship between stem density of *C. miniata* and elevation separated by year.

Table 3-6. Results of comparisons between *C. miniata* stem density elevation as a polynomial or linear predictor. Df = Degrees of freedom,  $\Delta$ BIC = Bayesian Information Criterion value compared to linear model, logLik=log likelihood, Chi sq. = chi-square value. n = 138 for 2009, and 140 for 2010 and 2011.

Model/Year	Df	$\Delta$ BIC	logLik	Chi sq.	p-value
linear/2009	4	--	-358.85		
polynomial/2009	5	-1	-355.83	6.05	0.01
linear/2010	4	--	-578.87		
polynomial/2010	5	2	-577.56	2.62	0.11
linear/2011	4	--	-543.32		
polynomial/2011	5	4	-543.07	0.51	0.47

Table 3-7 Fixed effects output from best ranked generalized linear mixed effects model of the variation in *C. miniata* stem density in 2011. wint = winter, snow\_days = estimated number of days of snow cover from September to June, precip = precipitation. n = 70. Std. err. = Standard error, z = z-score.

	Estimate	Std. err.	z	p-value
(Intercept)	5.391	7.921	0.681	0.496
poly(elevation,1)	232.380	44.671	5.202	<0.001
snow_days	-0.061	0.022	-2.806	0.005
av_precip	-2.943	0.609	-4.830	<0.001
pH	5.843	2.024	2.887	0.004
n	-0.323	0.121	-2.671	0.008
wint_min	-0.188	0.063	-2.968	0.003

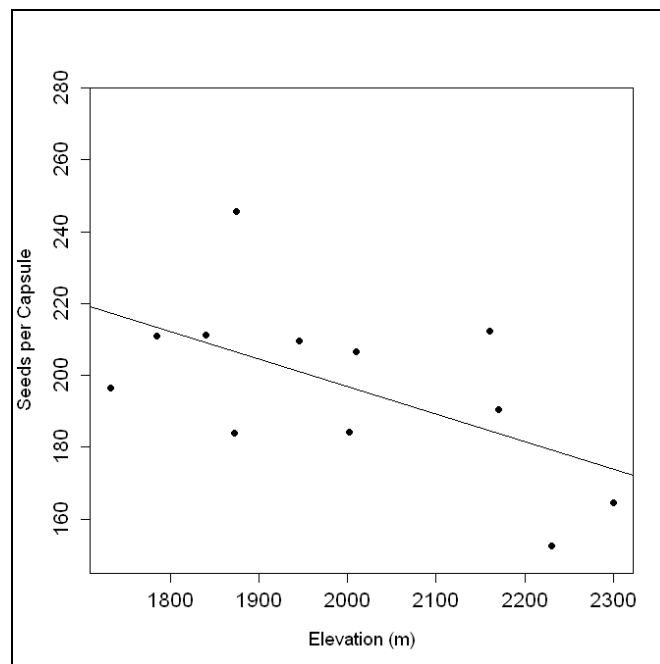


Figure 3-5. Mean number of seeds produced per seed capsule for *L. dalmatica* along the elevation gradient.  $p = 0.05$ .



Sexual Reproductive Output of the Test  
Species along the Elevation Gradient

The mean number of seeds produced per seed capsule declined with elevation for *L. dalmatica* ( $p = 0.05$ , Figure 2-5), but increased with elevation for *C. miniata* ( $p = 0.05$ , Figure 2-6).

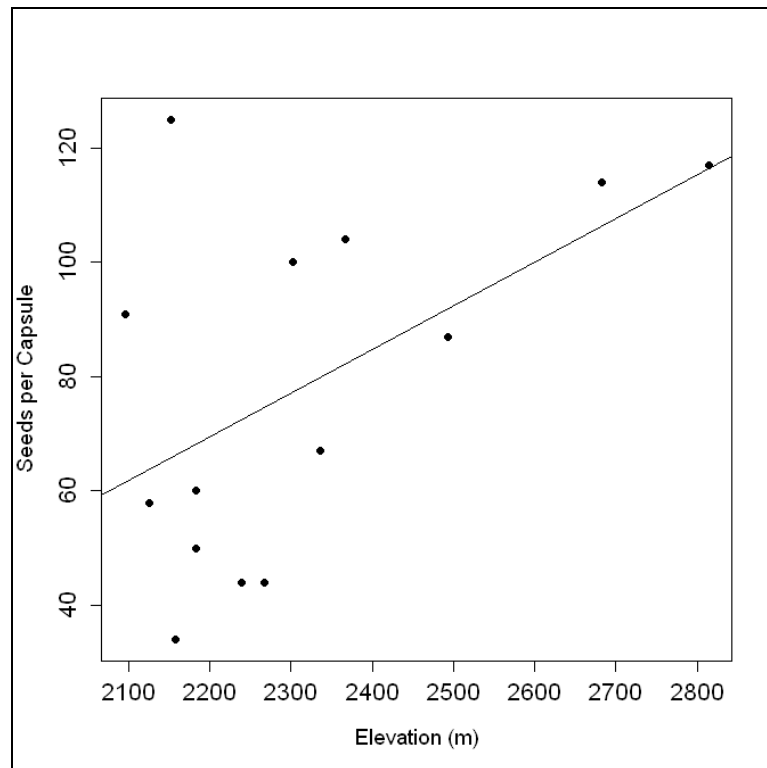


Figure 3-6. Mean number of seeds produced per seed capsule for *C. miniata* along the elevation gradient.  $p = 0.05$ .

Both species showed increasing mean total seed production per plot with increasing elevation, but this trend was not consistent from year to year. *L. dalmatica* showed no trend in total seed production in 2009, but had a positive linear trend for both 2010 and 2011 ( $p = 0.02$  for both years, Figure 2-7). Pooled analysis of the data with a year\*elevation interaction term included indicated that there was no significant difference

in these trends from year to year. *C. miniata* showed a positive linear increase in 2009 ( $p = 0.05$ , Figure 2-8) which was weaker in 2010 ( $p = 0.07$ , Figure 2-9), but showed no trend in 2011. Pooled analysis of these data indicated that there was no significant difference in these trends from year to year.

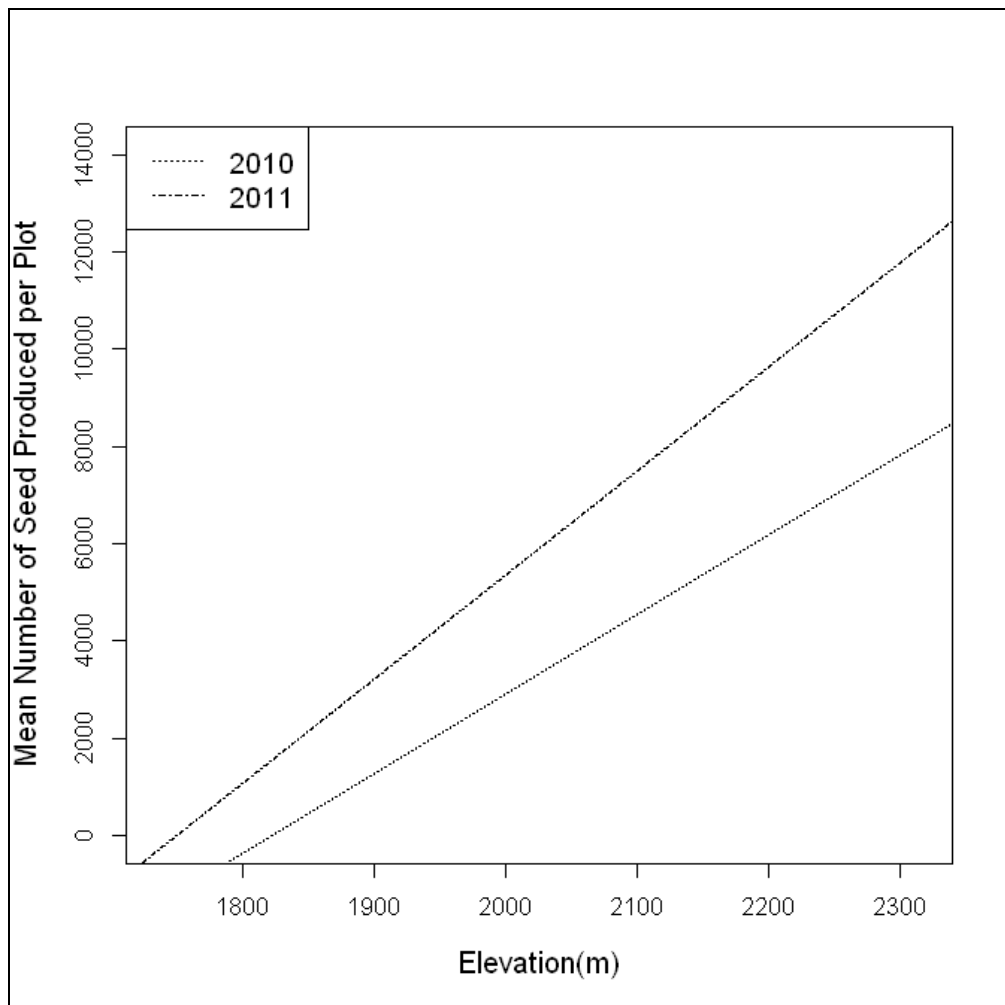


Figure 3-7. Trend in the mean number of seed produced per plot for *L. dalmatica* along the elevation gradient. Only years where this trend was significant ( $p < 0.05$ ) are shown above.  $n = 12$ .

Germinable seed production for *L. dalmatica* showed a weak unimodal trend in 2009 ( $p = 0.1$ , Figure 2-9), no trend in 2010, and a stronger unimodal trend in 2011 ( $p <$

0.05, Figure 2-9). Pooled analysis of these data indicated that there was no significant difference in these trends from year to year.

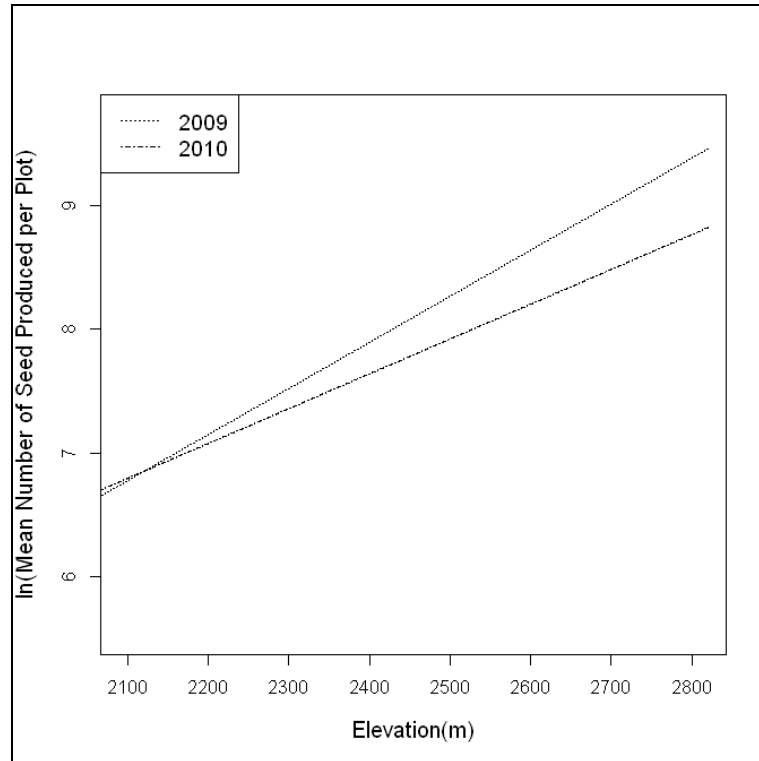


Figure 3-8. Trend in the mean number of seed produced per plot for *C. miniata* along the elevation gradient.  $p = 0.05$  for 2009, and  $0.07$  for 2010.  $n = 14$ .

### Seedling Survival for *Linaria dalmatica*

Seedling survival increased with increased elevation ( $p < 0.001$ ), and increased growing season precipitation ( $p = 0.001$ ,  $\Delta AIC$  from elevation model = -44), but was best described by mean minimum temperature ( $p < 0.001$ ,  $\Delta AIC$  from elevation model = -44, Figure 2-10). Out of the four high elevation sites which had seedlings from the low elevation site in addition to seedlings from that specific site, only one showed any difference in the mean number of seedling surviving from different seed sources. At that

site, the mean numbers of surviving seedlings from on-site and low elevation seed (4.2 and 2.6 respectively) were significantly different ( $p = 0.05$ ).

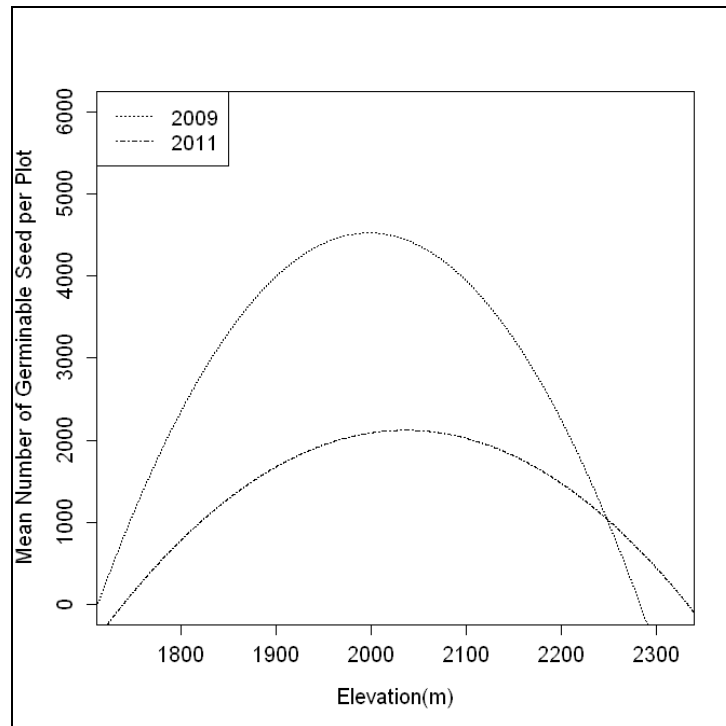


Figure 3-9. Trend in the mean number of germinable seed produced for *L. dalmatica* along the elevation gradient.  $p = 0.1$  for 2009, and  $< 0.05$  for 2011.  $n = 12$ .

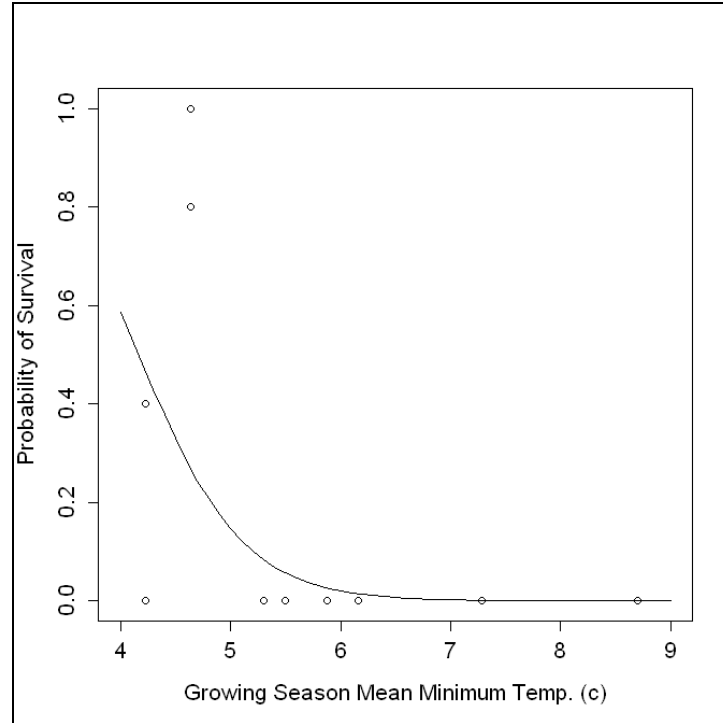


Figure 3-10. Probability of seedling survival versus growing season mean minimum temperature for *L. dalmatica* seedlings.  $p < 0.001$ .  $n = 10$ .

### Discussion

#### Climate and Environmental Variables along the Elevation Gradient

Overall, the trends in the climate variables that we observed along the elevation gradients were consistent with expectations based on general trends noted for climatic variables in mountain systems (Körner 2003). The only exception was for some of the mean and absolute minimum temperature trends. In winter 2010 (which included early 2011), both mean and absolute minimum temperature increased with increased elevation along the *L. dalmatica* section of the elevation gradients (i.e., essentially an inversion of the expected conditions). Absolute minimum temperature increased with elevation along

the *C. miniata* section of the elevation gradients in the 2011 growing season. This can be explained by the large snowpack that occurred during winter 2010/2011 and which persisted at high elevations in the area 17 days longer (July 11, 2011 NRCS snotel data for Parker Peak Station, Figure B-5) than the previous year. This snowpack at the higher elevation ranges of *L. dalmatica* most likely insulated those areas close to the ground from the lower temperatures experienced at lower elevations on the gradient where there was no snow during the winter. Early in the growing season, the persistent snowpack at the higher elevations of the *C. miniata* sections of the gradients had the same insulating effect, causing those sites higher in elevation to have higher absolute minimum temperatures near the ground (i.e. under snow). The opposite or non-significant trends in winter of 2009/2010 and growing season of 2010 show how influential extensive and persistent snowpack can be in relation to temperature near the ground.

Biotic and abiotic environmental and factors along the *L. dalmatica* section of the elevation gradient both showed different patterns. The variability in these factors reflects the transition from the dry sagebrush habitat at the lower range limit of the species to the more rocky, semi-forested habitat at the upper range of the species. Soil phosphorous increased with elevation, likely due to increased availability and weathering of parent materials at higher elevations along the gradient, where the soil was observed to be coarser and more large rocks were present at the surface. Similar trends in increased phosphorous from valley to ridge locations were described by Bowman et al. (2003).

Soil pH decreased slightly with increased elevation, with the mean falling from 7 to 6.7. Litter cover had a unimodal relationship with elevation, reflecting the presence of a more

heavily vegetated, semi-forested band of habitat in the middle of the range of *L.*

*dalmatica*. Canopy cover increased linearly with elevation, most likely because the upper limit of the species was within a more heavily forested belt of habitat whereas the lower range was in dry sagebrush steppe. Biotic and abiotic environmental factors along the *C. miniata* section of the elevation gradient both showed variation as well. While soil organic matter and vegetation cover both decreased, soil phosphorous and bare ground both increased. These changes likely reflect the transition from forested grassland habitat at the lower range of this species to the sub-alpine habitat present at its upper elevation range limit.

#### Density of Test Species in Response to Elevation, Climate, and Environmental Variables

Estimated number of days of pre-season snow cover and growing season climate variables were most influential in describing *L. dalmatica* stem density. Winter climate variables and biotic environmental variables did not improve the models, suggesting that these factors are not particularly influential on the stem density of this species.

Therefore, it seems that climate variables may be the primary drivers of establishment success for this species. Other studies have shown that climate can be influential on seedling establishment for a variety of species (Lloret et al. 2005; Jump et al. 2007; Vittoz et al. 2008; Shevtsova et al. 2009; Classen et al. 2010; Munier et al. 2010).

Environmental factors and resource levels may still impact this species, being influential on the growth of established individuals but not on establishment rates.

*L. dalmatica* stem density at the low elevation limits of the species, where growing season temperatures were warmer, was consistently low between years, accounting for the negative association between the number of growing season frost free days and stem density. The negative association between stem density and precipitation is more difficult to explain. When the number of days of snow cover was removed from the model, this relationship became positive, which suggests that these two variables are co-linear. Analysis revealed that both have positive associations with stem density when considered independently. However, the omission of either one from the model resulted in large increases in BIC, indicating that they are both influential in describing the current trend in stem density of *L. dalmatica* along the elevation gradient. Since the intent was to determine which factors were most influential on stem density, and not to actually make predictions about stem density, both variables were retained in the best model. If predictions were to be made, one of the collinear variables would need to be removed, or both would need to be combined (Bonate 1999) into a composite variable.

We had expected that the stem density of this species would also be lower at the upper end of its elevation range, and this was the case for 2008 and 2009. However, by 2011, stem density was actually the highest at the upper elevation range limit of the species. We believe that this may be related to increased number of days of snow cover at the higher elevations during the last year of the study, as discussed above. This is supported by our data. During model selection, removing the snow cover variable from the model resulted in large increases in BIC values, indicating that it was an important factor in relation to *L. dalmatica* stem density. In addition, the association between the



number of days of snow cover and stem density was positive. If increased snowpack does serve as insulation during winter months as discussed above, it could make conditions more favorable for the growth and survival of *L. dalmatica* at higher elevations, thus increasing stem density. This idea is supported by another study which found that seedling density and population growth increased with increased snow depth for the non-native species *Bromus tectorum* (Griffith and Loik 2010). However, it should be noted that the number of hours of spring snow was found to decrease bulbil biomass in another non-native species, *Oxalis pes-caprae*, on the island of Crete (Ross et al. 2008). Increased snow cover could also promote stem density by increasing the availability of early season soil moisture. However, our lack of actual snow cover data for all sites prohibited us from testing this theory rigorously.

*C. miniata* stem density was best explained by a combination of growing season and winter climate variables, as well as abiotic environmental variables. The trend in stem density throughout its current elevation range was similar to that of *L. dalmatica*, in that the shape of the relationship with increased elevation changed from unimodal to a linear increase throughout the course of the study. The fact that increased soil nitrogen was negatively associated with stem density for this species reflects the possibility that increased nitrogen levels can negatively impact plant growth in competitive environments (Brooks 2003; Badgery et al. 2005; Feng et al. 2007; Littschwager et al. 2010; Sharma et al. 2010), and suggests that *C. miniata* may be a weak competitor in areas with higher nitrogen availability. It also suggests that it may become a weaker competitor in sub-alpine environments, where the deposition of atmospheric nitrogen is expected to

increase (Körner, 2004). Growing season precipitation and pre-season snow cover displayed the same type of co-linear relationship for *C. miniata* as they did for *L. dalmatica*, and this is most likely the cause of the negative relationship between precipitation and stem density shown in our model.

The negative relationship between stem density and both number of days of pre-season snow cover and increased winter minimum temperature reflects the fact that there were more estimated days of pre-season snow cover from September to June at the lower elevation range of *C. miniata* (increasing winter minimum temperatures), where stem density was also lowest. It does not seem likely that either one of these climate variables would limit the stem density of *C. miniata* at lower elevations. However, even though growing season snow cover had a low correlation with stem density and was not used in the model, the only two sites with any growing season snow cover were coincidentally the two highest elevation sites, suggesting that snow cover in the early summer may serve the same purpose for *C. miniata* as the late winter snow cover does for *L. dalmatica*: insulating the plants from low temperatures during the earliest part of their respective growing seasons when low temperature events are likely and promoting increased stem density at higher elevations.

#### Sexual Reproductive Output of the Test Species along the Elevation Gradient

Neither one of the test species showed any indication that propagule pressure was an obstacle to upward expansion, but both had low rates of seed production at the lower elevation limit of their respective ranges. For *L. dalmatica* the fact that seed production

per seed capsule decreased with elevation was counterbalanced by increased seed production per plot at the higher elevations due to increased capsule production. However, when germination rates were taken into account, the number of germinable seed produced per plot decreased at both ends of the elevation range for *L. dalmatica*. For *C. miniata*, the number of seeds per capsule increased with elevation, as did the estimated seed production per plot. Unfortunately, seed germination data was not collected for this species.

#### Seedling Survival for *Linaria dalmatica*

We had hypothesized that seedling survival would be lowest at or just outside the current range limits of *L. dalmatica*. However, no seedlings survived within the current range of the species. One individual survived below the current elevation range limits of the species, and the predicted probability of survival above the current elevation range limits was around 0.2. The majority of seedling mortality took place later in the growing season when soil moisture was declining in most locations. Those seedlings that did survive were in shaded locations where precipitation was also greater. Our data show that both precipitation and growing season mean minimum temperature were associated with seedling survival. Since these two conditions interact to determine soil moisture levels it is likely that seedling survival for *L. dalmatica* is dependent on moisture availability, as has been shown in other studies (Defosse et al. 1997; Nagakura et al. 2005; Padilla and Pugnaire 2007; Fay and Schultz 2009). It should be noted that even though seedlings survived above the current elevation range limit for *L. dalmatica*, they were etiolated to the point that they were prostrate instead of growing upright. We

removed the surviving seedlings to avoid the risk of introducing this species to new areas, but had they been left there over the winter, their physical state at harvest suggested that they would not have survived. However, this highlights the need for further experimentation related to seedling survival and establishment for this species.

### Conclusions

Both *L. dalmatica* and *C. miniata* displayed similar trends in stem density, in that stem density of both species initially had a unimodal relationship with elevation which changed to a linear increase by the last year of the study. Given our data, combined with data from a climate monitoring station within the vicinity of the study area which measured snow level and duration, the most likely explanation is that increased pre-season snow cover for *L. dalmatica*, and increased growing season snow cover for *C. miniata* may have insulated individuals of these species from low temperature events early in their respective growing seasons. Later snow cover would also have led to greater moisture availability for both species at the high elevation limits of their ranges. As mentioned previously, the snowpack during late winter/early spring 2011 was much greater and lasted longer than in previous years, making this a likely explanation for the shifts in stem density at the high elevation limits of both species. Other studies have shown that increased snow pack can have positive effects of plant growth (Wipf et al. 2009; Griffith and Loik 2010; Peng et al. 2010), and serve a protective purpose for vegetation (Frey 1983; Molau 1996; Wipf et al. 2009).

Both species also had relatively consistent stem density levels at their lower elevation limits throughout the course of this study, suggesting that the lower elevation limits of both species within the study area are relatively stable. Since both species showed more limited propagule pressure at low elevations as compared to high elevations, it appears that both species are probably limited by a combination of propagule pressure and climatic/environmental variables at the lower elevations of their current ranges and by climate alone, if anything, at the upper range limits. For the lower range limits, it is likely that the lower observed propagule pressure is directly related to the warmer and drier conditions at the lower range limits of both species, as several studies have shown a decrease in seed production or size with increased drought stress (Stamp 1990; Bossard and Rejmanek 1994; Perez-Ramos et al. 2010; Jorgensen et al. 2011).

The main difference between the two species is that stem density for *L. dalmatica* was most related to pre-season snow cover and growing season climate variables, whereas *C. miniata* stem density was associated with soil properties and winter climate variables in addition to growing season precipitation and growing season snow cover. This suggests that the non-native *L. dalmatica* is more of a generalist species, capable of performing well under a greater variety of conditions, whereas the native *C. miniata* may be more limited in its capacity to cope with variance in environmental conditions. Such differences between native and non-native plant species in mountain systems have been suggested by Alexander et al. (2011), and this study therefore provides supporting

evidence for the theory of directional ecological filtering of non-native plant species in mountain systems.

In addition to propagule pressure and climate, disturbance is another possible factor which could affect the distributions of these species. Several other studies have noted that the distributions of non-native species can be related to disturbance (Parker et al. 1993; Duggin and Gentle 1998; Juttila and Grace 2002; Bellingham et al. 2005; Hendrickson et al. 2005; Hierro et al. 2006). We did not explicitly measure disturbance intensity as a part of this study, but instead tried to limit potential variation in disturbance intensity by selecting sites which were within a standard distance from the nearest anthropogenic disturbance and had no obvious signs of anthropogenic disturbance at the time of site selection. However, the entire study area has suffered from disturbances in the past, such as fire, grazing by native and introduced ungulates, and historical forest clearing by Native Americans. Thus, while it is unlikely that any of the observed trends were related to differences in current disturbance levels, the presence of *L. dalmatica* on the landscape may be related to past disturbances.

At present, the number of studies examining individual non-native species along elevation gradients in relation to climatic and environmental factors is relatively small. Studies have been conducted along environmental gradients, and associations have been found between various measures of plant growth and temperature (Grace and Norton 1990; Despland and Houle 1997; Chambers et al. 2007; Jakalaniemi 2011), precipitation levels (Mack and Pyke 1984; Tardif et al. 2006), soil water (Chambers et al. 2007), plant community (Ansari and Daehler 2010), plus duration (Ross et al. 2008) and depth

(Griffith and Loik 2010) of snow cover. Several of these studies were conducted in the context of mountain systems (Grace and Norton 1990; Chambers et al. 2007; Ross et al. 2008; Ansari and Daehler 2010; Griffith and Loik 2010; Jakalaniemi 2011). This suggests that climate conditions could serve as limiting factors for species ranges along elevation gradients (McDougall et al. 2009; Alexander et al. 2011). At present, the pool of detailed studies of individual species is too small for the development of any general theories of plant invasion at the species level in mountain systems. However, given the current level of interest in this topic, it seems likely that the number of these types of studies may reach a level which allows for some development of general theories that could potentially be applicable across many geographic contexts.

In addition, such studies could also address the issue of plant species distributional shifts under climate change scenarios in more detail. The importance of climate variables in the models describing stem density for both test species in this study suggests the possibility that future changes in climate could result in changes in the distribution of both species. While changes in the distribution of plant species in response to climate change (both actual and potential) have been noted elsewhere (Dullinger et al. 2004; McDougall et al. 2005; Shoo et al. 2006; Kelly and Goulden 2008; Lenoir et al. 2008; Salick et al. 2009), the need to consider biotic interactions (Pearson and Dawson 2003; Araujo and Luoto 2007; Brooker et al. 2007; Thuiller et al. 2008) and dispersal ability (Pearson and Dawson 2003; Thuiller 2004; Thuiller et al. 2008; Engler et al. 2009) of individual species when assessing the potential for distributional changes of species has also been noted. This also highlights the need for more studies incorporating

data on dispersal and biotic interactions for individual species, as such studies could add valuable information to the ongoing debate about the effects of climate change on plant species.

In terms of the concern about *L. dalmatica* spreading to higher elevations in the future, there is nothing in our data that provides strong evidence that this species is incapable of doing so under current climatic conditions. As such, populations at the upper elevation limits of this species should be managed to prevent further expansion. However, the results of this study fall short of providing evidence that the species can, with certainty, establish and persist at elevations above its current limits within the study area. The fact that the amount of germinable seed produced for this species declined at high elevations suggests one possible limitation for the establishment of this species at higher elevations. However, it should be noted that germination data was only collected for one season's seed lot. It is still possible that other aspects of this species' life cycle may be limited by harsh climatic conditions at higher elevations. We did not explicitly measure the effects of minimum growing season temperature on the establishment of seedlings of this species, and this is certainly worthy of further exploration. However, such studies would be a challenge to undertake in the field, as obtaining permission to plant weedy species in areas where they are not present is difficult. Thus, while there is some weak evidence that this species shows some establishment limitation at the high elevation limit of its current range, more data are needed to definitively say that this species will or will not expand upward in the future under current climatic conditions,



and to estimate what its potential distributional shift might be under future climate change scenarios.

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CHAPTER 4: DEMOGRAPHY OF A NATIVE/NON-NATIVE SPECIES PAIR  
ALONG AN ELEVATION GRADIENT IN THE GREATER YELLOWSTONE  
ECOSYSTEM

Introduction

Plant communities in mountainous areas of the world are facing an uncertain future. Climate change has the potential to alter the range of both native (Crimmins et al. 2009; Engler et al. 2009), and non-native (Becker et al. 2005; McDougall et al. 2005; Marini et al. 2009; Pauchard et al. 2009) plant species, and could potentially result in increased success of non-natives plants at higher elevations (McDougall et al. 2005; Crimmins et al. 2009). In addition, increased use of these mountainous areas by humans could result in more opportunities for non-native species establishment due to an increase in dispersal vectors and suitable habitat related to altered land use (McDougall et al. 2009; Pauchard et al. 2009). Hence, mountainous regions are not as immune to non-native plant invasions as they were once thought to be (McDougall et al. 2009).

When considering the fate of non-native plant species in mountain systems, it has been found that non-native plant species richness tends to decrease at higher elevations, and that this trend is a global phenomenon (Alexander et al. 2011; Seipel et al. 2012). This response has been observed in some cases to be somewhat linear (Becker et al. 2005; McDougall et al. 2005), and to be hump shaped in other cases (Tassin and Riviere 2003; Arevalo et al. 2005). One recent exception to this generality was found by (Paiaro et al. 2011), who observed that non-native species richness increased at both ends of an

elevation gradient in central Argentina. When considering individual non-native species, several studies have noted decreases in occurrence and population size and/or vital rates with elevation (Trtikova et al. 2010; Liang et al. 2008; Alexander et al. 2009; Monty and Mahy 2009; Pollnac et al. 2012) and at least one has noted increased success at higher elevations (Ansari and Daehler 2010).

Although there are general trends as noted above, the presence of some exceptions to those trends suggests that elevation alone is not a suitable explanatory factor when trying to understand the process of non-native plant species distributions in mountain systems. Nonetheless, these generalities do suggest that there are factors which are capable of limiting the presence of non-native species in mountain systems. It is clear that there are several other factors besides elevation which influence non-native plant species in mountain systems. Arguably, many of these factors, such as temperature, soil moisture, and precipitation, change as a result of elevation, but not all of these change in consistent ways from one mountainous area to the next (Körner 2004). Furthermore, the effects of these factors on any given species could manifest themselves in subtle ways (seed production or viability) such that if a survey of only one factor (e.g. density) is conducted, a large part of the story could be missed. It follows that if questions related to the future fate of a non-native species in a mountainous area are to be addressed, the demographic details of populations of the species throughout its current range can offer many insights.

The differences in the growth rate ( $\lambda$ ) of populations of a plant species between its range limits and its interior range has been hypothesized to be different based on whether

or not that species has reached the limits of its potential range (Gaston 2003; Angert 2006; Eckhart et al. 2011). For example, if a species has filled its potential range,  $\lambda$  at the margins should be lower than  $\lambda$  for the interior populations because the marginal populations have theoretically encountered some limiting factor which suppresses growth and prevents them from expanding further (Gaston 2003, and references therein). Alternatively, for a species which has not yet reached the limits of its potential range, marginal populations may exhibit higher  $\lambda$  values due to the fact that the species is in suitable habitat where potentially limiting density dependence has not yet been encountered due to lack of other individuals of the same species (Gaston 2003, and references therein). Eckhart et al. (2011) take this theory farther, stating that: 1) covariance between population  $\lambda$  and environmental factors known to influence it suggests lack of adaptation as the primary limit to a species' current range and, 2) lack of association between  $\lambda$  and range position, or increases in  $\lambda$  at range limits both implicate dispersal as the primary factor defining range limits. As such, comparisons of  $\lambda$  for interior vs. edge populations can provide some insight into whether or not a non-native species has reached the limits of its potential range within an area, and what the causes of this limitation might be. In a mountainous area, this allows one to assess the potential for the species to become established in upslope or down slope habitats under current climate conditions.

The first objective of this study was to examine the relationships between specific vital rates and environmental and climatic factors for a particular non-native plant species, *Linaria dalmatICA* (L.) Mill, along an elevation gradient in the Greater

Yellowstone Ecosystem (GYE). Here, we hypothesized that vital rates would vary along the studied gradient in relation to climatic and environmental predictor variables. Our second objective was to compare the trends in vital rates for *L. dalmatica* to those of a closely related native species, *Castilleja miniata* (Douglas ex Hook.), found along the same elevation gradient. We hypothesized that vital rates of *C. miniata* might not vary as much as those of *L. dalmatica* since it has been present in the area for a much longer period of time. Our third objective was to model population growth of *L. dalmatica* and to perform sensitivity analyses for each of the study sites. We hypothesized that population growth rates would be lower at the upper elevation range limit of this species. Since *L. dalmatica* is a perennial species, we also hypothesized that population levels for this species would be most sensitive to the survival rate of mature individuals.

## Materials and Methods

### Study Area and Site Selection

This study was conducted along an elevation gradient within the GYE in the vicinity of Gardiner, MT, 45°01'60" N, 110°42'33" W, 1,598 m elevation. Three networks of linked roads were chosen as replicate elevation gradients in the area, and will henceforth be referred to as elevation transects (Figure E-1). In general, each of these transects proceeded from elevations near the bottom of the Yellowstone River Valley in Gardiner, MT to elevations just short of the highest elevation extent for the specific peak, but represent the highest point of road access (2,900 m for transect 1, 2400 m for transect 2, and 2200 m for transect 3). See figure E-1 for map of study area.

During July and August of 2008, the three elevation transects were surveyed for the presence of *L. dalmatica* and *C. miniata*, both hereafter referred to collectively as the test species. During initial surveys, an effort was made to identify every distinct population of the test species present within 5 to ~200 m of the elevation transects (roads) from their lowest elevations up to the highest extent that was navigable in a vehicle. Each population's center was marked with a Global Positioning System (GPS, Trimble GeoXT 2008 Series), and if multiple discrete patches were present at a site, the boundaries of these patches were also mapped by walking the perimeters. During early spring 2009, three study sites were established on each one of the three elevation transects. Sites were selected from the pool of surveyed sites to represent a relatively even spread of elevations along each elevation transects. The sites essentially represented the low, medium, and high ranges for *L. dalmatica* and *C. miniata* in their respective local elevation distributions. Four 1 m<sup>2</sup> monitoring plots were established at each one of these sites. Plots were placed randomly in areas where the test species was present. Each plot was marked with rebar and its position recorded with a GPS to enable easy relocation during subsequent visits.

#### Estimation of Vital Rates

Vital rates were collected for each species for the purposes of: 1) determining which climate and environmental factors influenced the vital rates for each species, 2) comparing patterns of variability in vital rates between the test species, and 3) building demographic population models for *L. dalmatica*. Plots were monitored during early June and late August of each field season from 2009-2011. During each session, a 1 m<sup>2</sup>

frame divided into 16ths was placed over each plot. The location of each stem in the grid was then drawn on a piece of tracing paper, noting if the stem was a seedling, vegetative stem, or flowering stem, using a different symbol for each. Stems which were obviously arising from a common root crown were drawn to be touching on the mapping data sheet, such that individuals could be counted more precisely.

To estimate vital rates from early spring to late summer, sheets from subsequent monitoring sessions were overlaid (for example August 2009 was placed over June 2009) for each plot, and the number of stems which had: 1) transitioned from vegetative to flowering, 2) stayed vegetative, or 3) died, were counted, as were the number of individuals which had either survived or died. Similarly, looking at the time period from the August to the following June, the number of individuals that either survived or perished was recorded. This yielded information on stem production, spring individual survival, transition to flowering stem, estimated rhizomatous ramet production (for *L. dalmatica* only), and fall individual survival rates. Seedlings were almost never observed, so that seedling survival could not be estimated from these data. Spring vital rates (individual survival, stem production, transition to flowering stem, rhizomatous ramet production [for *L. dalmatica* only], and seed production) were collected for three successive years (2009, 2010, and 2011). The vital rate of individual survival from spring to fall was only collected for two successive years (2009 and 2010).

For *L. dalmatica*, seed production estimates were based on the number of seed capsules counted each year. The number of seed capsules for *L. dalmatica* was adjusted based on data collected at each site which quantified the proportion of capsules which

had viable seed at the end of the growing season (see chapter 3 methods for details). The adjusted number of seed capsules was then multiplied by the average number of seeds found per capsule (as discussed in chapter 3) at each site to estimate seed production rates. Seed predation data was also collected at each site using four 8 cm x 8 cm plastic trays. Each tray had 2 holes drilled in the bottom, one for drainage and one for securing the tray to the ground using a nail. Trays were placed such that they were flush with the ground surface. They were filled with sand and 50 *L. dalmatica* seeds were scattered on the surface of the sand. After 10 days, the remaining seeds were collected and counted. These data were used to reduce seed production rates for each site in the population model.

Seed germination, longevity and seedling survival were only evaluated for *L. dalmatica*. To accomplish this, several seeds were harvested during the late summer of 2008. Seeds were divided into 5 lots of 400 seeds for each site. The first lot of 400 seeds for each site was used for immediate germination and viability tests. To test for germination, 4 batches of 50 seeds per site were placed into plastic containers containing blotting paper which was wetted with distilled water. These containers were placed in a germination chamber at 15° C alternating 12 hours light/12 hours dark and germination was monitored weekly for 5 weeks. These data were used to estimate current season germination rate. These conditions were chosen based on the work of Robocker (1970) which noted that the highest level of germination occurred under temperature conditions of 15-20° C. Four batches of 25 seeds were then tested for viability using a tetrazolium

test (Peters 1970). Seeds were cut in half, and then placed in a 1% TZ solution for 24 hours at 30° c before evaluating.

The remaining lots of seeds were placed in nylon sacks (200 seeds/sack) with 40 ml of sand. Eight of these sacks were then buried at each of the sites to be recovered in random pairs in subsequent years. The location for seed burial was randomly chosen. At each seed burial site, a meter stick was laid on the ground, either end was marked with a piece of rebar and a spike with a blue road hair, and the point was recorded with a GPS (Trimble Geo XT 2008 Series). Two sacks were then buried adjacent to each other at the 20, 40, 60, and 80 cm marks on the meter stick such that the top of the sack was approximately 0.5 cm below the surface. Each year following the initial burial, in late September, a pair of sacks was removed randomly from the 20, 40, 60, or 80 cm mark at each site. The seed material was separated from the sand using a 0.5 mm sieve and counted, and the procedures described above for germination and viability testing were performed. Seed decay rate on a per year basis was estimated using the three years of viability and seed loss data.

To estimate seedling survival for *L. dalmatica*, during the spring and summer of 2011, seedlings were placed at five sites along the two elevation transects outside of Yellowstone National Park (see Figure E-1). Three of these sites were within the current range of *L. dalmatica*, with the remaining two sites being above and below the current elevation range of the species. Seedlings used for each site were grown from seeds collected there during fall 2010 which were then stored in cold, dry storage at 4° C. Seeds for the sites outside of the current range were from the nearest site along the



gradient. Seedlings were transplanted in 8.9 cm round pots filled with soil (equal parts peat, loam, and sand). From our data and Robocker (1970), it was determined that 55 growing degree days using 10° C as the base temperature were sufficient for the germination of *L. dalmatica*. Five pots of five seedlings were thus placed at a given site on the date at which that site had accumulated 55 growing degree days the previous year. Seedlings were started in a greenhouse (18° C) at staggered dates such that seedlings were all in the cotyledon stage when they were planted at each of the different sites. Seedlings were subjected to rapid acclimatization to ambient conditions over a 24 hour period. Seedlings were monitored weekly after planting until early September to establish seedling survival rates along the elevation transects. All pots were protected within a wire mesh cage (0.63 cm grid size) to prevent larger herbivores from eating seedlings and were removed after the final survey to prevent new populations from establishing.

The only rate used in the model which was not based on field measurements was seedling competitive ability. Since seedlings of *L. dalmatica* are weak competitors with established vegetation (Gates and Robocker 1960; Robocker 1970), germinable seed crop was further reduced in the model by multiplying by (1- mean proportion of bare ground measured at each site), assuming random dispersal and random seed decay. That is, if a seed landed on existing vegetation, it was expected to die, but if it landed on bare soil, it was subject to germination. It is quite possible that seed decay and predation could be related to the environment in which a seed lands, but we did not have data to test this hypothesis.

For *C. miniata*, an estimate of seed production was achieved by randomly harvesting 10 flowering heads from outside of the monitoring plots at each of the *Castilleja miniata* sites in the late summer of 2009. These flowering heads were dried at constant temperature (43° C) for several weeks and then dissected such that for each seed capsule, the number of seeds could be counted. Seed germination and seed decay rates for this species were not measured.

### Data Analysis

#### Variance in Vital Rates along Elevation Gradients

All analyses were performed using R 2.14.1 (R-Development-Core-Team 2011). Before producing any population dynamics models, we wished to see if vital rates varied from site to site for each test species, and to see if there was any difference in the degree to which vital rates varied from site to site between species. To address these objectives, vital rate data collected directly from study plots (spring and fall individual survival, stem production, transition to flowering stem, rhizomatous ramet production [for *L. dalmatica* only], and seed production) from different years were averaged for each plot, such that in the analysis, each plot at each site had one vital rate value, yielding a sample size of 4 per site (36 total) for each vital rate for each species. Climate data collected in successive years (number of weeks until the permanent wilting point was reached [weeks to wilt], growing season mean minimum temperature, growing season absolute minimum temperature, number of growing season frost free days, growing degree days, growing season precipitation, winter mean minimum temperature, winter absolute minimum

temperature, number of winter days at or below zero) were averaged for each site because the overarching interest was in how the trajectory of population growth might be affected by changes in vital rates as influenced by climatic factors over time. Although yearly fluctuations in climatic variables likely produce fluctuations in vital rates, the time lag is between the two is unknown, and population growth over time is a product of the averages of such fluctuations.

An Information Criterion approach (Burnham and Anderson 2002) was used to determine which set of environmental and climatic predictor variables best explained the variance in each of the vital rates analyzed (stem production, spring individual survival, transition to flowering stem, seed production, rhizomatous ramet production [for *L. dalmatica* only], and fall individual survival). Examination of residuals from the models described below revealed that none of the assumptions of linear regression were violated, so this approach was used to analyze the data. Seed production was square root transformed to meet model assumptions.

Full models contained elevation and all of the environmental (percent canopy closure, percent litter cover, percent bare ground, and percent vegetation cover, soil nitrogen, soil pH, soil phosphorous, and soil organic matter) and climatic predictor variables and any second order polynomial terms deemed necessary by examination of diagnostic plots of each vital rate plotted against individual predictor variables. Interactions were not included due to the low number of replicates (4) for each site and autocorrelation between variables. Including elevation (unique for each site) in the model allowed us to determine if any unmeasured environmental variables were

influential. Backward selection was employed on the full model and the model with the lowest Akaike's Information Criterion (AIC) score was selected as the best model.

#### Population Growth Rate along Elevation Gradients

To estimate stochastic population growth rate ( $\lambda$ ), vital rates were used to construct population dynamics models. Detailed information on seed germination, seed predation, and seed decay were not collected for *C. miniata*. Additionally, seed production for this species was estimated in a much less precise fashion than for *L. dalmatica*. As such, population dynamics models were only constructed for *L. dalmatica* because the absence of several factors from the *C. miniata* models would most likely influence  $\lambda$  values, making these models less precise and consequently not comparable to the *L. dalmatica* models. Comparisons between the two species were therefore confined to the observed vital rates discussed in the previous section.

For *L. dalmatica*, population dynamics were modeled for each of the four separate plots at each site with the data on vital rates collected from each plot using a difference equation model (see Appendix D for model diagram and code) to accommodate the two yearly (spring to fall and fall to spring) transitions. Initial population conditions were specified for each plot. The number of mature individuals in each plot was set based on observations from each unique plot in spring of 2009, and the number of seeds was arbitrarily set at 25. Preliminary runs of the models suggested that the initial start conditions had no effect on the distribution of  $\lambda$ . To simulate one generation, the initial population of each of the four plots at each site was multiplied by

the spring to fall vital rates for that plot, and then the resulting population was multiplied by the fall to spring vital rates for that plot. For the projection of populations to estimate  $\lambda$ , the environment for each site was assumed to fall into one of three states which corresponded with the three years observed in the study, and the three years of data on vital rates were viewed as linked to those three unique environmental states (i.e. environmental state 1 resulted in the distribution of vital rates observed in year 1, environmental state 2 resulted in the distribution of vital rates observed in year 2 etc.). For each plot at each site, the first three generations of the model used the three environmental states (and the vital rate distributions linked to them) in the sequence in which they were observed (i.e. environmental state 1, environmental state 2, and environmental state 3). After the third generation, an environmental state was randomly selected with replacement from the distribution of environmental states following Caswell (2001), and vital rates recorded *in that year (environmental state) in that plot* were used. In this way,  $\lambda$  was modeled independently for each of the four plots at each site, starting with a chronological sequence of observed transition rates for three generations and then continuing out to 30 generations using transition rates from a randomly chosen environmental state. At the end of 30 generations, the geometric mean  $\lambda$  was calculated for each plot, and the mean of the four plot  $\lambda$  values was calculated to yield an overall  $\lambda$  for each site.

This approach assumed that the mean observed vital rates varied during any given year based on: 1) variation in conditions from plot to plot within each site, and 2) variations in conditions from site to site. Since differences in mean vital rates in any

given year between sites were believed to be due to actual differences in overall growing conditions, vital rates from sites were not randomly assigned between sites in the models (e.g. site 1 plot 1 vital rates were never randomly assigned to site 2 plot 3 etc.).

Similarly, since the differences in transition rates between plots at each site in any given year were believed to be due to actual microsite heterogeneity, each plot was modeled separately and plot transition rates within each site were neither randomly swapped between plots nor randomly applied to the whole site (e.g. plot 1 site 1 vital rates were never randomly assigned to any other plots within site 1 nor to the entire site). The overarching assumption was that the variance structure of the vital rates of plots within each site during any given year was based on stable properties of the site, just as the variance structure of the vital rates between sites during any given year was based on properties which were stable along the environmental gradient (i.e. this variance was true sample variance). By simulating each plot independently at a site and then deriving a mean  $\lambda$  value for the site based on plot values, inclusion of sample variance in the simulation was minimized in an effort to reduce the chances of overestimating the true variability of the population at each site (Boyce 1992). The observed distributions of vital rates were thus viewed as linked to an environmental state in which differences in microsite conditions within a site and overall growing conditions between sites were stable over time.

A mean distribution of possible  $\lambda$  values for each site was achieved by the non-parametric bootstrap method (Caswell 2001). The simulation described above was repeated 1000 times, using a randomly drawn sequence of transition rates specific to each

plot after generation 3 each time. In this way, we believe that the structure of the bootstrapped data followed the structure of the observed data (Caswell 2001) as described above (i.e. distribution of vital rates unique to each plot and site which varied from year to year based on the environmental state).

The distribution of  $\lambda$  for each site was highly non-normal, so a quantitative comparison of  $\lambda$  based on site conditions using traditional statistical methods was not possible. Median  $\lambda$  values were assessed qualitatively for differences based on site characteristics using box and whisker plots. If the notches of compared plots did not overlap, this was considered evidence that the medians of those plots differed (Chambers et al. 1983). We looked for obvious shifts from  $\lambda > 1$  to  $\lambda < 1$  based on environmental characteristics, and then used the overlap of the notches as a way to determine whether or not these shifts were significant. In addition, instances where the highest or lowest median value of  $\lambda$  was positioned at either end of the range of the climate or environmental variable being examined were viewed as indications that extreme values of  $\lambda$  may be related to extreme levels of the variable.

#### Vital Rate Sensitivity Analysis of Population Growth

In order to determine the influence of each of the measured vital rates of *L. dalmatica* on overall population density, a vital rate sensitivity analysis (VRSA)(Fefferman and Reed 2006) was employed. This method is very similar to traditional sensitivity analyses in that it describes the proportional change in the population based on proportional changes in vital rates. However, instead of describing

changes in  $\lambda$ , it quantifies changes in the population density, and therefore does not rely on the population having a stable age distribution (Fefferman and Reed 2006). The analysis is also sensitive to initial population conditions, and is therefore useful when considering comparisons between populations which vary in initial density (Fefferman and Reed 2006). To perform the VRSA, the population model for each site described above was modified so that an additional 1000 run simulation could be executed in parallel using the same sequences of vital rates, but with a selected vital rate being decreased by 10%. At the end of the simulation, the mean % decrease in the population between the original and the modified vital rate model was calculated and used as the sensitivity value.

## Results

### *Linaria dalmatica* Vital rates

*L. dalmatica* sites were found to be variable in terms of both climate and environmental conditions (Table 3-1). Vital rates also qualitatively appeared to vary from site to site (Figure 3-1). No suitable regression models were found to describe the variation in stem production or spring individual survival rates. The model which best described the variation in the transition to flowering rate included growing season mean minimum temperature and its 2<sup>nd</sup> order polynomial term as predictors (Table 3-2). In this model, transition to flowering had a convex association with increased growing season mean minimum temperature (Table 3-2). The best model for fall (over winter) individual survival rate included winter mean minimum temperature and the number of winter days



at or below zero as predictors (Table 3-3). In this model, fall individual survival rate was positively associated with both increased winter mean minimum temperature and the number of winter days with temperatures at or below 0° C (Table 3-3). The best model for rhizomatous ramet production contained winter mean minimum temperature and the number of winter frost days as predictors, and showed negative associations between rhizomatous ramet production and both predictor variables (Table 3-4). Finally, the best model for seed production contained elevation, growing season mean minimum temperature and its 2<sup>nd</sup> order polynomial, and number of frost free days during the growing season as predictors (Table 3-5). This model showed positive associations between seed production and both increased elevation and increased number of growing season frost free days (Table 3-5). There was a slight concave but generally decreasing relationship between seed production and increased growing season mean minimum temperature (Table 3-5). The response variables rhizomatous ramet production and seed production were square root transformed prior to analysis in order to help meet the assumption of normality.

Table 4-1. Environmental and climate characteristics of the nine *L. dalmatica* study sites. Gs = growing season, Wint. = winter, min. temp. = minimum temperature, perm. wilt. = permanent wilting point, \* = calculated with base 10° C. For site, the first number is the transect identifier, and the second number is the site identifier (1 = low elevation, 2 = mid elevation, 3 = high elevation). NA = not available due to failure of data logger.

Site	1_1	1_2	1_3	2_1	2_2	2_3	3_1	3_2	3_3
Bare ground (%)	54.5	25.3	67.0	32.2	47.3	37.5	80.7	38.3	38.0
Canopy closure (%)	0.0	8.0	3.0	0.0	23.8	30.9	0.0	0.0	18.7
Elevation	1737	2002	2237	1876	2015	2318	1785	1875	2159
Growing degree days*	1117.1	572.3	888.5	NA	960.6	781.4	1224.1	NA	895.8
Gs. frost free	91	74	88.5	89	91	86	91	90	87
Gs. mean min. temp. (C)	7.3	2.76	6.46	6.05	7.07	5.21	8.16	6.16	5.23
Gs. min. temp. (C)	-1.75	-4.75	-1.75	-3	-1.5	-3	-0.75	-2.5	-3.25
Litter cover (%)	16.7	19.8	8.0	30.5	12.7	6.2	3.0	24.0	20.2
pH	7.1	6.5	6.9	7.1	7.2	6.6	7.1	6.7	6.7
Precipitation (cm)	6.1	7.0	5.1	6.1	7.4	10.5	3.7	6.2	7.5
Soil Nitrogen (ppm)	1.5	4.5	2.5	2	1.5	5.5	1.5	3	1.5
Soil Organic Matter (%)	3.6	9.3	4.3	4.9	2.4	4.2	3.2	7.7	5.3
Soil Phosphorous (ppm)	13.0	29.0	27.0	19.0	10.0	27.0	13.0	29.0	26.0
Soil Potassium (ppm)	534.0	560.0	323.0	553.0	419.0	442.0	478.0	533.0	340.0
Vegetation cover (%)	28.8	54.8	26.8	37.3	40.0	56.3	16.5	37.7	41.8
Weeks to perm. wilt.	6.0	7.0	7.5	6.0	6.5	7.0	4.0	6.0	7.0
Wint. frost	211.5	251	224	NA	217.5	168.5	206	NA	230.5
Wint. mean min. temp. (C)	-5.09	-6.43	-6.42	NA	-4.33	-3.26	-4.41	NA	-3.99
Wint. min. temp. (C)	-29.3	-29.3	-29.3	NA	-25.3	-20.3	-26.8	NA	-23.8

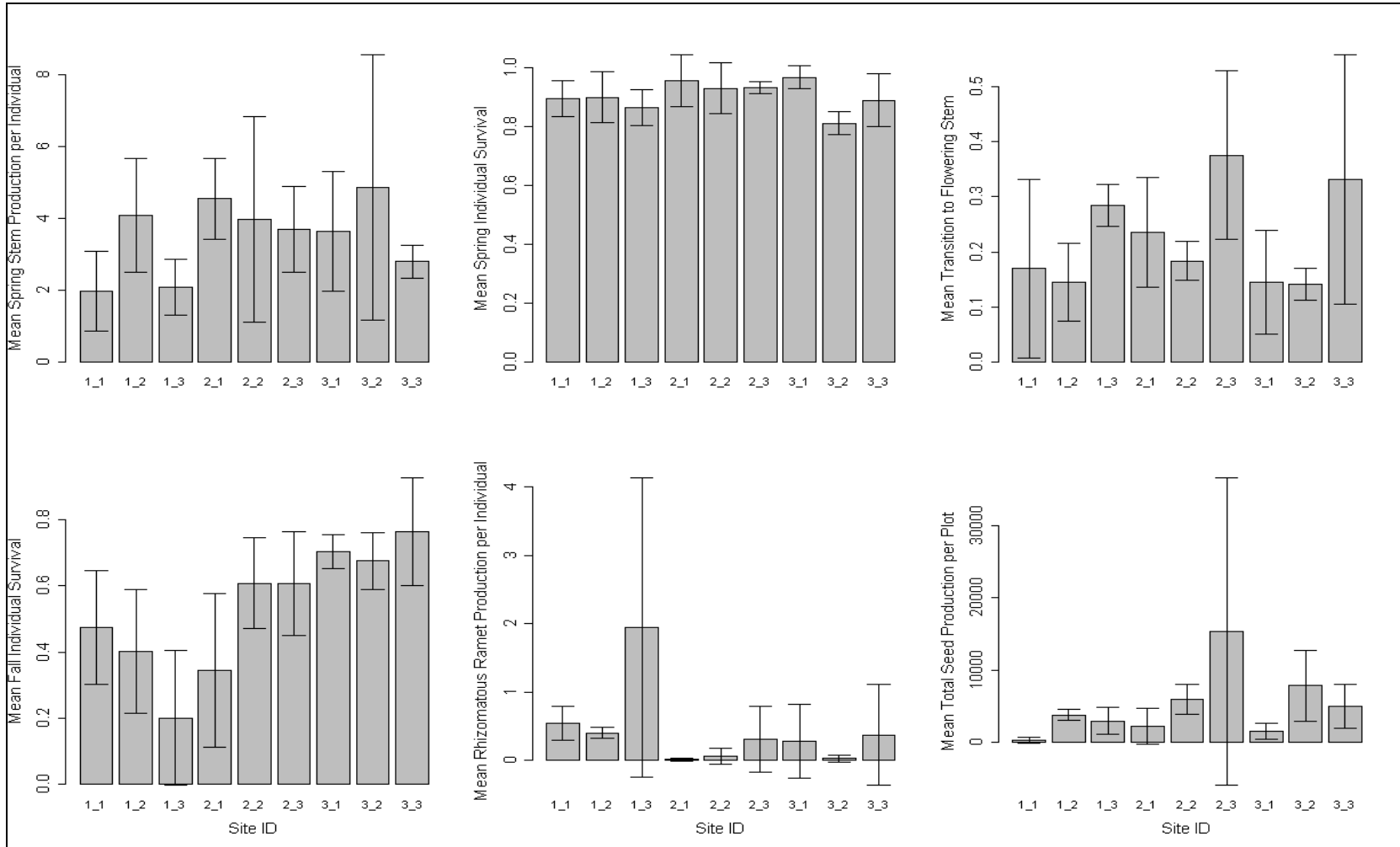


Figure 4-1. Mean transition rates for each *L. dalmanica* site. Error bars represent 95% confidence interval for the mean. For Site ID, the first number is the elevation transect identifier, and the second number is the site identifier (1 = low elevation, 2 = mid elevation, 3 = high elevation). n = 36.

Table 4-2. Values for best model for *transition to flowering* rate.

Gs = growing season, min. temp. = minimum temperature.

Model  $R^2 = 0.27$ , model p-value = 0.01. n = 36.

	Estimate	Std. error	t- value	p-value
Intercept	-0.41	0.23	-1.78	0.089
Gs mean min. temp.	0.28	0.09	3.10	0.005
Gs mean min. temp. <sup>2</sup>	-0.03	0.01	-3.23	0.004

Table 4-3. Values for best model for *fall individual survival* rate.

Wint. = winter. min. temp. = minimum temperature. Wint. frost =

number of days at or below 0° C. Model  $R^2 = 0.55$ , model p-value

= &lt;0.01. n = 36.

	Estimate	Std. error	t- value	p-value
Intercept	0.51	0.30	1.703	0.1027
Wint. mean min. temp.	0.21	0.04	5.285	<0.001
Wint. frost	0.05E-01	0.02E-01	2.554	0.02

Table 4-4. Values for best model for the square root of

*rhizomatous ramet production* rate. Wint. = winter, min. temp. =

minimum temperature. Wint. frost = number of days at or below 0°

C. Model  $R^2 = 0.31$ , model p-value < 0.01. n = 36.

	est	std err	t	p
Intercept	-1.80	5.44	-0.331	0.74353
Wint. mean min. temp.	-2.41	0.70	-3.436	0.00236
Wint. frost	-0.056	0.03	-1.782	0.08858

Table 4-5. Values for best model for for the square root of *seed**production* rate. Gs = growing season, min. temp. = minimumtemperature. Model  $R^2 = 0.35$ , model p-value = 0.01. n = 36.

	Estimate	Std. error	t- value	p-value
Intercept	-1.65E+03	8.20E+02	-2.009	0.058
Elevation	2.26E-01	7.76E-02	2.91	0.009
Gs mean min. temp.	-3.37E+02	1.76E+02	-1.915	0.070
Gs mean min. temp. <sup>2</sup>	2.35E+01	1.22E+01	1.923	0.070
Gs frost free days	2.71E+01	1.49E+01	1.819	0.084

### Castilleja miniata Vital Rates

*C. miniata* sites showed variability in climate and environmental conditions (Table 3-6), but vital rates appeared to be less variable in relation to both climate and environmental conditions than those of *L. dalmatica* (Figure 3-2). Only one vital rate for this species (seed production) was described by any of the climate or environmental variables that were measured. Seed production was best described by elevation and winter mean minimum temperature, and increased with increases in each of these predictor variables (Table 3-7).

### Population Growth Rate of *Linaria dalmatica*

The mean projected population growth rate ( $\lambda$ ) for *L. dalmatica* was found to be variable between sites (Figure 3-3) but there was no clear trend in  $\lambda$  along the elevation gradient (Figure 3-4). There were very few instances in which the distribution of  $\lambda$  showed any consistent pattern across levels of the climatic and environmental variables measured at each site. However, some weak patterns were noted. For growing season precipitation, population growth ( $\lambda > 1$ ) appeared to be related to increased levels of precipitation in general (Figure 3-4), although one site with the lowest level of precipitation had the highest  $\lambda$  value. Lambda also appeared to decrease as the number of weeks to permanent wilting point increased (Figure 3-4). Winter minimum temperature appeared to have some influence on  $\lambda$ , in that the only sites where  $\lambda < 1$  had minimum temperatures of  $-29.5^{\circ}\text{C}$  (Figure 3-5). Lambda did not show any notable relationships with any soil characteristics (Figure 3-6). The highest value of  $\lambda$  was observed at the highest value of growing season mean minimum temperature (Figure 3-4), the lowest

value of vegetation cover (excluding *L. dalmatica*) and the highest value of % bare ground (Figure 3-7). For litter cover, the highest and lowest values of  $\lambda$  were observed at the lowest and highest values of litter cover, respectively (Figure 3-7).

Table 4-6. Environmental and climate characteristics of the nine *C. miniata* study sites. Gs = growing season, Wint. = winter, min. temp. = mean minimum temperature, perm. wilt. = permanent wilting point, \* = calculated with base 10 ° C. For site, the first number is the transect identifier, and the second number is the site identifier (1 = low elevation, 2 = mid elevation, 3 = high elevation).

Site	1 1	1 2	1 3	2 1	2 2	2 3	3 1	3 2	3 3
Bare ground (%)	0.0	21.5	29.8	1.5	2.3	5.0	0.3	0.0	3.5
Canopy closure (%)	39.4	26.3	33.2	47.6	35.4	12.0	43.8	77.4	60.5
Elevation	2096	2683	2812	2151	2303	2368	2159	2183	2239
Growing degree days*	NA	432.3	337.0	667.8	769.9	507.5	913.0	723.4	NA
Gs. frost free	NA	76	63	84.5	82.5	81	87.5	86	NA
Gs. mean min. temp. (C)	NA	4.66	4.12	4.30	4.84	3.93	5.52	4.18	NA
Gs. min. temp. (C)	NA	-3.50	-2.50	-3.50	-3.50	-3.25	-2.75	-2.50	NA
Litter cover (%)	27.2	29.2	46.0	16.8	23.2	21.2	21.8	32.5	26.8
pH	6.3	6.0	6.0	6.9	6.2	6.4	6.3	6.4	5.8
Precipitation (cm)	NA	NA	NA	9.3	11.3	15.7	7.7	6.6	10.2
Soil Nitrogen (ppm)	1.0	3.5	4.5	2.5	7.5	5.0	9.5	0.5	1.5
Soil Organic Matter (%)	9.3	6.6	4.0	6.2	9.0	7.3	11.4	7.2	27.2
Soil Phosphorous (ppm)	16.0	52.0	30.0	4.0	17.0	33.0	29.0	40.0	18.0
Soil Potassium (ppm)	258.0	603.0	316.0	238.0	400.0	358.0	471.0	371.0	372.0
Vegetation cover (%)	95.4	51.8	25.8	89.6	84.1	85.1	86.2	77.1	72.3
Weeks to perm. wilt.	8.0	9.0	9.5	9.5	8.5	12.0	9.5	11.0	12.0
Wint. frost	256.5	246	243.5	242	238.5	245	227	206	226
Wint. mean min. temp. (C)	-8.56	-4.21	-2.99	-7.49	-3.84	-6.84	-1.37	-3.16	-1.83
Wint. min. temp. (C)	-33.50	-29.00	-21.25	-30.00	-22.00	-30.00	-22.00	-19.00	-17.50

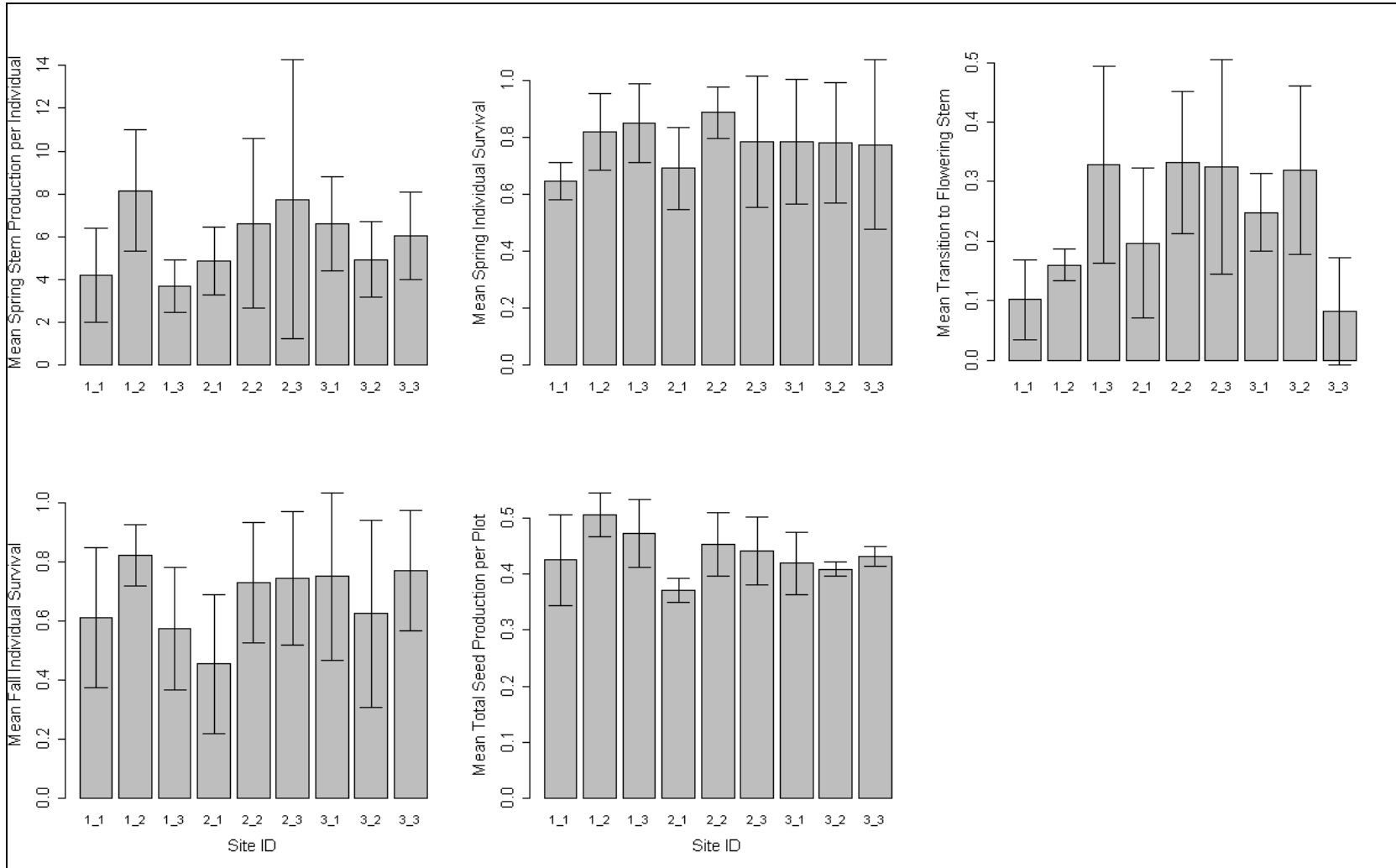


Figure 4-2. Mean vital rates for each *C. miniata* site. Error bars represent 95% confidence interval for the mean. For Site ID, the first number is the transect identifier, and the second number is the site identifier (1 = low elevation, 2 = mid elevation, 3 = high elevation) n = 36.



Table 4-7. Values for best model for the square root of *seed production* rate. Wint. = winter, min. temp. = minimum temperature. Model  $R^2 = 0.25$ , model p-value = 0.04. n = 36.

	Estimate	Std. error	t- value	p-value
Intercept	1.14E-01	2.02E-01	0.567	0.56
Elevation	2.51E-04	9.23E-05	2.716	0.02
Wint. Mean min. temp.	6.09E-03	3.49E-03	1.745	0.1

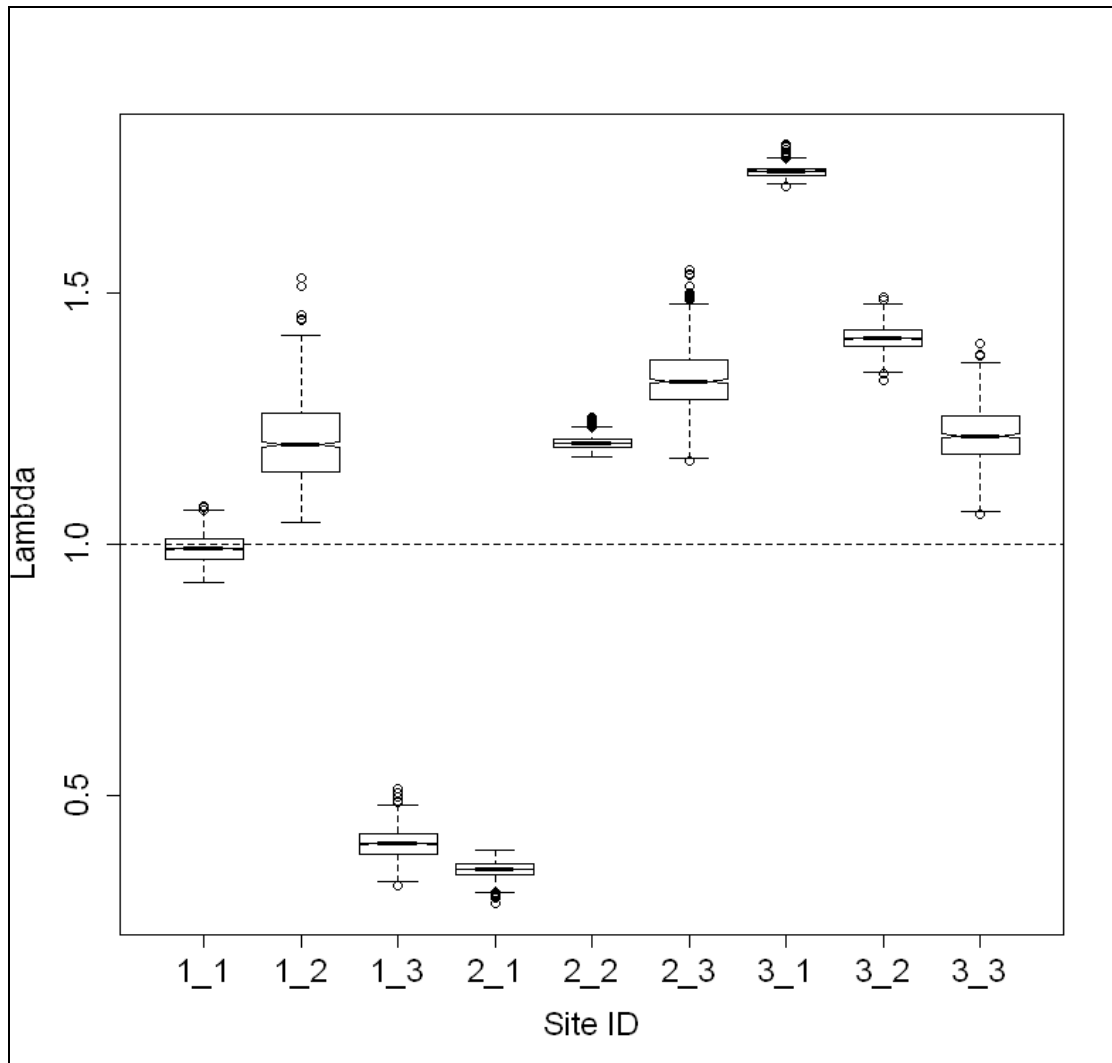


Figure 4-3. Boxplots of the distribution of growth rate (lambda) values by site (site ID) from 1000 simulations of a 30 generation model using a random sequence of transition rates for each iteration of the simulation. n = 1000 for each site. For Site ID, the first number is the transect identifier, and the second number is the site identifier (1 = low elevation, 2 = mid elevation, 3 = high elevation).

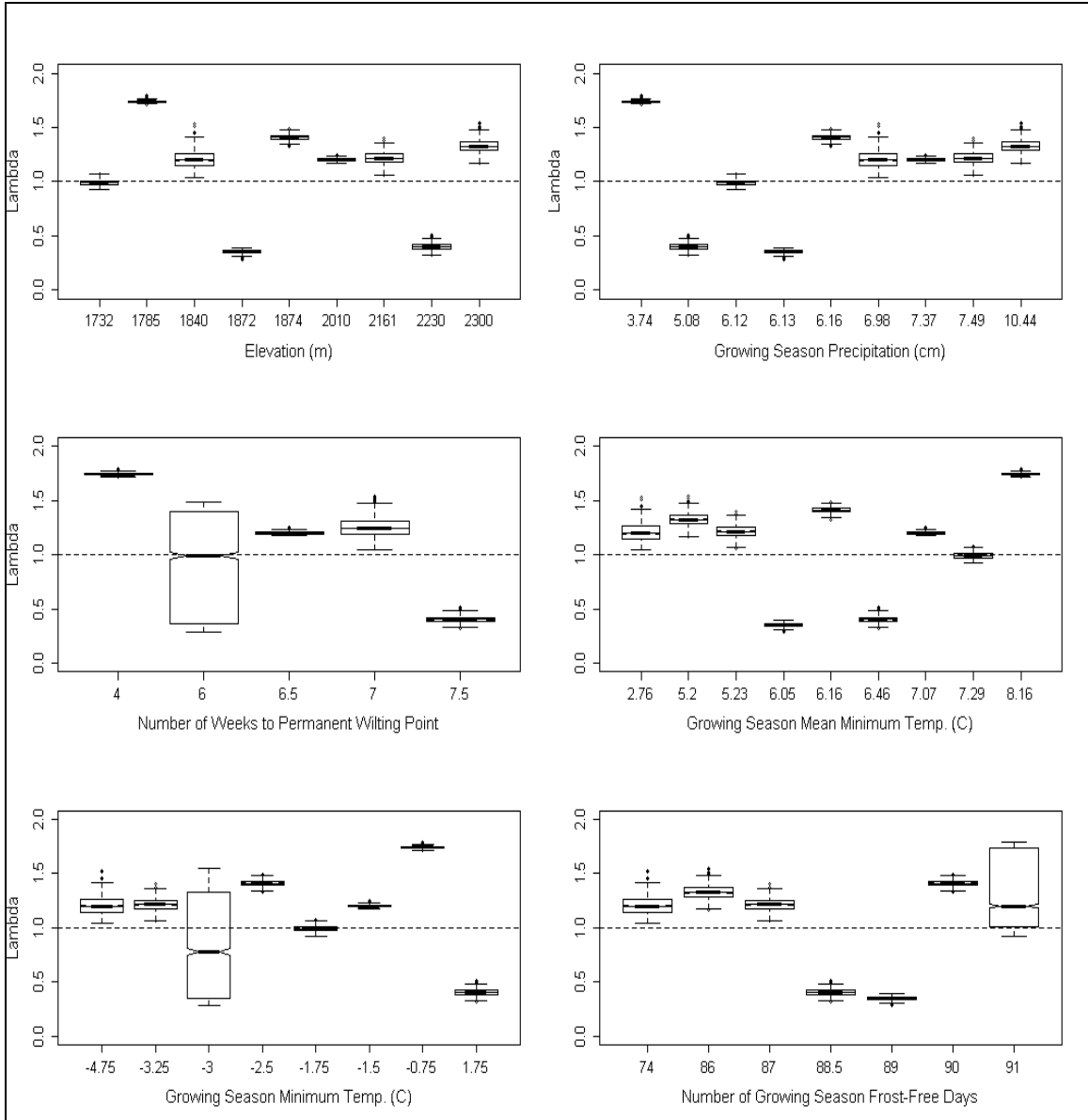


Figure 4-4. Boxplots of distribution of growth rate (lambda) values by elevation and growing season climate variables from 1000 simulations of a 30 generation model using a random sequence of transition rates for each iteration of the simulation.

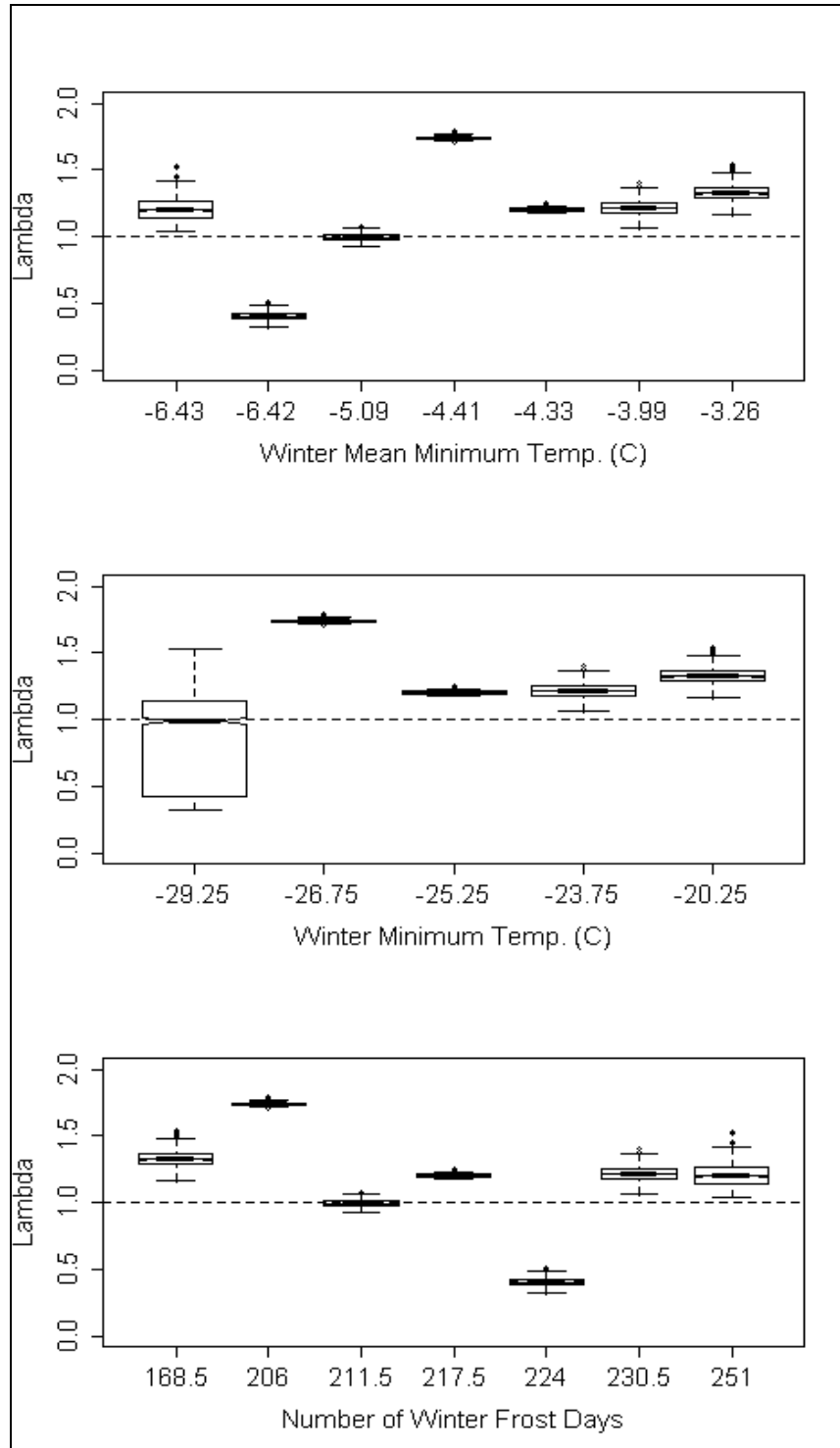


Figure 4-5. Boxplots of distribution of growth rate (lambda) values by winter climate variables from 1000 simulations of a 30 generation model using a random sequence of transition rates for each iteration of the simulation.

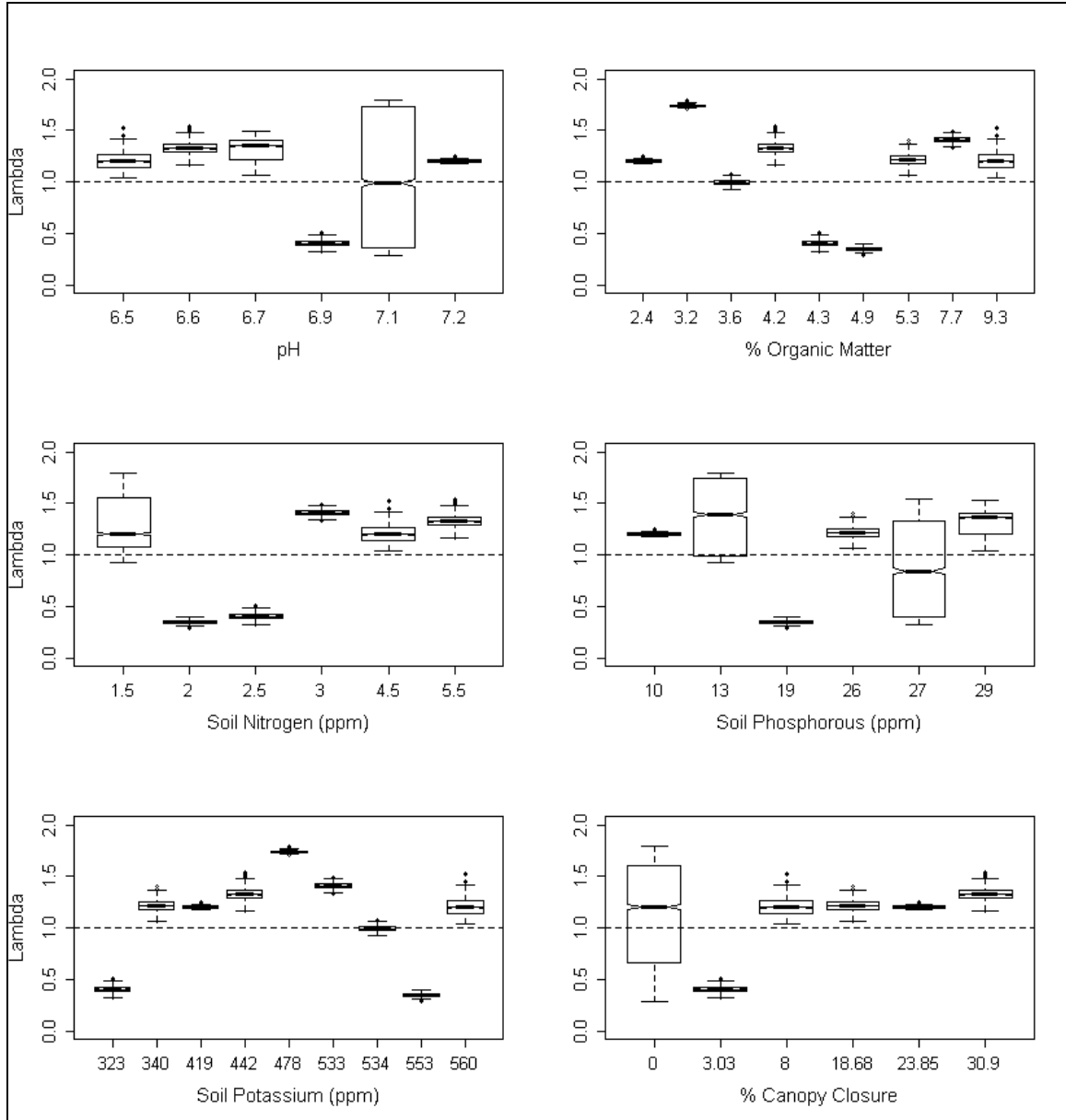


Figure 4-6. Boxplots of distribution of growth rate (lambda) values by environmental variables from 1000 simulations of a 30 generation model using a random sequence of transition rates for each iteration of the simulation.

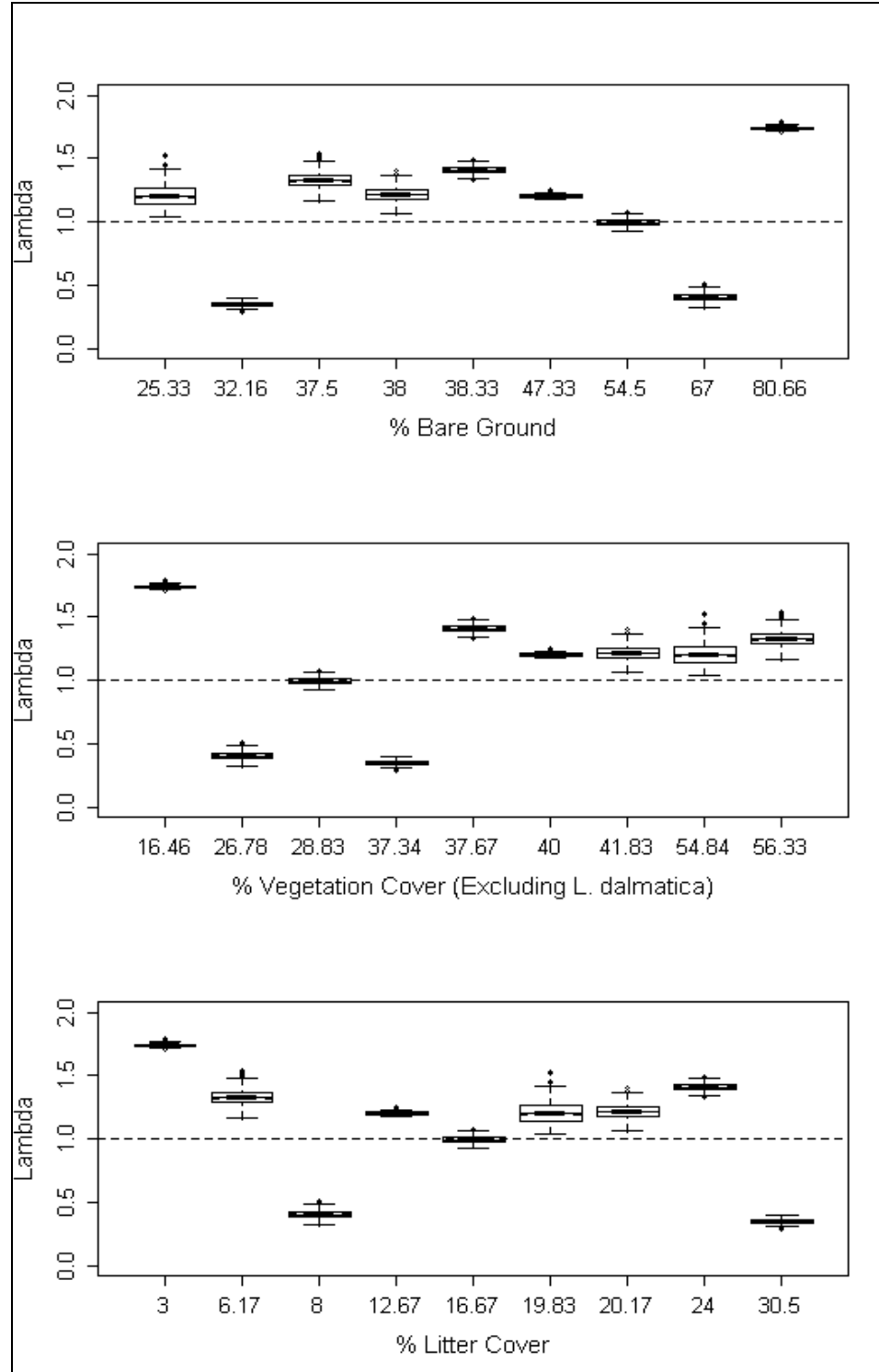


Figure 4-7 Boxplots of distribution of growth rate ( $\lambda$ ) values by environmental variables from 1000 simulations of a 30 generation model using a random sequence of transition rates for each iteration of the simulation.

Vital Rate Sensitivity Analysis  
of *Linaria dalmatica*

The vital rate sensitivity analysis for *L. dalmatica* revealed that population levels of *L. dalmatica* were most sensitive to changes in mature individual survival rate for the fall to spring transition, followed by mature individual survival rate for the fall to spring transition (Table 3-8). These sensitivity values were consistently high among sites.

Sensitivity of the population to changes in all other vital rates was extremely variable (Table 3-8).

Table 4-8. *L. dalmatica* mean growth rate ( $\lambda$ ) values and population sensitivity values for all vital rates for all sites. For Site ID, the first number is the transect identifier, and the second number is the site identifier (1 = low elevation, 2 = mid elevation, 3 = high elevation).

	Site ID	1 1	1 2	1 3	2 1	2 2	2 3	3 1	3 2	3 3
Lambda		0.99	1.21	0.4	0.35	1.2	1.33	1.74	1.41	1.22
Spring Individual Survival		0.82	0.88	0.7	0.35	0.71	0.35	0.79	0.65	0.83
Rhizomatous Production		0.39	0.75	0.52	0.03	0.03	0.01	0.6	0.13	0.71
Stem Production		0.0007	0.04	0.2	0.45	0.22	0.51	0.24	0.27	0.16
Transition to Flowering Stem		0.0006	0.04	0.2	0.44	0.22	0.51	0.24	0.27	0.16
Seed Production		0.0005	0.04	0.2	0.45	0.22	0.51	0.24	0.27	0.16
Germination		0.002	0.04	0.2	0.45	0.21	0.51	0.25	0.27	0.16
Seed Survival		0.005	0.1	0.55	0.78	0.3	0.77	0.33	0.41	0.21
Winter Individual Survival		0.96	0.95	0.87	0.77	0.93	0.8	0.93	0.92	0.94
Seedling Survival		0.002	0.04	0.21	0.45	0.21	0.51	0.25	0.27	0.16

### Discussion

#### *Linaria dalmatica* and *Castilleja miniata* Vital Rates

Several of the vital rates for *L. dalmatica* showed significant associations with climate and environmental predictors, as has been shown for other plant species along

environmental gradients (Mack and Pyke 1984; Carlsson and Callaghan 1994; Chambers et al. 2007; Purves 2009; Eckhart et al. 2011; Gimenez-Benavides et al. 2011). The rate at which vegetative stems transitioned to flowering was a hump shaped (convex) pattern which was highest at intermediate values of growing season mean minimum temperature. Another study (chapter 3) showed that growing season mean minimum temperature declined linearly as elevation increased within the study area, suggesting that the transition to flowering is suppressed at both ends of the current elevation range of this species by both high and low temperatures. Other studies have shown that flowering can be reduced by both high (Lang 1952; Hillman 1959; Menzel et al. 1987) and low temperatures (Lang 1952).

Over winter individual survival of *L. dalmatica* increased with both increased winter mean minimum temperature and increased number of winter days at or below zero. The relationship with these two variables together suggests that perhaps over winter survival of this species is affected by snow pack. Other studies have shown that increased snow pack can have positive effects of plant growth (Wipf et al. 2009; Griffith and Loik 2010; Peng et al. 2010), and serve a protective purpose for vegetation (Frey 1983; Molau 1996; Wipf et al. 2009).

Rhizomatous ramet production decreased under colder winter mean minimum temperatures and increased number of winter days at or below zero. It has been speculated that rhizomatous reproduction is a viable strategy for reproduction in harsh environments (Körner 2003) and that perhaps plants reproduce more vegetatively in these environments. Our data support this hypothesis, in that *L.dalmatica* appears to produce

more rhizomes in areas with colder winter temperatures, but also shows that rhizomatous production may actually decrease if conditions remain cold for too long.

Overall seed production for *L. dalmatica* increased with elevation. While another study showed that seed production per capsule declined with elevation, the large number of capsules produced at some of the high elevation sites counteracted this effect (chapter 3). These high sites had some of the lowest growing season mean minimum temperatures. Additionally, the higher number of seeds produced per capsule at low elevations (with high growing season mean minimum temperatures) was enough to counteract the lower number of capsules produced there. Together, this resulted in the slightly concave but generally decreasing relationship between growing season mean minimum temperature and seed production rate.

The vital rates of *C. miniata* were found to be much less dependent upon climatic and environmental conditions in comparison to the vital rates of *L. dalmatica*, as we hypothesized. The only vital rate which was described by climate or environmental variables for this species was seed production, which increased with increases in both elevation and winter mean minimum temperature. This suggests that warmer winter mean minimum temperatures may promote enhanced seed production for this species.

The fact that none of the other vital rates for *C. miniata* were shown to vary significantly based on climate or environmental variables is not surprising. In chapter 3, it was shown that none of the winter climate variables showed any significant variation along the *C. miniata* section of the elevation gradient. However, growing season climate variables did show variation along that section of the elevation gradient. Thus, perhaps



the lack of variability in vital rates based on climate and environmental conditions is due in part to the fact that these conditions were less variable over the surveyed range for *C. miniata* than they were for *L. dalmatica*. This would suggest that *C. miniata*, having had more time to equilibrate within its range, has filled a niche where its vital rates are relatively stable due to more constant climatic conditions. Another interesting possibility is that *C. miniata* has had time to adapt to the variable conditions within its current range such that its vital rates can remain stable in spite of climatic variation, as has been hypothesized by Eckhart et al. (2011). Although we cannot formally test either of these hypotheses, our data suggest that it is a combination of both, given that there is less variability in some (but not all) of the climatic conditions along this species' elevation range, and that whatever variability there is does not seem to affect the vital rates of the species to any great extent. In contrast, *L. dalmatica* is a relative newcomer to the area, and therefore may be more susceptible to climatic/environmental variations because it has not had time to adapt to all of the environments in which it is now present. This generally reflects the concept of the taxon cycle which states that species with longer residence times tend to exhibit contracted ranges in interior habitats whereas newer colonizing species exhibit expanded ranges in marginal habitats (Wilson 1959).

#### Population Growth Rate of *Linaria dalmatica*

We did not find that the population growth rate of this species decreased at the upper limit of its current elevation range. In fact, there was no discernible trend in  $\lambda$  for this species as elevation increased. The lack of a decrease in  $\lambda$  at the current elevation limit of this species suggests that this species may not yet have reached the limits of its

potential range (Gaston 2003). There was weak evidence that  $\lambda$  for this species was influenced by some of the measured climatic or environmental variables, which suggests that: 1) dispersal may not be the primary limit to this species' current range (Eckhart et al. 2011), and 2) this species' range may be climate limited. Population growth appeared to increase with increased levels of precipitation, but also appeared to increase with decreased number of weeks until the permanent wilting point was reached. This relationship is easily explained, in that most of the precipitation in this area occurs early in the growing season, and that *L. dalmatica* can take advantage of this early season moisture via large taproots (Robocker 1974). Those sites with more persistent soil moisture generally had higher levels of vegetative cover and lower levels of bare ground (Table 3-1). The fact that the highest value of  $\lambda$  for this species occurred where both vegetation cover and litter were the lowest and where % bare ground was the highest further suggests that the relationship between  $\lambda$  and weeks to wilting point is related to increased growth of other vegetation and consequent litter production in sites where soil moisture is retained longer into the growing season. Robocker (1974) noted that this species has low competitive ability in established perennial communities. Other studies have also shown associations between single non-native species abundances and vegetative community characteristics such as native species richness (Knight and Reich 2005) or native species diversity (Ortega and Pearson 2005), and that increased plant litter can decrease establishment of non-native plants (Hager 2004; Bartuszevige et al. 2007).

The general lack of strong relationships between  $\lambda$  and many of the measured climate variables suggests that *L. dalmatica* may be able to tolerate a broad range of climatic conditions. Other studies have suggested that non-native plants which successfully invade mountain systems must be broadly adapted to cope with the variable climatic conditions found along the elevation gradients in these areas (Alexander et al. 2011). However, winter minimum temperature had an interesting relationship with  $\lambda$ , in that the only sites where  $\lambda < 1$  corresponded to the lowest measured winter minimum temperature. This suggests that this species may only be broadly adapted to a point, and that success of this species above its current elevation range may be limited by extremely low winter temperatures, as is common with plants in cold environments (Stocklin and Baumler 1996; Hobbie and Chapin 1998). Thus, if climate warms, this species may be more likely to expand its range upwards.

Despite the lack of any general trend in  $\lambda$  along the elevation gradient, the projected  $\lambda$  values for these sites are reflective of the trend that was observed in stem density for *L. dalmatica* in chapter 3, Figure 3. Initially, *L. dalmatica* stem density had a hump shaped relationship with elevation in 2008 and 2009. However, by 2011, this association was a linear increase. This indicated that the populations above  $\sim 1,900$  m must have experienced a net increase in size from 2008 to 2011. The projected values of  $\lambda$  for four out of the five sites above was  $\geq 1.2$ , with the fifth having  $\lambda = 0.4$ . This general trend of increase corresponds to the change in trends of stem density from 2008 to 2011.

Vital Rate Sensitivity Analysis  
of *Linaria dalmatica*

The vital rate sensitivity analysis of *Linaria dalmatica* indicated that populations of this species are most sensitive to the survival rates of mature individuals during the fall to spring and the spring to fall transitions. This makes sense for a perennial species which reproduces both sexually and asexually, since the presence of individuals from one year to the next can rely heavily upon the survival of individuals from previous years. Seed production, germination, and seedling survival can also be important, but this is not the case for *L. dalmatica*. The mature individual survival rates were the most important in determining population size for this species. Populations were less sensitive to those vital rates related to seeds and seedlings, most likely because rates of seedling survival for this species were very low. This reflects the fact that seedlings of this species were never observed in plots, such that seedling survival had to be estimated as discussed in the methods. Establishment via seedlings must take place for this species (and thus it was given a very low rate in the model) since it has spread discontinuously from its place of introduction in the study area, but these events would seem to be very rare based on our observations. Since this species has such low levels of seedling establishment and reproduces rhizomatously, management methods which focus on the seed/seedling classes would be ineffective for reducing existing populations. However, populations at the upper range limits of this species should be managed in a way that will also limit seed production and thereby reduce the risk of rare/episodic establishment of new populations from seedlings at higher elevations.

### Conclusions

As we had hypothesized, *L. dalmatica* vital rates were associated with variation in climatic conditions to a greater extent than those of the closely related native species *C. miniata*. This is most likely due to the difference in the level of adaptation of each species to its environment (Echkart et al. 2011) based on the length of time that each species has had to adapt to conditions within its current range. In the population models, the projected population size of *L. dalmatica* was found to be most sensitive to changes in over winter survival rates. Other studies have shown that increased snow cover can act as a protective layer for vegetation (Frey 1983; Molau 1996; Wipf et al. 2009) and the positive association between over winter survival and both increased winter mean minimum temperatures and number of days at or below zero indicates that increased snowpack may increase the survival of this species (since increased snowpack would both increase winter mean minimum temperature by buffering the area from lower temperatures and increase the number of days where temperatures are near 0° C). On the other hand, it also suggests that increasing winter temperatures under a warming climate could increase survival of this species. Since the populations which were decreasing were all at sites which had the lowest measured minimum winter temperatures, this suggests that extremely low winter temperatures are a strong factor in determining the success of this species. Anything that would tend to increase winter temperatures, be it insulation due to increased snow pack or increased air temperatures under a warming

climate, may favor the survival of this species and allow it to colonize new areas above its current elevation distribution.

Although the vital rates of *L. dalmatica* were found to be variable along the elevation gradient, this did not result in a decrease in  $\lambda$  with increased elevation as we had hypothesized. Instead of responding to climate in a progressive way,  $\lambda$  appeared to be limited by extremely low winter minimum temperatures. Thus, even though there is no clear trend in  $\lambda$  for this species along the elevation gradient indicating successively more limited population growth due to increasingly harsh climatic conditions, this species may be experiencing a climatic barrier due to extremely low winter temperatures based on: 1) the observed decrease in the overwinter survival rate of this species with decreased winter mean minimum temperature and 2) the qualitatively observed decline in  $\lambda$  at sites with the lowest winter mean minimum temperatures. We have hypothesized that the location of this barrier could be shifted in the future based on increased snow pack prior to extremely cold temperature events and/or a warming climate. In addition, properties of the vegetative community appear to be exerting more influence on  $\lambda$  of *L. dalmatica* throughout its current elevation range. Together, this suggests that the current range of this species may be limited by climate, but within its current range the species may be primarily limited by characteristics of the vegetative community.

In the future, more specific tests of establishment and survival need to be conducted to test the theory that this species is currently experiencing a climatic limit to further spread. The lack of rigorous tests of this climatic limitation theory coupled with the absence of any other climatic factors associated with  $\lambda$  suggest that this species is

broadly adapted within its current range, and that it could potentially spread outside of this range under current climatic conditions. The lack of a consistent decrease in  $\lambda$  at the upper elevation limits of this species is further evidence of this. Additionally, the fact that propagule pressure for this species is not constrained at higher elevations (chapter 3) suggests that it could successfully spread upward in the absence or reduction of climatic barriers. It is still possible that climate may be limiting the establishment of *L. dalmatica* above its current elevation limits, but our data do not provide enough conclusive evidence of this.

Due to the sensitive nature of alpine habitats and the large proportion of plant diversity and endemic species contained therein (Körner et al. 2011), the impacts of non-native plant species in these areas could be particularly harsh. This, in itself, may be enough justification to increase efforts to limit invasions of non-native plant species, such as *L. dalmatica*, into these areas. Although established *L. dalmatica* plants are viewed as competitive in that increased *L. dalmatica* density has been shown to be associated with decreased density of other plants (Robocker 1974; Wilson et al. 2005), whether or not this species is capable of *displacing* other vegetation is still questionable. Seedlings are noted to not be particularly competitive with established vegetation (Gates and Robocker 1960; Robocker 1974) so this species may have difficulty establishing in heavily vegetated areas. However, the alpine zone is subject to frequent natural soil disturbances (frost heaving and animal burrowing) and is relatively sparse in established vegetation. In the absence of climate constraints, this would seem to be an ideal habitat for *L. dalmatica* establishment. Since *L. dalmatica* has been shown to be broadly adapted and

we have not been able to provide any conclusive evidence of any climatic limitation for this species, populations at its upper range limits should not be ignored in management efforts. In addition, areas above its current elevation range should be surveyed frequently for the presence of this species in order to prevent the spread of this species into higher elevation environments.



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CHAPTER 5: USING DIRECTIONAL ECOLOGICAL FILTERING AS A MODEL  
FOR THE EXPANSION OF A NON-NATIVE SPECIES (*LINARIA DALMATICA*) IN  
MOUNTAIN SYSTEMS

Introduction

Recent interest in the dynamics of non-native plant species invasions in mountain systems has increased due to the fact that these systems are not yet as heavily invaded by non-native plants as lowland systems (Pauchard et al. 2009). Also, due to their steep environmental gradients and the recent nature of many plant species introductions, mountain systems are viewed as a unique opportunity to examine the dynamics of non-native plant invasions (Becker et al. 2005; Pauchard et al. 2009). The potential changes to these areas in the near future also add some urgency to providing an understanding of the causes and effects of plant invasions. Climate change has the potential to alter the current range of non-native plant species (Becker et al. 2005; McDougall et al. 2005; Marini et al. 2009; Pauchard et al. 2009) and could potentially result in increased success of non-natives plants at higher elevations (McDougall et al. 2005; Crimmins et al. 2009). In addition, the increased use of these mountainous areas by humans could result in more opportunities for non-native species establishment due to an increase in dispersal vectors and suitable habitat (McDougall et al. 2009; Pauchard et al. 2009). For many recent invasions, it is obviously impossible to determine long term effects. However, one study has suggested that non-native plants may impact alpine communities in the long term by limiting pollination of native plants if present at high enough densities (Munoz and

Cavieres 2008). It has also been shown that non-native plants can homogenize plant communities across the landscape (McKinney 2004). It is therefore possible that, in addition to upward range shifts which could cause homogenization of alpine plant communities (Jurasinski and Kreyling 2007), non-native plants could intensify the degree of plant community homogenization in the alpine landscape on a longer timescale (McKinney 2004).

The role of non-native plant species in the landscape in general is a hotly debated topic. While many studies support the hypothesis that non-native plant species have detrimental impacts on native plant communities (Collier et al. 2002; Chen et al. 2007; Galbraith-Kent and Handel 2008; Ens et al. 2009; Flory and Clay 2010; Vila et al. 2010; Brewer 2011; French et al. 2011), others suggest that the presence of non-native plants may be more a symptom of disturbance than a direct threat to native plant communities (MacDougall and Turkington 2005; Maskell et al. 2006). Although interest is primarily focused on the effects of non-native plants on native plants, it is also necessary to consider the effect that native plant species richness has on non-native plant abundance. The concept of invasibility as a property of native plant communities has been discussed extensively (Rejmánek 1989; Lonsdale 1999; Davis et al. 2000; Naeem et al. 2000; Prieur-Richard et al. 2000; Wardle 2001; Brown and Peet 2003; van Ruijven et al. 2003; Walker et al. 2005; Maron and Marler 2007; Belote et al. 2008). However, studies quantifying the effects of the native community on individual non-native species abundance are not common.

Native plant species richness is often used as a metric by which to gauge the impact of non-native plant species on the landscape. This, in itself, has added to the uncertainty of the matter, largely because non-native plant species are associated differently with native plant species richness depending on the scale of observation (Lonsdale 1999; Davies et al. 2005; Knight and Reich 2005; Fridley et al. 2007; Powell et al. 2011). Studies that have examined this relationship at multiple spatial scales have found the relationship to be negative at small spatial scales (e.g. plot scale studies) and positive at large spatial scales (Davies et al. 2005; Knight and Reich 2005). When considering the concept of invasibility, the same rule seems to apply. Studies which examined the relationship between invasibility and native species diversity or richness at multiple scales found a positive relationship at larger scales, but a negative relationship at smaller scales (Brown and Peet 2003; Knight and Reich 2005). Experimental or observational studies conducted only at smaller scales have found a negative relationship (Naeem et al. 2000; Prieur-Richard et al. 2000; van Ruijven et al. 2003; Von Holle and Simberloff 2005; Maron and Marler 2007), whereas those conducted only at larger regional scales have found a positive relationship (Stohlgren et al. 1999; Stadler et al. 2000) between native species richness or diversity and invasibility. Despite all of the interest in the concept of invasibility, there still are no unifying theories which would allow one to predict the invasibility of a plant community or ecosystem based on its attributes. However, in relation to the concept of non-native plant invasions in mountain systems, one general theory has the potential to detail the general process underlying the observed trends in non-native plant species richness in these areas.



The theory of directional ecological filtering, as explained by Alexander et al. (2011), has shed some light on the phenomenon of non-native plant community assembly in mountain systems. Although this theory deals with non-native plant species as a group, it does have potential applications in a single species context. This theory states that the non-native flora of a given mountainous area is often composed of nested subsets of lowland adapted species. As elevation increases, the number of species from the lowland pool which can survive decreases as a result of environmental filters (Alexander et al. 2011). Thus, as one moves upslope, fewer and fewer non-native species are encountered. This trend has been observed in several studies (Tassin and Riviere 2003; Arevalo et al. 2005; McDougall et al. 2009; Pauchard et al. 2009; Alexander et al. 2011; Seipel et al. 2012). One of the main concepts of this theory is that successful mountain invaders will be broadly adapted species which are capable of surviving in many different microclimates (Alexander et al. 2011). As a result, these species will be widespread throughout elevation gradients, occurring at both low and high elevations (Alexander et al. 2011). In contrast, native plant species along elevation gradients have shown a tendency towards endemism (Kessler 2000) and decreased range sizes (Kessler 2001) and might therefore be expected to have narrower elevation range widths than non-native species along the same elevation gradients (Alexander et al. 2011). To test the validity of this, the range size of a non-native plant species could be compared to the mean range width of native plant species along the same elevation gradients. The hypothesis would be that successful mountain invaders will have a much broader range than the majority of

the native plants, such that the invader's range encompasses the ranges of the majority of the native plant species present in the same area.

The general goal of this study was to examine the relationship between the successful mountain invader *Linaria dalmatica* (L.) Mill, in the Greater Yellowstone Ecosystem and the native plant communities and species within its current distributional range. Our study was set up to address four main objectives. Our first objective was to examine the current range of *L. dalmatica* as compared to the range sizes of individual native species to see if there was any support for the theory of directional ecological filtering taking place for this species. Specifically, we hypothesized (H1) that if *L. dalmatica* fit within the framework of directional ecological filtering, its current elevation range width would be broader than the mean range width of the native species found within the same elevation range. Another key component to the theory of directional ecological filtering is that the non-native plant communities found at higher elevations are nested subsets of the non-native plant community found at lower elevations. A previous study conducted in the same general geographic area (Alexander et al. 2011) found that non-native plant richness decreased with elevation and that non-native plant communities had a higher degree of nestedness (i.e. the species in species poor communities were subsets of more species rich communities) than would be expected by chance. We hypothesized (H2) that these relationships would hold specifically within the context of our study area. Confirmation of both of these hypotheses would lend support to the theory of directional ecological filtering as a mechanism of non-native plant

community assembly in mountain systems and demonstrate that this theory can be tested within the context of the range of a single non-native plant species.

Our second objective was to determine if there was any trend in the occurrence (which incorporates establishment and mortality) of *L. dalmatica* along the elevation gradient within the study area. Based on several previous studies of non-native species richness along elevation gradients (see Pauchard et al. 2009), we hypothesized (H3) that the probability of occurrence of *L. dalmatica* would either decrease at both ends of the current elevation range of the species, or decrease at the upper limit of the species. Our third objective was to test for relationships between *L. dalmatica* cover and vegetative community characteristics which might indicate that there were some plant communities which were more resistant to invasion of this species. We hypothesized (H4) that several potential vegetative community characteristics such as native and non-native plant species richness, plant diversity, perennial, annual and total plant species cover, bare ground, and litter cover could account for variation in *L. dalmatica* cover within its current range. Since elevation has been shown to influence stem density for this species (Chapter 3) we also hypothesized (H5) that it would account for some of the variation in *L. dalmatica* cover.

Our fourth objective was to see if any of the characteristics of the vegetative community varied systematically between areas with *L. dalmatica* and those areas without *L. dalmatica*. We hypothesized (H6) that the presence of *L. dalmatica* could be associated with the plant community characteristics discussed above in relation to H4. Testing both H4 and H6 gave us some ability to make comments about the direction of

influence between the native plant community and *L. dalmatica*. For example, if there were associations between *L. dalmatica* cover and the vegetative community (H4) and the presence of *L. dalmatica* was associated with changes in those community characteristics (H6), this would indicate that *L. dalmatica* was driving the plant community associations proposed by H4. Alternatively, if the communities with and without *L. dalmatica* were similar in composition, then this would suggest that *L. dalmatica* was not driving the association and that the vegetative community was more influential in the associations proposed by H4.

## Materials and Methods

### Study Area and Site Selection

This study was conducted along an elevation gradient within the Northern Range of Yellowstone National Park, in the vicinity of Gardiner, MT, 45°01'60" N, 110°42'33" W, 1,598 m elevation. Three networks of linked roads were chosen as replicate elevation gradients in the area, and will henceforth be referred to as elevation transects. See figure E-1 for map of study area. During July and August of 2008, the three elevation transects were surveyed for the presence of *L. dalmatica* to determine the elevational extent of the species within the study area. During initial surveys, an effort was made to identify every distinct population of *L. dalmatica* present within 5 to 200 m of the elevation transects (roads) from their lowest elevations up to the highest extent of the species. Six *L. dalmatica* survey sites were then selected from the pool of sites on each elevation transect to evenly represent the elevation range of the species from the lower limit of its range to

the upper limit of its range. Six 1/4 m<sup>2</sup> vegetation survey plots were randomly established within *L. dalmatica* populations at each one of the study sites. Each plot was marked and its position recorded with a GPS (Global Positioning System, Trimble GeoXT 2008 Series). At each site, four additional 1/4 m<sup>2</sup> vegetation survey plots were randomly placed outside of but within 25 m of *L. dalmatica* populations. Within each of the survey plots, the percent of bare ground (including rocks), litter (including mosses and lichens), species richness, *L. dalmatica* cover, and the percent cover of all other plant species were recorded individually by a single observer during the growing season of 2011. Since individual species occurred in different layers of vegetation, total cover of the plot was not bounded at 100%.

We also wanted to investigate the probability of establishment of *L. dalmatica* along elevation gradients within the study area in general. This was not possible using the data collected as described above, since all of the survey plots were within the current range of the species, and had been purposefully stratified based on the presence of *L. dalmatica*. Therefore, it was necessary to use other data collected during a comprehensive survey of the Northern Range of Yellowstone National Park. Transects of 1km length (379 total) were surveyed for the presence of non-native plants during four summers (2001-2004) (Rew et al. 2005). Transects were 2km in length and started at random locations along either trails or roads. Successive 10 m by 10 m plots were observed travelling perpendicular to the trail or road along these transects. The presence of any non-native plant species was recorded for each plot using a GPS unit and this data

was then converted to occurrence (presence/absence) data. More detailed methods are described in Rew et al. (2005). Here, we selected only transects that started from roads.

### Data Analysis

#### *L. dalmatica* in Relation to Directional Ecological Filtering Theory

All data analysis was completed using R version 2.14.1 (R-Development-Core-Team 2011). To address the first objective, the elevation range width of each plant species surveyed within *L. dalmatica*'s range along the three elevation transects was calculated. Native species range widths were then compared to the elevation range width of *L. dalmatica* using a one sided one sample t-test. The null hypothesis for this test was that the mean elevation range width of native species would be equal to 568 m, which is the current elevation range of *L. dalmatica* within the study area. The alternative hypothesis was that the mean elevation range width of native species would be less than 568 m. Non-native species richness was regressed against elevation in a Poisson generalized linear model (GLM) to determine if there was any relationship between non-native species richness and elevation within the study area. Following the methods of Alexander et al. 2011, a nestedness analysis was performed for the native and non-native plant communities within the range of *L. dalmatica* using the oecosimu function in R. This function derives the probability that the observed matrix of presence/absences for species (columns) at different sites (rows) is more or less nested than randomized matrices after a specified number of successive randomizations (1000 for this analysis). For this analysis, the observed matrix rows were ordered by increasing elevation of site

and columns were ordered by decreasing occurrence of species, following the methods of Alexander et al. (2011). During randomizations, the species richness of each site was maintained while the species composition was randomized (method R1 in oecosimu), and the ordering of rows and columns was also maintained (nestfun = nestednodf and order = F in oecosimu). This allowed us to test the hypothesis that the plant communities of species-poor, high elevation sites are nested subsets of plant communities in species-rich, low-elevation sites (Almeida-Neto et al. 2008; Alexander et al. 2011).

#### Occurrence of *L. dalmatica* along the Elevation Gradient Within the Study Area

To address the second objective, data from the YNP survey was used. From this data, only transects that began on a road were used in order to keep the survey area (near roads) consistent with that of this study. For each of the 164 transects which had plots in close proximity to a road, 10 plots were randomly sampled from within 250 m of the road. Each plot had a binary presence/absence value for *L. dalmatica*, and this variable was regressed against elevation and its polynomial term using a binomial GLM.

#### Relationship Between *L. dalmatica* Cover and the Vegetative Community

To address the third objective, the response variable *L. dalmatica* cover was logit transformed and used as the response variable in linear regressions. A simple model regressing *L. dalmatica* cover against elevation and the polynomial of elevation was investigated first, based on trends previously noted with stem density for this species along elevation gradients. Next, full models were run regressing *L. dalmatica* cover

against total species richness, non-native species richness, native species richness, total vegetation cover, annual species cover, perennial species cover, species diversity, percent bare ground, and litter cover individually. *L. dalmatica* was excluded from the data when calculating levels of species richness, diversity, and cover for the predictor variables. In addition to these vegetative community predictor variables, elevation and elevation transect ID were also included in the full models, along with all possible pairwise interactions between elevation, elevation transect ID, and the individual vegetative community predictor variables. Polynomial relationships were examined for all continuous predictor variables. Non-significant variables and interactions were systematically removed from models until a final model was achieved for each vegetative community predictor variable.

#### Relationship Between *L. dalmatica* Presence and the Vegetative Community

To address the fourth objective, the vegetative predictor variables listed above were used as *response* variables to evaluate if these vegetative community characteristics varied based on the presence of *L. dalmatica* within its current range of invasion. Response variables pertaining to percent cover were logit transformed prior to analysis. For each site, four out of six survey plots within *L. dalmatica* populations were randomly drawn from the dataset to pair with the four survey plots outside of *L. dalmatica* populations to achieve a balanced design for analysis. Predictor variables for these models were the type of plot (inside population or outside of population), and elevation. A nested ANCOVA approach was used to analyze these data, with elevation as the



continuous predictor variable two nested variables (site within plot type, and elevation transect within plot type) as factor covariates.

## Results

### *L. dalmatica* in Relation to Directional Ecological Filtering Theory

The mean range width of native species within the current range of *L. dalmatica* was 217.6 m, and was significantly less than the range (568 m) of *L. dalmatica* ( $p < 0.001$ ). Non-native plant species richness declined with increasing elevation ( $p = 0.055$ ). Nestedness within the current range of *L. dalmatica* was found to be significantly greater than that expected by random chance for the non-native plant communities, but not for the native plant communities ( $p < 0.001$  and 0.19 respectively, Figure 4-1).

### Occurrence of *L. dalmatica* along the Elevation Gradient Within the Study Area

In the examination of the probability of establishment of *L. dalmatica* along elevation gradients within the study area, elevation was found to have a polynomial relationship with the probability of establishment for the YNP Survey data ( $p < 0.05$ , Figure 4-2)

### Relationship Between *L. dalmatica* Cover and the Vegetative Community

We found that elevation alone (either as a linear or polynomial predictor) did not describe a significant portion of the variation in *L. dalmatica* cover (Table 4-1).

Elevation, elevation transect ID, and all pairwise interactions between elevation, elevation transect ID, and the individual vegetative predictor variables were found to be

non-significant for all of the vegetative community predictor based models. Thus, the final models included only the individual vegetative community variables as predictors. Total richness, native richness, total vegetation cover, and perennial cover were all negatively associated with *L. dalmatica* cover ( $p < 0.05$ , Table 4-1), while there was weak evidence of a positive association between non-native species richness and *L. dalmatica* cover ( $p = 0.07$ , Table 1). None of the other variables tested had significant associations with *L. dalmatica* cover (Table 4-1.)

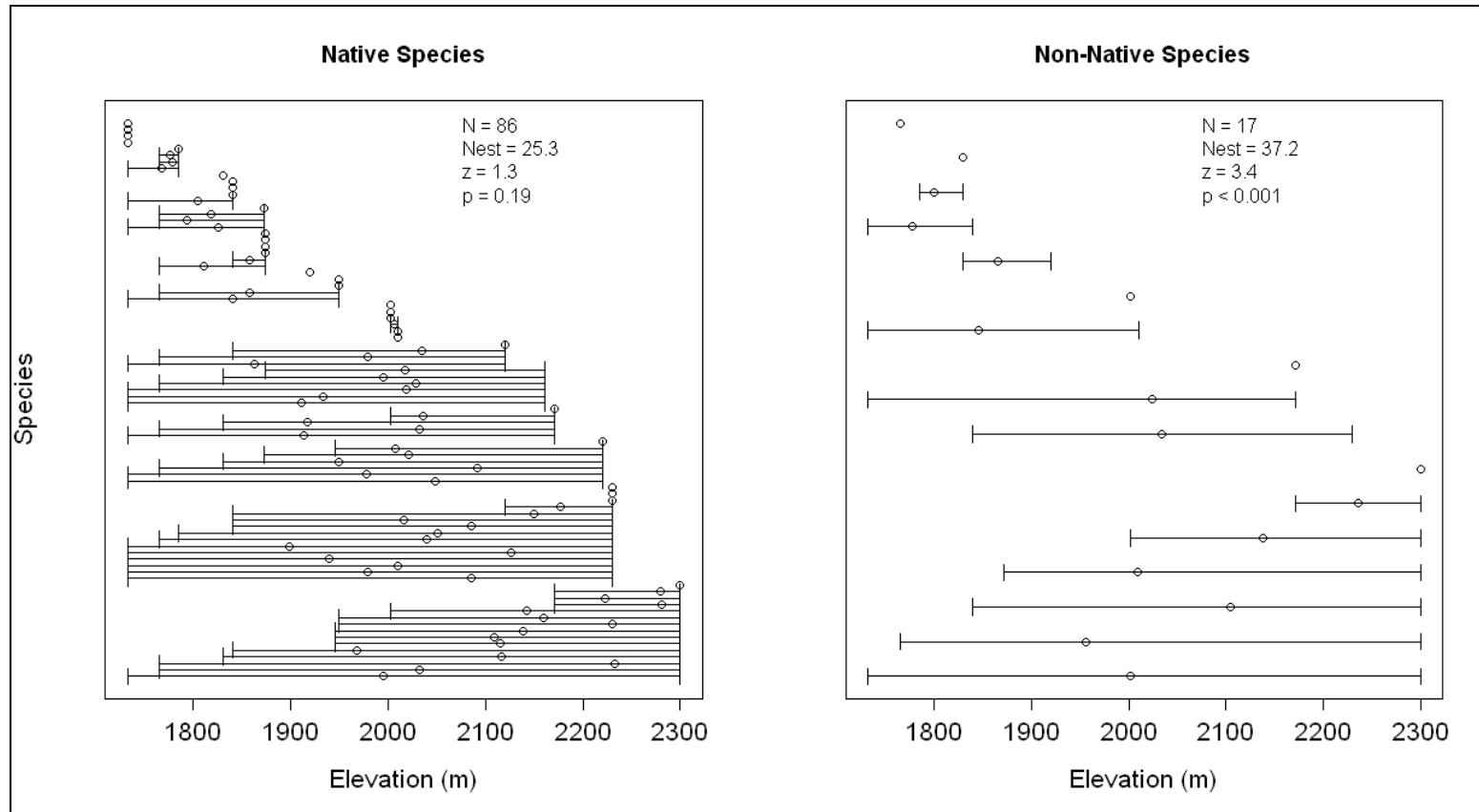


Figure 5-1. Mean, minimum and maximum elevation of occurrence for native and non-native species within the current range of *L. dalmatica*. Each horizontal line indicates the elevational range of an individual species. Open circles indicate mean elevation of occurrence. N = number of species. Nest = calculated nestedness value, z = z-score, and p = p value. Only values from the analysis of nestedness among sites are presented. Nest and z increase with increasing nestedness. Z scores significantly less than or greater than 0 indicate that species composition is respectively less than or greater than would be expected by random chance. Y-axis is dimensionless.

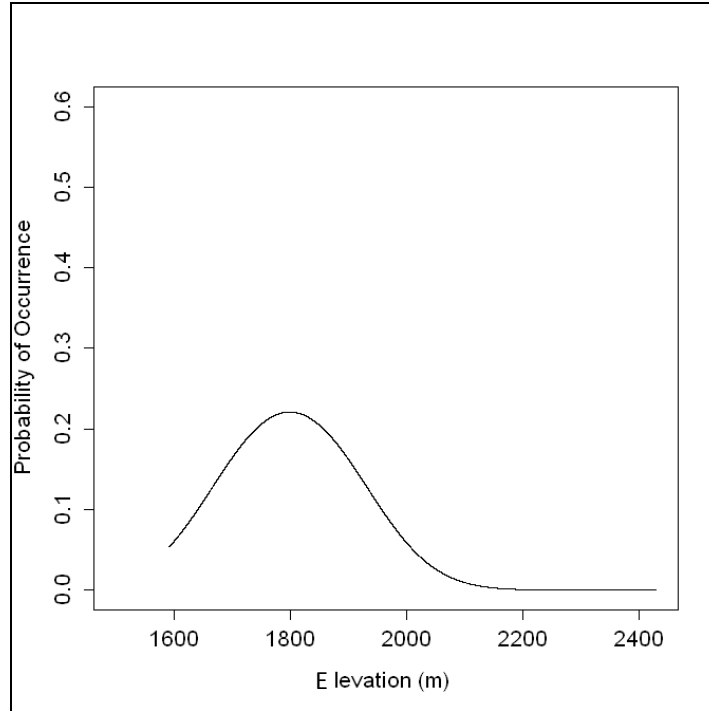


Figure 5-2. *L. dalmatica* probability of occurrence predicted from Yellowstone National Park survey data, within the Greater Yellowstone Ecosystem. p-value for curve < 0.05, n = 1,639.

Table 5-1. Results of models of individual vegetative community predictor variables versus logit *L. dalmatica* % cover. n = 69 for all regressions.

Predictor Variable	Estimate	Std. Error	t-value	p-value	Adj. R <sup>2</sup>
Elevation	-8.51E-03	2.16E-02	-0.395	0.69	
+ elevation <sup>2</sup>	2.02E-06	5.35E-06	0.378	0.71	-0.02
Elevation	-0.00038	0.000791	-0.479	0.63	-0.01
Total richness	-0.17	0.06575	-2.541	0.01	0.07
Native richness	-0.21	0.06233	-3.393	<0.01	0.13
Non-native richness	0.25	0.1351	1.828	0.07	0.03
Vegetation cover	-0.01	0.006059	-1.962	0.05	0.04
Perennial cover	-0.02	0.005799	-2.607	0.01	0.08
Annual cover	0.01	0.01638	0.79	0.43	-0.00556
Litter	-0.01	0.00772	-0.98	0.33	-0.00059
Bare ground	-0.003	0.005282	-0.506	0.61	-0.01106
Diversity	-0.7887	0.6728	-1.172	0.245	0.005

Relationship Between *L. dalmatica*  
Presence and the Vegetative Community

There was no evidence that any of the vegetative community variables above had associations with the type of survey plot (inside vs outside of *L. dalmatica* population) except for the variables of non-native plant species richness (excluding *L. dalmatica*) and plant litter cover. There was evidence that mean non-native plant species richness was higher in plots inside than it was in plots outside of *L. dalmatica* populations (means = 1.1 +/- 0.11 SE and 0.8 +/- 0.11 SE respectively,  $p = 0.03$ , Figure 4-3) after accounting for the effects of elevation and the nested factors. Mean native species richness for plots inside vs outside of *L. dalmatica* populations was identical at 4.7 species. There was strong evidence that plant litter cover was higher in plots outside than it was in plots inside of *L. dalmatica* populations (means = 18 +/- 1.96 SE and 26 +/- 2.36 SE respectively,  $p < 0.01$ , Figure 4-4) after accounting for the effects of elevation and the nested factors.

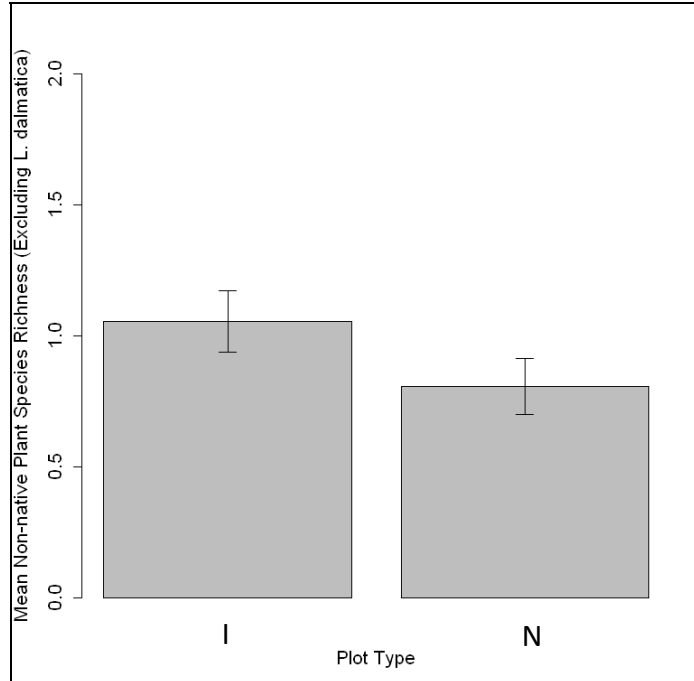


Figure 5-3. Mean non-native plant species richness with standard error bars by plot (0.25 m<sup>2</sup>). I = inside *L. dalmatica* patch (n=72), N = outside of *L. dalmatica* patch (n=72). p-value for difference in means from model = 0.03.

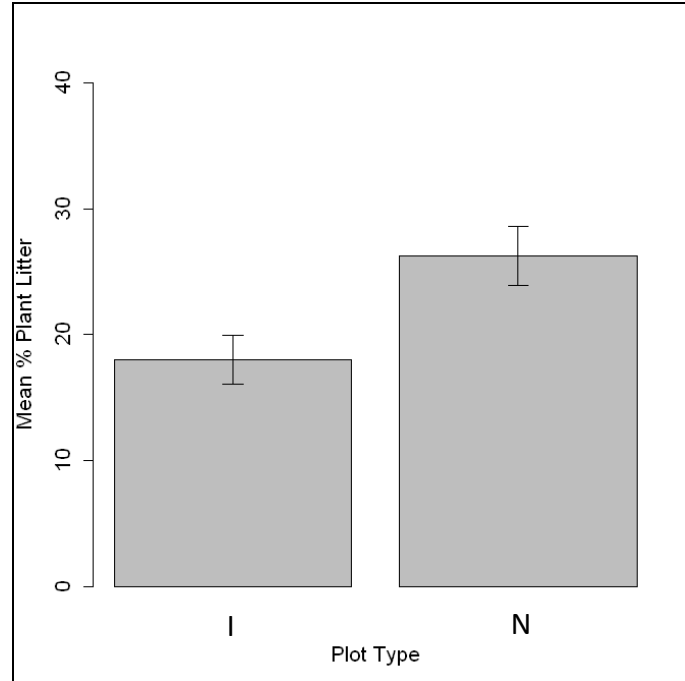


Figure 5-4. Mean percent plant litter cover with standard error bars by plot (0.25 m<sup>2</sup>). I = inside *L. dalmatica* patch (n=72), N = outside of *L. dalmatica* patch (n=72). p-value for difference in means from model = 0.002.

### Discussion

Based on the analyses of range width, *L. dalmatica* appears to fit the profile of a non-native species which has undergone directional ecological filtering since its introduction to the area roughly 60 years ago. Its range width is significantly greater than the mean range width of native species within its current range, confirming H1. This suggests that it has broader climatic tolerance than the native species within its current range, as suggested by directional ecological filtering theory (Alexander et al. 2011). In terms of the nestedness analysis, our results agree with those of Alexander et al (2011). We found that non-native species richness decreased with elevation, and that the

relatively species poor non-native communities at higher elevations were nested subsets of the relatively species rich non-native communities at lower elevations, confirming H2.

*L. dalmatica* cover was associated with many of the vegetative community characteristics along the elevation transects. Other studies have shown similar relationships, whereby the cover of a single non-native species was associated with vegetative community characteristics such as native species richness (Knight and Reich 2005) or native species diversity (Ortega and Pearson 2005). This confirms our hypothesis (H4) that vegetative community characteristics would influence cover of this species. Since associations were present between *L.dalmatica* cover and the vegetative community characteristics, but there was no real difference in those vegetative community characteristics based on whether or not *L.dalmatica* was present (H6), this would suggest: 1) that the vegetative community characteristics were influencing the cover of *L. dalmatica* and 2) that the presence of *L. dalmatica* was not, on average, effecting vegetative community characteristics. However, we did find that the typical scenario where decreased native species richness is associated with increased non-native species richness existed within our study plots after accounting for the effects of elevation ( $p < 0.001$ ), as has been found in several other studies (Naeem et al. 2000; Prieur-Richard et al. 2000; van Ruijven et al. 2003; Von Holle and Simberloff 2005; Maron and Marler 2007). There was a weak association indicating that mean non-native species richness tended to be higher in plots within *L. dalmatica* patches, and a stronger association indicating that mean litter cover tended to be higher in plots outside of *L. dalmatica* patches. This suggests that while *L. dalmatica* is not influential on native



species richness by itself, it is part of a group of non-native species whose increasing richness is associated with decreased native species richness. In other studies, plant litter has been shown to decrease establishment (Hager 2004; Bartuszevige et al. 2007) and alternatively to increase survival (Schramm and Ehrenfeld 2010) of non-native plants. Since non-native plant richness was associated with plant litter in our study area, further evaluation of the role of plant litter with native and non-native plant germination and survival is necessary.

We did not find that *L. dalmatica* cover was associated with elevation as we had hypothesized (H5) based on relationships we had noted between stem density and elevation (chapter 3). The fact that this association was lacking suggests that, for this species, stem density and percent cover are not equivalent measures. In an analysis for plots where *L. dalmatica* cover and stem density was measured, there was a positive correlation between the two ( $p < 0.01$ ,  $r^2 = 0.2$ ), as one would expect. However, as indicated by the  $r^2$  value, the variation in stem density explained by cover or vice versa was relatively low. The reason for this could be that percent cover relates to both stem density and the vigor of individual stems. Therefore, if the vigor of individuals changes across the surveyed area, percent cover will most likely capture this effect. Stem density, on the other hand, does not necessarily capture the vigor of individuals of a species, as a stem could have large or small cover values, but would still be counted as only 1 stem. While stem density does not account for vigor of plants, it does provide some measure of establishment/reproductive success, in that each stem represents the successful establishment of a seedling or a vegetative ramet. For *L. dalmatica*, individuals can

produce multiple stems from a common root crown. In the other study (chapter 3) stem density for this species was measured on a per plot basis from 1 m<sup>2</sup> plots. For this study, cover was measured within 0.25 m<sup>2</sup> plots, but stem density was not measured. Therefore, it is not possible to estimate *L. dalmatica* cover on a per stem or per individual basis from our data. Thus, in light of the relationship between stem density and elevation we can only hypothesize that the lack of association between *L. dalmatica* cover and elevation is due to differential vigor of individuals along the elevation gradient.

In contrast to the lack of association between elevation and *L. dalmatica* cover, elevation was significantly associated with probability of *L. dalmatica* occurrence (H3). This pattern was hump shaped, indicating that the probability of occurrence decreased at both ends of the current elevational range of *L. dalmatica* and peaked at the interior of its current range. Similar results have been found for the relationship between general non-native plant species richness in the same study area (Alexander et al. 2011; Seipel et al. 2012), and in other parts of the world (Pauchard et al. 2009; Haider et al. 2010; Alexander et al. 2011). The differences in association between elevation and 1) *L. dalmatica* cover, and 2) probability of *L. dalmatica* occurrence, suggest that elevation primarily determines where *L. dalmatica* can become established by influencing establishment and/or survival rates. However, once the species is established in an area, then biotic factors associated with the composition of the vegetative community are primarily responsible for limiting cover of the species. These results agree with the findings of other studies that have suggested that non-native species are probably influenced by both abiotic and biotic factors along elevation gradients (Haider et al. 2010;

Pollnac et al. 2012). Since stem density is related to establishment as discussed above, this could also explain why stem density was found to be associated with elevation while cover was not.

In conclusion, our data have shown that while the pattern of increased non-native richness was associated with decreased native species richness along the surveyed elevation gradients, *L. dalmatica* by itself has little to do with that pattern, other than being part of the group of non-native species. In addition, we have shown that elevation has little to do with the cover of *L. dalmatica* along the gradients, although it is important for stem density. In this case, the occurrence of *L. dalmatica* (as a proxy for successful establishment) appears to be strongly associated with elevation, while vegetative community factors have the direct influence on the cover of this species once it becomes established.

This study also provides evidence in support of the theory of directional ecological filtering of non-native plant species along elevation gradients, and shows that this theory can be tested on an individual non-native plant species basis. Information on whether or not an established non-native species fits into the framework of this theory can provide managers with useful information. If a species fits the profile of the broadly adapted mountain invader as specified by the theory (Alexander et al. 2011), this means that there may be nothing aside from dispersal opportunities constraining the species from spreading higher or lower along the gradient. Thus, in lieu of any information indicating that the species is unlikely to spread higher due to dispersal limitation or climatic and/or environmental conditions, the upper populations of such species should

be actively managed in an effort to prevent further spread into alpine environments. For established non-native species which do not fit the pattern and have narrow or comparable range widths in comparison to native species, this would indicate that the species either has very poor dispersal or has relatively narrow environmental tolerances, and is unlikely to spread at a rapid rate beyond its current range unless its dispersal is augmented or the species undergoes some form of adaptation (Gaston 2003; Becker et al. 2005). In this case, unless dispersal is likely to be augmented in some way, such species may be a lower priority for managers.

Unfortunately, there is no way to tell whether or not a newly introduced non-native species will be capable of spreading upwards along an elevation gradient other than informed guesses made by researching the climate of its native range. Although cold adapted non-native species are not a common occurrence in mountainous areas (Alexander et al. 2011; Seipel et al. 2012), any newly introduced non-native species in a mountainous area which is pre-adapted to alpine habitats should be a high priority for managers in these areas. An example of this provided by (McDougall et al. 2005) would be a non-native alpine plant being cultivated at high elevation tourist resorts. In the case of *L. dalmatica*, this species has proven to be a broadly adapted mountain invader, as defined by Alexander et al. (2011). Dispersal of this species into higher elevation areas is not limited, as it is primarily wind dispersed (Robocker 1970). In addition, the location of this species at roadsides probably presents additional opportunities for both dispersal on motor vehicles (Clifford 1959; Zwaenepoel et al. 2006; Von der Lippe and Kowarik 2007; Wichmann et al. 2009; Pickering and Mount 2010; Veldman and Putz 2010) and

establishment in disturbed areas along roadsides (Arevalo et al. 2005; Hansen and Clevenger 2005; Hendrickson et al. 2005; Arteaga et al. 2009; Veldman and Putz 2010; Paiaro et al. 2011; Pollnac et al. 2012). Although the establishment of this species may be limited by lower germination (chapter 3) and survival rates (chapter 4) at higher elevations, population models for this species did not show that population growth rate for this species was universally below replacement levels ( $\lambda < 1$ ) at its current high elevation limits (chapter 4). Thus, this species should be managed at its high elevation limits to prevent spread into alpine areas.

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## CHAPTER 6: PROJECT SUMMARY AND FUTURE RESEARCH

The findings of this project suggest that *L. dalmatica* is a broadly adapted non-native plant species. This is consistent with the theory of directional ecological filtering of non-native plants in mountain systems. Where comparisons were possible between *C. miniata* and *L. dalmatica*, it was apparent that these species differed in terms of how they respond to conditions along their respective elevation gradients. While variation in stem density of *L. dalmatica* along the elevation gradient was best explained by a combination of climate variables, the variation in stem density of *C. miniata* was best explained by both climate and soil characteristics. This suggests that stem density of *C. miniata* may be more sensitive to site specific soil characteristics, and that *L. dalmatica* is less responsive to subtle differences in substrate in terms of overall stem production.

Comparison of the vital rates of the two species provided interesting results. Several of the vital rates of *L. dalmatica* were found to vary based on differences in climatic conditions such as growing season and winter temperatures. However, only one of the vital rates for *C. miniata* (seed production), showed any associations with any of the measured climate or environmental variables. Overall, there appeared to be less variability in the vital rates of *C. miniata* than for *L. dalmatica*. However, there was also less measured variability in climate conditions along the section of the elevation gradient where *C. miniata* was present. This would obviously explain the lack of variation in *C. miniata* vital rates. However, it is interesting that: 1) *C. miniata* is found in a less climatically variable band of elevation than *L. dalmatica*, and 2) that, in spite of some climatic variation, the vital rates of *C. miniata* still appear to be relatively stable. This

suggests that perhaps *C. miniata* is more closely matched to an “ideal” habitat than *L. dalmatica*. Having had a longer time for population dynamic processes to operate and promote success in more suitable environments and extinctions in less ideal environments is one possible explanation. *C. miniata* has also had a longer time to adapt to local conditions, such that the species may be able to optimize its vital rates in spite of variation in climate throughout its current range. In contrast, *L. dalmatica* is a relative newcomer to the area. Being broadly adapted has allowed it to establish across a broad range of environments. However, the species has not yet had enough time to, and perhaps never will, adapt to local conditions across the gradient such that vital rates can be optimized across the range of environments in which it is currently present.

Despite the variance in vital rates of *L. dalmatica*, no consistent trends in population growth of this species were evident along the elevation gradient. We had hypothesized that if this species was climate limited, population growth rates would decrease at the upper extents of its current elevation range where climatic conditions were increasingly harsh. This was not the case. Population growth showed no trend with elevation. There were some interesting associations however. All of the sites where  $\lambda < 1$  were located in areas where the winter minimum temperature was lowest. In addition, high values of  $\lambda$  appeared to be related to low vegetation cover, low litter cover, and higher proportions of bare ground cover. Together these associations suggest that population growth of this species may be limited by extremely low temperatures, and that it may also be reduced in areas where vegetation cover is higher.

Examining probability of occurrence and percent cover of *L. dalmatica* revealed that the occurrence of this species is currently associated with elevation, but that cover is not. Instead, cover appears to be negatively associated with native species richness and perennial species cover. This, coupled with the lack of difference in these vegetative community characteristics between plots with and without *L. dalmatica* suggests that the native community is influencing the cover of *L. dalmatica* and not vice versa.

All of the results discussed above suggest that *L. dalmatica* is broadly adapted, in that it is experiencing positive population growth and stem production across a variety of environments. There is no strong evidence of climatic or propagule pressure limitation at the current upper limits of this species. The current trends in stem density, as well as the projected population growth of this species, suggests that populations at the upper elevation limits of this species may experience growth in the coming years. It is unclear, however, if this population growth will result in the spread of this species beyond its current upper elevation limits. Even though no climatic limits were proven conclusively, some of our results suggest that the species may be limited once a certain winter minimum temperature is reached. This could potentially serve to limit the spread of this species higher along the elevation gradient. The apparent negative associations of this species with increased vegetation cover for both percent cover and population growth suggest that the presence of more heavily forested habitat higher on the elevation gradient may also limit the upward expansion of this species. However, in these days of increased anthropogenic influence, it is quite possible that propagules of *L. dalmatica* could be transported through the heavily forested zone to the sub-alpine/alpine zones within the

study area where vegetation cover begins to decrease. If this were to happen, the presence or absence of climatic limitation would have a great effect on whether or not this species could establish in these areas. Therefore, in an effort to determine whether or not this species will be able to spread into these sub-alpine/alpine zones, experiments should be undertaken which quantify germination, establishment, and long term survival of *L. dalmatica* in these higher elevation environments. Since it is unlikely that permission would be granted to conduct such research in natural environments, growth chamber experiments could be conducted to simulate the cold temperatures over winter and during the early germination periods for the species. In addition, post germination low temperature events of varying intensities and durations could be simulated to determine the effects of such events on seedling survival. Such experiments would give a much clearer sense of whether or not this species would be able to establish and persist at higher elevations than it is currently present.

Another interesting possibility would be to simulate the introduction of this species into intact sub-alpine/alpine plant communities under controlled circumstances. If a facility was available where small sub-samples of intact sub-alpine/alpine plant communities could be maintained under relatively representative conditions, seeds of *L. dalmatica* could be introduced to these communities. This would test the competitive ability of *L. dalmatica* seedlings in an environment where this has not previously been tested.

Stepping away from *L. dalmatica* and considering the broad group of non-native plant species that have been found in mountain systems, there is much work still to be

done. Some promising general theories have been developed in terms of the phenomenon of non-native plant species invasions in mountain systems. In order to confirm or refute the general theories that have already been proposed, they will need to be tested or validated in the context of the behavior of individual species in mountain systems. Such single species information will also be necessary if we have any desire to provide managers in these mountainous areas with information that they can actually use to go out and manage non-native plants. The general theories are wonderful in terms of their ability to provide insights into what might be occurring, but they often fall short of providing information that managers can apply to their management programs. At present, the availability of single species data is still relatively low. This study in particular has provided evidence for the validity of the theory of directional ecological filtering as the mechanism of the assembly of non-native plant communities in mountain systems, and has hopefully provided information that will be useful to managers dealing with *L. dalmatica* in mountainous areas.

In closing, the phenomenon of non-native plant species expansion into mountainous areas is an exciting area of study. As other individuals and groups involved in this area of study have already observed, we have the opportunity in mountain systems to examine the early stages of plant invasions and to provide information which might help to prevent further invasions in these diverse mountain habitats. I would therefore encourage anyone who is interested in either non-native plant invasions or the preservation of sub-alpine/alpine habitats to consider this area of study in the pursuit of those interests.



## EPILOGUE

I will open the epilogue with a disclaimer. This final segment has no scientific information related to *L. dalmatica*, or anything else for that matter. It is simply a random collection of my personal observations on the process of completing my PhD project. If you are still interested, please keep reading. Working on this project for the last four years has been an experience. Like most PhD projects, I think, it has had its high points and its low points. However, when it all gets mixed together in the bucket, it has definitely been a positive experience. It gave me the opportunity to do one of the things that I enjoy the most, which is just to learn something new, and to apply that knowledge to an important issue. Through the global nature of the problem which this project dealt with, and the generosity of my advisor, I was also able to travel to some truly amazing places and interact with like-minded individuals who are also tackling the issue of non-native plant species in mountain systems. Those experiences were invaluable to the evolution of both this project and of myself. Thanks Lisa.

So why am I carrying on about all of this? I presume that if you are actually taking the time to read an epilogue in a dissertation, you have some curiosity in regards to the process of getting a PhD for the purposes of making a decision, gaining some sort of perspective, or maybe just some finding some helpful advice. I think I have managed to distill why the experience was so valuable to me already, so I suppose now it is time to dispense some advice to those who are seeking it. If you are thinking of pursuing a PhD or have already begun to do so, make sure that you have a good understanding of why you are doing so. I mean this in both a personal and professional sense. Knowing

specifically why you, as a person, are pursuing a PhD, and why you are working on the particular project that you are working on, is probably the most valuable information that you can have during the experience of completing your degree. The process of completing a PhD undoubtedly takes one to some odd and sometimes unpleasant places. By places, I mean both mental (e.g. why am I still awake at 3am thinking about population models?) and physical (e.g. why am I walking down this dirt road by myself in a sleet storm, in June?). Circumstances differ for everyone, but if one finds oneself asking the big question of “Why am I doing this?”, it is nice to have answers. So figure that out as soon as you can.

Don't forget to take time away from your project. Working on a PhD can be especially hard at times, both for the person doing the work and for those that, through lack of foresight, decided to live with/marry/carry on some sort of personal relationship with the person working towards the degree. Completing a PhD does require a lot of work, but it is important to realize that you (and any close associates if applicable) deserve a break from the craziness every once in a while. I took a week off about 6 weeks before my dissertation was due to my committee. Some of this time was spent at a professional meeting, but the rest was spent with my wife, relaxing and exploring a place that neither one of us had ever been. Yes, I freaked out a bit when I got back and realized how few days there were until my dissertation needed to be handed to my committee, but as of now it looks as though it will get done on time. Taking that bit of time off has made it that much easier to sit in front of the computer for the long hours required to get everything done. So go somewhere, and don't feel guilty about it! Everyone needs some

rest. However, you might not want to go to a nice island. You will just end up wanting to move there.

As for the actual writing of the dissertation, start early. Start with a comprehensive literature review if that is required. Leaving this until the end is a BIG mistake. Literature reviews take a lot of energy to write. Typically, towards the end of the dissertation writing ordeal, one only has enough energy to incorporate revisions and write rambling epilogues. In addition, you will often find information which will make data collection/analysis/project justification easier in the process of writing a literature review. Also, despite what everyone says, I have found it easier to write my introductions first, not last or next to last. They may need to be tweaked once the data analysis is finalized, but I found it to be tremendously helpful to write the introductions to all of my chapters back in August, before I began my final analyses. Doing so helped me to refine my objectives, and to come up with some ideas for additional analyses that I had not considered previously. Overall, I believe that this helped to generate a better end product. It was also one less thing that I had to do over the last few weeks. So just write up whatever you can when you have time to do it. Literature reviews, introductions, methods, and even loose ideas for discussion points can be written well before analyses are finalized. If you have the time to get these started early, do so.

Start to think about the next step while you are finishing up. Start applying for jobs, even ones that you may not be qualified for. This serves two purposes. First, it helps to have some sense that there is going to be something to move on to after the PhD is done. Even if you do not actually successfully land a job before you graduate, at least

you will be trying to do so. Applying for jobs forces you to think about what you actually want to do when you are finished, which may be different than you had imagined before you thought about it in depth. Besides, doing nothing in this regard generally produces no results, whereas trying may actually get you somewhere. The second purpose is that applying for jobs serves as a productive alternative to writing your dissertation etc. Some days it just doesn't come together. Lack of sleep, burnt toast, lack of coffee, lack of motivation, and general exhaustion can all become obstacles to a long day of working on a dissertation. When the day or the afternoon does not lend itself to productive dissertation manufacturing, job searching and resume updating are viable alternatives. They often require less creative effort, and you can end the day feeling like you did something productive as opposed to feeling like you are a lost cause. But remember, it is OK to just take time off if needed. Working through exhaustion just ends up making it worse in the end.

And now for the random bits that don't really need a paragraph's worth of elaboration. If you are going to mark plots with fiberglass road-hairs (those 6" fiberglass tassels that you drive into the ground with a big nail), use the blue ones. All of the other colors fade after 1-2 seasons. There is no ideal time to get a dog. If you want one "at some point", don't bother waiting or putting it off, especially if your significant other really wants one. Resistance is futile in this situation. Follow Bruce Maxwell on his dinner excursions in strange cities only if you are willing to accept the odds. 50% of the time you end up with a good dinner. 10% of the time you end up with a good dinner AND some weird circumstances that make for an interesting story. 50% of the time you

just end up with the interesting story. This has been scientifically proven. Don't just sit at your desk all day. Go for a walk, go to the gym, go swimming, or whatever it takes to avoid trips to the chiropractor and bouts of insanity. Lastly, always remember that you decided to pursue an advanced degree for a reason. Don't lose sight of that reason.

APPENDICES

APPENDIX A

DETAILED METHODS

Owing to the array of measurements taken in the field throughout the course of this project, the materials and methods sections of the preceding chapters needed to be condensed in order to prevent them from becoming prohibitively dense in material. As such, certain fine details of the methods used in certain parts of this study may have been left vague. This appendix represents the complete version of the methods used for this project, and is given here in an effort to answer any questions that may arise in the future.

Before delving into the details, a brief statement of the overall goal of this project is necessary. The main objective of this project was to monitor populations of *Linaria dalmatica* and *Castilleja miniata* along elevation gradients in an effort to determine what factors effectively limit the current ranges of these two species. *Linaria dalmatica* was chosen as the non-native test species for two reasons: 1) it is a species of concern within the study area, listed as a category 2B noxious weed on the Montana State Noxious Weed List, and is thus subject to management, and 2) it currently has a wide distribution along elevation gradients within the study area. *Castilleja miniata* was chosen as the complimentary native species because it is closely related to *L. dalmatica* and is also present across a wide range of elevations in the study area. Sites were selected based on the presence of either one of these species, and all of the observations taken as a part of this study consequently fall within the current range of one or both of these species.

#### General Study Area

This study was conducted along three elevation gradients within the Northern Range of Yellowstone National Park, in the vicinity of Gardiner, MT, 45°01'60" N, 110°42'33" W, 1,598 m elevation. Three networks of linked roads were chosen as



replicate elevation gradients in the area, and will henceforth be referred to as elevation transects. Elevation transect one was located within Yellowstone National Park (YNP) and proceeded from the Boiling River parking area, 44°59'34" N, 110°41'35" W 1,713 m elevation, to a point below the summit of Mt Washburn, 44°47'12" N, 110°26'36" W, 2,800 m elevation. This transect was mostly paved, apart from a section which followed the one way ~9 km Black Tail loop road and the final ~2 km of the transect on the slopes of Mt Washburn. Both of these sections were dirt roads. Elevation transect two was located just north of Gardiner, MT, and proceeded from a point on Travertine Road, 45°02'25" N, 110°42'09" W, 1,795 m elevation, to a point on Bear Creek Rd, 45°05'45" N, 110°36'02" W, 2,237 m elevation. Elevation transect three was also located just north of Gardiner MT and proceeded from the start of Forest Service Rd 3243, 45°02'40" N, 110°40'30" W, 1,872 m elevation to a point near the end of this road, 45°05'25" N, 110°39'51" W, 2,490 m elevation. Elevation transects 2 and 3 were both dirt roads. In general, each of these transects proceeded from elevations near the bottom of the Yellowstone River Valley in Gardiner, MT to elevations just short of the highest elevation extent for the specific peak, but represent the highest point of road access. Each transect ended 322 m, 326 m, and 90 m short of its respective peak.

### Study Site Selection

During July and August of 2008, the three elevation transects were surveyed for the presence of *L. dalmatica* and *C. miniata*, both hereafter referred to collectively as the test species. The first criterion for site selection was that the populations not be directly adjacent to the road in order to avoid attracting undue attention to plot markers and to

minimize the possibility, especially for *L. dalmatica*, that the plants at the site would be affected by weed control efforts. Another criterion for site selection was that we could identify multiple discrete patches of the test species at the site that could serve as replicate populations. This was possible for the vast majority of *L. dalmatica* sites, but *C. miniata* tended to be present in diffuse patches upon which decisive boundaries could not be laid. During initial surveys, an effort was made to identify every distinct population of the test species present within 5 to 200 m of the elevation transects (roads) from their lowest elevations up to the highest extent that was navigable in a vehicle. Each population was marked with a GPS, and if multiple discrete patches were present, the boundaries of these patches were mapped. Sites were selected from the pool of sites to represent a relatively even spread of elevations along each elevation transect.

For *L. dalmatica*, six sites were established on each one of the three elevation transects. For *C. miniata*, six sites were initially selected on elevation transect one, and four each on elevation transects two and three. However, during the summer of 2009, two of the sites on elevation transect one had to be removed because they had inadvertently been placed in a Bear Management Area within Yellowstone National Park. These two sites were subsequently replaced by two new sites, one on elevation transect one and one on elevation transect two. Since the two sites that had been removed were at the highest extent that *C. miniata* was found on transect one, the two replacement sites were also located at the upper range of the species. Fewer sites per elevation transect were possible for *C. miniata* due to the fact that the elevation range at which it occurred on transects two and three was more limited than that of *L. dalmatica*.

### Plot Placement

During August of 2008, ten 1 m<sup>2</sup> monitoring plots were semi-permanently established (for the duration of this project) at each one of the study sites. These plots were established so that individuals of the test species could be monitored over subsequent years of observation. At each site, discrete patches were identified where possible, and plots were placed randomly among all patches of the test species that were present. At some sites, it was difficult to identify discrete patches. This was mainly an issue for *C. miniata*, but some *L. dalmatica* sites were also problematic. When a population at a site was large and diffuse it was considered to be one patch. To permanently establish each plot, a 1 m<sup>2</sup> frame was placed on the ground in a random location as noted previously. The upper left and lower right corners of each plot were marked with a blue road hair driven into the ground on a 6" metal spike. The upper left marker also had an aluminum number tag affixed to the top of the spike with wire. Facing the plot such that the number tag was in the upper left corner, a compass bearing was taken facing towards the far edge of the plot, and the location of the plot was recorded with a GPS. Details of the exact locations of these plots can be found in Appendix E.

It should be noted that although the color of road hairs used to mark plots may seem a trivial consideration, blue was actually a fortunate choice. Over the last 4 years we have observed that the common colors of road hair (red, yellow, pink, and orange) fade very quickly to the point where they are completely bleached within 1 or 2 field

seasons. The blue road hairs, however, retained their color throughout the duration of this study (four field seasons).

### Monitoring the Test Species

#### Stem Density Counts

Stem density of the test species was measured within each plot at every site. These measurements were taken during mid to late August each season from 2008-2011. At each set of plot markers, a frame was placed on the ground and the number of stems within the frame was counted. Stems were counted as flowering, vegetative, or grazed. Given the size of grazed stems, it was assumed that these would have flowered if they had not been grazed. During the progress of the study, it was also observed that some stems had apparently been damaged by insects, as indicated by leaf damage. Therefore, starting in 2010, the number of stems with insect damage was also noted for each plot. For *L. dalmatica* and *C. miniata*, stems were counted as separate stems only if they diverged from a common point at the ground (root crown) or were truly isolated stems. Stems which branched off of a main stem above the ground were not counted as separate. The height of the tallest plant in each plot was also measured and recorded at the same time that density counts were completed.

#### Estimation of Reproductive Output

*Linaria dalmatica*. During late August of each field season, the number of seed capsules present within each plot at each site was counted as a rough estimate of reproductive output. To get a better idea of the actual amount of seed produced, seed was

collected and counted for a subset of sites. At four sites along each elevation transect (sites 1, 2, 4, 7, 15, 16, 18, 22, 27, 28, 29, and 31; Appendix E) seed capsules were collected throughout the end of the growing season in 2008 and 2009. Forty-five capsules were collected from plants outside of the monitoring plots and placed in individual envelopes at each of the sites listed above. Seed capsules were collected such that 15 were collected from each of the low, middle, and highest regions of the stems, with no more than 1 capsule being collected from a given stem. In 2008, many of the capsules which were collected had opened, and thus had potentially lost seed material. In 2009, capsules were collected just prior to opening such that seed material inside of the capsule would be fully developed, but none would have been lost. Capsules were then dried at constant temperature (43° C) and each capsule was individually measured (length, width, and depth), opened and the seed material within was counted, weighed, and coloration was noted. A paired t-test comparing the mean number of seeds per capsule at each site in 2009 to closed capsules that were collected in 2008 revealed that there was no significant difference ( $p = 0.34$ ) in the mean number of seeds per capsule at each site between years.

In late September of 2010, a late season survey of seed capsules was conducted to get a better idea of what proportion of seed capsules were mature at the end of the growing season. At the same sites from which seed was collected (see above), ten stems were randomly selected for surveying. On each stem, the number of capsules which were open and the number that were closed were recorded. Additionally, 20 closed capsules were collected from each site. The closed capsules were brought back to MSU and put in

cold storage for 3 months. Each capsule was then opened and the contents were examined and saved in envelopes. Seeds were rated as either immature or mature based on appearance. This methodology was followed so that we could 1) gain a better idea what proportion of capsules matured enough to disperse seeds by the end of the growing season, and 2) determine what proportion of capsules that were not mature on visual inspection contained mature seeds. The contents of the seed capsules were then tested for germinability.

Throughout the course of these observations, it became apparent that seed capsules were being removed from *L. dalmatica* throughout the growing season before they had matured by some sort of predation. Although it was evident that some capsules had been removed due to remnant capsule stalks, these were not counted as part of the seed production estimations, as they had been removed before maturity. However, it was determined that having an idea of the magnitude of capsule predation at each site would be of interest. Consequently, during the 2011 field season, 10 stems were randomly selected for monitoring throughout the season at each site. Each week, the number of flower buds, flowers, and capsules was counted. This was done so that the magnitude of seed capsule predation could be measured across all sites.

*Castilleja miniata*. Reproductive output for this species was estimated in a more coarse fashion based on the number of flowering heads present within plots at each site, as measured during stem density counts. Individual seed capsules were not counted because it was extremely difficult to count the number of capsules on any given flowering head without causing extensive damage to the plant. To get a better idea of

actual seed production, 10 flowering heads were randomly harvested from outside of the monitoring plots at each of the *C. miniata* sites in the late summer of 2009. These flowering heads were dried at constant temperature (43° C). They were then measured for length and dissected such that for each seed capsule, the number and appearance of seeds and presence of insect damage could be evaluated.

#### Estimation of Vital Rates for Demographic Models

Estimation of vital and transition rates for demographic models was accomplished in essentially the same way for both of the test species. At a subset of 3 sites per species along each elevation transect (sites 1, 4, 7, 16, 18, 22, 27, 29, and 31 for *L. dalmatica* and sites 9, 12, 13, 19, 21, 23, 25, 26, and 33 for *C. miniata*; Appendix E) four plots per site were randomly selected during the summer of 2009 to serve as demographic monitoring plots. The sites essentially represented the low, medium, and high range for each species in its elevational distribution. Each one of the selected plots at the sites was modified from the description above in that the road hair on the bottom right of the plot was replaced with a length of rebar driven into the ground, and the upper right corner of the plot was also marked with a piece of rebar. This was done such that a frame could be more precisely placed over the plot in subsequent monitoring sessions, and so that the markers would be less likely to be moved by animals or frost heaving. These plots were monitored during early June and late August of each field season from 2009-2011. During each session, a 1 m<sup>2</sup> frame which was divided into 16ths was placed over each plot. The location of each stem was then drawn on a piece of tracing paper, noting if the stem was a seedling, vegetative stem, flowering stem, grazed, or broken using different

symbols. Stems which were obviously arising from a common root crown were drawn to be touching on the mapping data sheet, such that individuals could be counted more precisely.

To estimate vital and transition rates from early spring to late summer, sheets from subsequent monitoring sessions were overlaid (for example August 2009 was placed over June 2009) for each plot, and the number of stems which had: 1) transitioned from vegetative to flowering, 2) stayed vegetative, or 3) died, was counted, as were the number of individuals which had either survived or died. Similarly, looking at the time period from the August to the following June, the number of individuals that either survived or perished was recorded. Seedlings were almost never observed, so that seedling survival could not be estimated from these data.

Seed germination, longevity and seedling survival were only estimated for *L. dalmatica*. This was mainly because it was very difficult to get seeds of *C. miniata* within the study area due to extensive insect predation on this species. Therefore, the following methods only pertain to the subset of *L. dalmatica* sites listed above. At each site, several seeds were harvested during the late summer of 2008. Seeds were brought back to Montana State University and divided into 5 lots of 400 seeds for each site. The first lot of 400 seeds for each site was used for immediate germination and viability tests. To test for germination, 4 batches of 50 seeds per site were placed into plastic containers containing blotting paper which was wetted with distilled water. These containers were placed in a germination chamber at 15° C alternating 12 hours light/12 hours dark and germination was monitored weekly for 5 weeks. These conditions were chosen based on



the work of Robocker (1970) which noted that the highest level of germination occurred under temperature conditions of 15-20° C. Four batches of 25 seeds were then tested for viability using a tetrazolium test. Seeds were cut in half, and then placed in a 1% TZ solution for 24 hours at 30° C before reading.

The remaining lots of seeds were placed in nylon sacks (200 seeds/sack) with 40 ml of sand which had been sieved with a 0.5 mm brass sieve. This particular size of sieve was used because this was the largest size through which no *L. dalmatica* seeds would pass. Eight of these sacks were then buried at each of the *L. dalmatica* sites listed above to be recovered 2 at a time in subsequent years. At each site, the location was randomly chosen. At the seed burial site, a meter stick was laid on the ground, either end was marked with a piece of rebar and a spike with a blue road hair, and the position was marked with a GPS. Two sacks were then buried at the 20, 40, 60, and 80 cm marks on the meter stick such that the top of the sack was approximately 0.5 cm below the surface. Each year following the initial burial, in late September, a pair of sacks was removed (randomly from the 20, 40, 60, or 80 cm mark) from each site. The seed material was separated from the sand using a 0.5 mm sieve, and the procedures described above for germination and viability testing were performed.

Seedling survival was assessed during the spring and summer of 2011 at three sites along the two elevation transects outside of Yellowstone National Park (sites 16, 18, 22, 27, 29, and 31; Appendix E). During April of 2011, several seeds of *L. dalmatica* were started in a greenhouse for later placement at sites. Since the primary goal was to assess seedling survival as it would result from natural events, seedlings were started for

each site using seeds that had been collected there during fall 2010 and stored in cold, dry storage at 4°C. In addition, one extra lot of seedlings was started for each of the highest and lowest sites along the elevation transect for placement above and below the current elevational range of the species using seeds from the nearest site along the gradient. A second goal was to assess the ability of seedlings grown from seed from the lowest elevation sites to survive at higher elevations along the elevation gradients. As such, another lot of seedlings was started for the highest sites using seeds from the lowest site along that elevation gradient. Once seedlings had germinated, they were transferred to 8.9 cm round pots filled with potting soil (equal parts sand, loam, and peat) such that there were five seedlings per pot. Enough pots were established in this fashion so that five pots for each seed lot (seed from site/nearest site or seed from lowest site) could be placed at each site. Seedling pots were placed out in the field in mid-May to mid-June based on the number of growing degree days accumulated at each site. It was determined that 55 growing degree days using 50 degrees Fahrenheit as the base temperature were sufficient for the germination of *L. dalmatica*. Seedlings were thus placed at a given site on the date at which that site had accumulated 55 growing degree days the previous year. Seedlings were monitored weekly thereafter to establish seedling survival rates along the elevation transects. In addition, pots that contained a known number of seeds from a site were placed at each site. This was done to evaluate seed germination under field conditions. All pots were protected with a ¼" wire mesh cage to prevent larger herbivores from eating seedlings.

### Climate and Environmental Measurements

In addition to monitoring the test species, fine scale climate and environmental data were collected from each one of the study sites used for this project. The overall purpose of this was to enable us to determine which environmental factors might be responsible for any of the patterns that appeared along the elevation transects in terms of stem density, reproductive output, and the like.

#### Measurement of Daily Minimum Temperature

Daily minimum temperature was measured at each site using one Lascar EL-USB 1 temperature data logger (temperature logger) set to record temperature on an hourly basis. The majority of the temperature loggers were deployed on June 27, 2009, with the exception of site 9 which was deployed on July 17, 2009, site 33 which was deployed on July 21, 2009, and site 34 which was deployed on July 8, 2010. Temperature loggers at sites 9 and 33 were deployed later due to lack of access, and the temperature logger at site 34 was deployed a year late because this was a new site which was not yet in place as of early summer 2009.

Temperature loggers were placed within protective ¼" wire mesh cages prior to placement. These cages were then secured to the North side of existing vegetation at a height of roughly 1-2 feet from the ground surface in an attempt to accurately capture the minimum air temperature at the height of most of the vegetation of interest and to avoid the influence of radiant heat from the ground during the summer months. To avoid the

loss of any temperature probes, the cages were also secured to a metal anchor in the ground via a metal cable.

Data was periodically downloaded from the temperature loggers every September (at which point batteries were also replaced) and June for the duration of the project until September 2011. These data were imported into Microsoft Excel for each site and then collated using R. Complete details and R code for this process are located in Appendix D

### Measurement of Soil Moisture

Soil moisture was measured at each site using three randomly placed Delmhorst gypsum blocks. The majority of the gypsum blocks were placed at each site in early June of 2010. Access to sites 9, 12, 33, and 34 was delayed for one week due to snow, and access to site 8 was delayed until July of 2010 due to a road closure, thus gypsum block placement at these sites was delayed.

Gypsum blocks were placed at a depth of 15 cm in the ground following the procedure described in Aho and Weaver (2008). They determined that placing the gypsum blocks in a slurry, as per recommendation of the manufacturer, could lead to biased readings for many weeks or even months after placement. Through a controlled experiment, they determined that if the gypsum blocks were placed in soil without the addition of water, they would equilibrate to the moisture level of the soil in roughly 150 hrs. Gypsum blocks were monitored weekly and moisture level was recorded with a Delmhorst KS-D1 meter from June to late September of 2010 and 2011. The gypsum blocks were left in the ground over the winter of 2010/2011. The readings taken from the

gypsum blocks were converted to water potential in mpa following Aho and Weaver (2008)

#### Measurement of Precipitation

Rain gauges (Taylor Pro-Gauge) were placed at each site in early June of 2010 and again in early June of 2011. Rain gauges were removed in mid-September to avoid damage caused by freezing over the winter months. One rain gauge was placed at each site in an area where there was no canopy cover or tall vegetation overhead which would intercept precipitation. Each gauge was placed within a bracket and mounted to a 3 ft wooden stake which had been pounded into the ground. Wherever possible, stakes were placed such that they were camouflaged by existing short vegetation so that they would not draw unwanted attention. Stakes were also spray painted grey for further concealment. Since the rain gauges could be tipped easily out of their mounting brackets, they were also secured to the stake using zip ties. Upon placement, 3 ml of machine oil was placed in each rain gauge to prevent evaporation of precipitation between survey times. Throughout the growing season, rain gauges were monitored weekly and the amount of precipitation was recorded.

#### Canopy Cover and Percent of Bare Ground, Litter, and Vegetation Cover

Canopy cover was measured at each site using a spherical densitometer at four random locations at each site during the summer of 2010. Holding the densitometer at waste height and approximately 1.5 feet from the body, each of the 24 squares on the densitometer was mentally divided into 4, and the number of quarter squares without

canopy cover was counted. This procedure was repeated at each of the four locations for each compass direction. The average of the four measurements at each random location was then multiplied by 1.04 and subtracted from 100 to estimate the degree of canopy closure at that location. Percents of bare ground, litter, and vegetation cover were estimated by randomly selecting six out of the ten 1 m<sup>2</sup> vegetation monitoring plots at each site. A ¼ m<sup>2</sup> frame was centered within each plot and the percents of bare ground (including rock cover), litter (including moss and lichens), and vegetation cover were estimated by a single observer.

### Soil Properties

During the summer of 2010, soil samples were taken from each site. Ten soil samples were taken to a depth of 10cm (approximately 285 cm<sup>3</sup>) from random locations at each site. These ten samples were then thoroughly mixed together and sub-sampled for further analysis two days after collection. Sub-samples were stored 4° C until the time that they were analyzed for pH, organic matter, nitrogen, phosphorous and potassium content.

APPENDIX B

CHAPTER 3 ADDITIONAL TABLES AND FIGURES

Table B-1. Fixed effects output for 2008 model with stem density of *L. dalmatica* as response and elevation and 2<sup>nd</sup> order polynomial elevation as predictors. n=180.

	est	std err	z	p val
(Intercept)	2.23442	0.08169	27.352	<2e-16
poly(elevation,2)1	3.35178	1.15057	2.913	0.00358
poly(elevation,2)2	-3.2702	1.10584	-2.957	0.0031

Table B-2. Fixed effects output for 2008 model with stem density of *L. dalmatica* as response and elevation as predictor. n=180.

	est	std err	z	p val
(Intercept)	2.241	0.101	22.195	<2e-16
poly(elevation,1)	3.55	1.407	2.524	0.0116

Table B-3. Fixed effects output for 2009 model with stem density of *L. dalmatica* as response and elevation and 2<sup>nd</sup> order polynomial elevation as predictors. n=179.

	est	std err	z	p val
(Intercept)	2.40161	0.09081	26.445	<2e-16
poly(elevation,2)1	2.68252	1.29839	2.066	0.0388
poly(elevation,2)2	-2.9029	1.23479	-2.351	0.0187

Table B-4. Fixed effects output for 2009 model with stem density of *L. dalmatica* as response and elevation as predictor. n=179.

	est	std err	z	p val
(Intercept)	2.4155	0.1051	22.975	<2e-16
poly(elevation,1)	2.8555	1.4881	1.919	0.055

Table B-5. Fixed effects output for 2010 model with stem density of *L. dalmatica* as response and elevation and 2<sup>nd</sup> order polynomial elevation as predictors. n=180.

	est	std err	z	p val
(Intercept)	2.84566	0.07882	36.11	<2e-16
poly(elevation,2)1	1.63527	1.07484	1.52	0.128
poly(elevation,2)2	-0.4643	1.05344	-0.44	0.659



Table B-6. Fixed effects output for 2010 model with stem density of *L. dalmatica* as response and elevation as predictor n=180.

	est	std err	z	p val
(Intercept)	2.84654	0.08024	35.48	<2e-16
poly(elevation,1)	1.65044	1.09393	1.51	0.131

Table B-7. Fixed effects output for 2011 model with stem density of *L. dalmatica* as response and elevation and 2<sup>nd</sup> order polynomial elevation as predictors. n=180.

	est	std err	z	p val
(Intercept)	2.2739	0.1831	12.417	<2e-16
poly(elevation,2)1	5.4185	2.505	2.163	0.0305
poly(elevation,2)2	1.1836	2.4014	0.493	0.6221

Table B-8. Fixed effects output for 2011 model with stem density of *L. dalmatica* as response and elevation as predictor. n=180.

	est	std err	z	p val
(Intercept)	2.2716	0.1783	12.738	<2e-16
poly(elevation,1)	5.3765	2.4446	2.199	0.0279

Table B-9. Fixed effects output for 2009 model with stem density of *C. miniata* as response and elevation and 2<sup>nd</sup> order polynomial elevation as predictors. n=138.

	est	std err	z	p val
(Intercept)	2.238	0.104	21.530	<2e-16
poly(elevation,2)1	5.339	1.314	4.062	<0.001
poly(elevation,2)2	-3.138	1.191	-2.635	0.008

Table B-10. Fixed effects output for 2009 model with stem density of *C. miniata* as response and elevation as predictor. n=138.

	est	std err	z	p val
(Intercept)	2.242	0.121	18.591	<2e-16
poly(elevation,1)	5.747	1.523	3.774	0.001

Table B-11. Fixed effects output for 2010 model with stem density of *C. miniata* as response and elevation and 2<sup>nd</sup> order polynomial elevation as predictors. n=140.

	est	std err	z	p val
(Intercept)	2.539	0.154	16.481	<2e-16
poly(elevation,2)1	4.631	1.972	2.348	0.019
poly(elevation,2)2	-2.866	1.745	-1.643	0.100

Table B-12. Fixed effects output for 2010 model with stem density of *C. miniata* as response and elevation as predictor. n=140.

	est	std err	z	p val
(Intercept)	2.542	0.162	15.717	<2e-16
poly(elevation,1)	5.141	2.053	2.504	0.012

Table B-13. Fixed effects output for 2011 model with stem density of *C. miniata* as response and elevation and 2<sup>nd</sup> order polynomial elevation as predictors. n=140.

	est	std err	z	p val
(Intercept)	2.135	0.229	9.317	<2e-16
poly(elevation,2)1	7.115	2.914	2.442	0.015
poly(elevation,2)2	-2.042	2.557	-0.798	0.425

Table B-14. Fixed effects output for 2011 model with stem density of *C. miniata* as response and elevation as predictor. n=140.

	est	std err	z	p val
(Intercept)	2.129	0.245	8.699	<2e-16
poly(elevation,1)	7.601	3.085	2.464	0.014

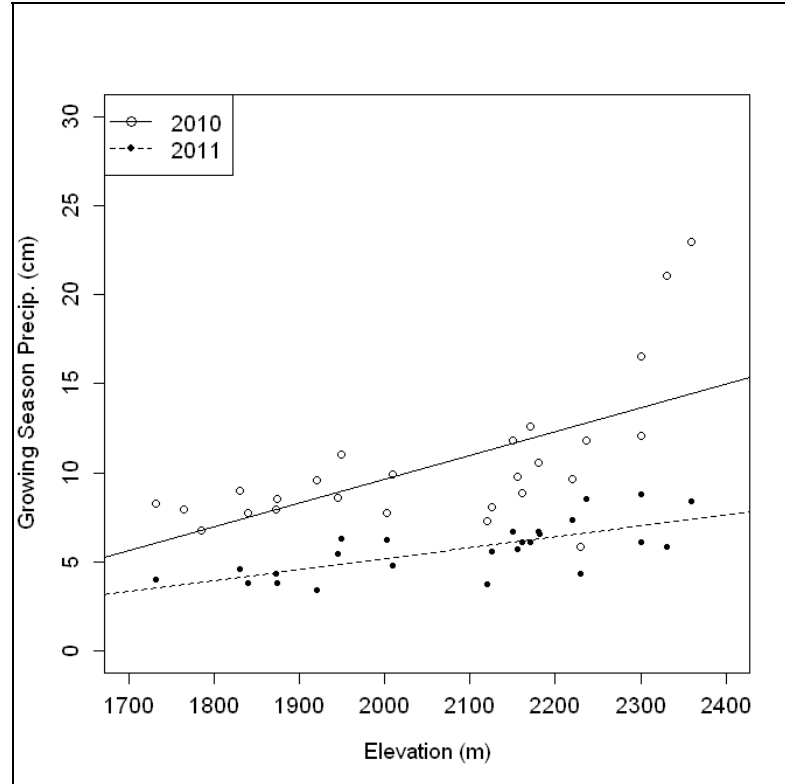


Figure B-1. Growing season precipitation versus elevation for the entire length of the surveyed elevation gradients in 2010 and 2011. Relationships significant at  $p < 0.01$ .  $n = 26$  for 2010 and 26 for 2011.

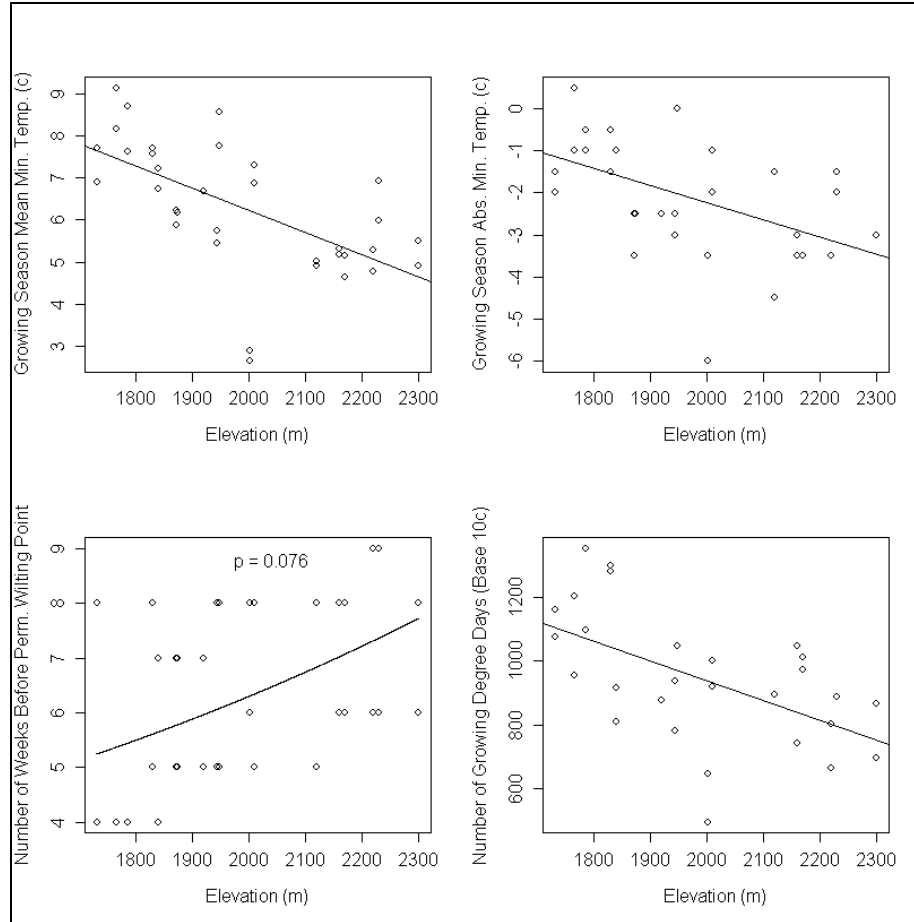


Figure B-2. Plots of the significant relationships of growing season response variables versus elevation for the *L. dalmatica* elevation gradients. All relationships significant at  $p < 0.01$  unless labeled otherwise.  $n = 34$  (growing season mean and absolute minimum temp.), 36 (number of weeks before perm wilting point), and 28 (growing degree days).

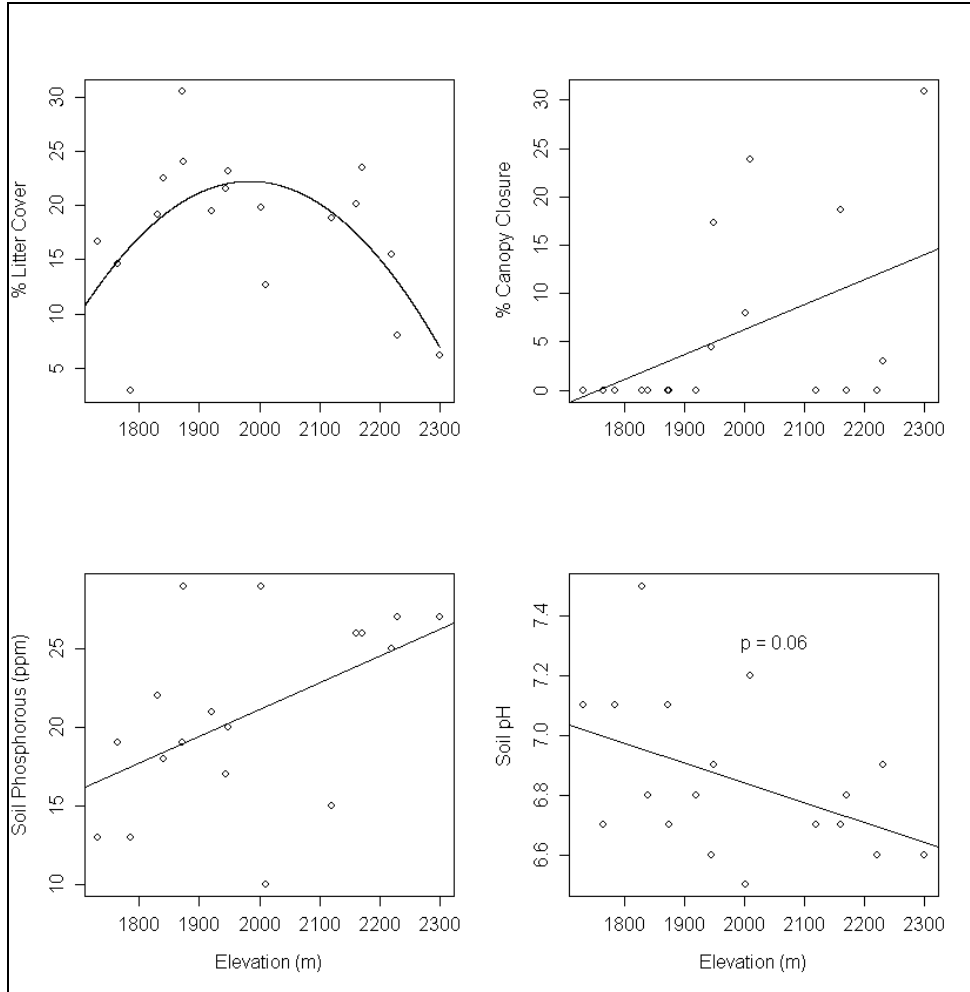


Figure B-3. Plots of the significant relationships of environmental variables versus elevation for the *L. dalmatica* elevation gradients. All relationships significant at  $p \leq 0.05$  unless labeled otherwise.  $n = 18$  for all regressions.

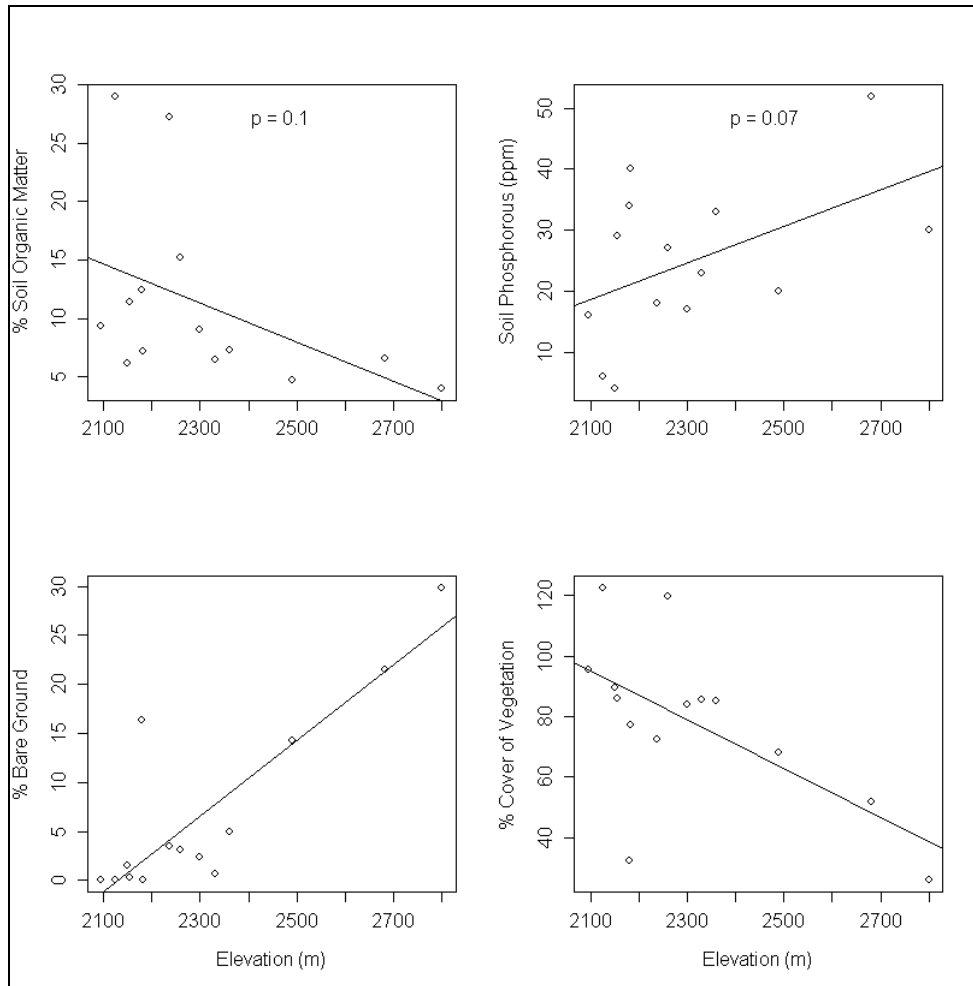


Figure B-4. Plots of the significant relationships of environmental variables versus elevation for the *C. miniata* elevation gradients. All relationships significant at  $p \leq 0.05$  unless labeled otherwise.  $n = 14$  for all regressions.

Table B-15. Table of fixed effects from *L. dalmatica* stem density Generalized Linear Mixed Effects candidate models and associated  $\Delta$  Bayesian Information Criterion (BIC) scores compared to elevation only model. Random effects in all models were site and *L. dalmatica* patch. Gs = growing season, wint = winter, meanmin = mean minimum temperature, min = minimum temperature, frostfree = frost free days (minimum temperature  $>0^{\circ}$  c), frost = frost days (minimum temperature  $\leq 0^{\circ}$  c), snow\_days = estimated number of days of snow cover from September to June, precip = precipitation, wks\_wilt = number of weeks in growing season until permanent wilting point was reached), ph = soil pH, om = soil % organic matter, p = soil phosphorous, n = soil nitrogen.

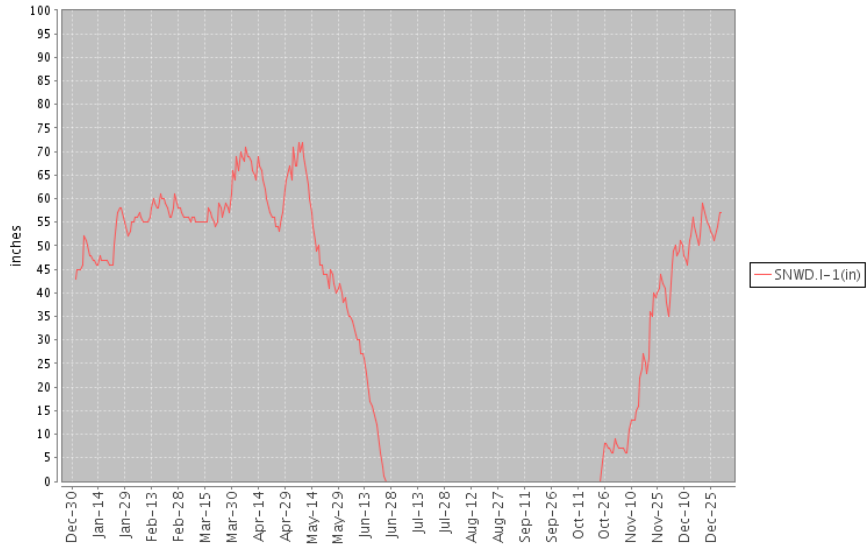
Model	Fixed effects	$\Delta$ BIC
full	elevation+gs_meanmin+snow_days+gs_frostfree+gs_min+gs_precip+wks_wilt+ph+om+p+n	-436
1	elevation+gs_meanmin+snow_days+gs_frostfree+gs_min+gs_precip+wks_wilt+ph+om+p	-427
2	elevation+gs_meanmin+snow_days+gs_frostfree+gs_min+gs_precip+ph+om+p	-430
3	elevation+gs_meanmin+snow_days+gs_frostfree+gs_min+gs_precip+ph+p	-434
4	gs_meanmin+snow_days+gs_frostfree+gs_min+gs_precip+ph+p	-432
5	elevation+gs_meanmin+snow_days+gs_frostfree+gs_min+ph+p	-335
6	elevation+gs_meanmin+gs_frostfree+gs_min+gs_precip+ph+p	-80
7	elevation+gs_meanmin+snow_days+gs_frostfree+gs_min+gs_precip+p	-439
8	elevation+snow_days+gs_frostfree+gs_min+gs_precip+p	-440
9	elevation+snow_days+gs_frostfree+gs_precip+p	-444
10	elevation+snow_days+gs_frostfree+gs_precip	-448
11	elevation+snow_days+gs_frostfree+gs_precip+wint_min	-445
12	elevation+snow_days+gs_frostfree+gs_precip+wint_meanmin	-444
13	elevation+snow_days+gs_frostfree+gs_precip+wint_frost	-444
14	elevation+snow_days+gs_frostfree+gs_precip+wint_frost+canopy closure	-444
15	elevation+snow_days+gs_frostfree+gs_precip+wint_frost+bare ground	-445
16	elevation+snow_days+gs_frostfree+gs_precip+wint_frost+vegetation cover	-444
elevation only	elevation	--

Table B-16. Table of fixed effects from *C. miniata* stem density Generalized Linear Mixed Effects candidate models and associated  $\Delta$  Bayesian Information Criterion (BIC) scores compared to elevation only model. Random effects in all models were site and *C. miniata* patch. Gs = growing season, wint = winter, meanmin = mean minimum temperature, min = minimum temperature, av = average (averaged over two years), frostfree = frost free days (minimum temperature  $>0^{\circ}$  c), frost = frost days (minimum temperature  $\leq 0^{\circ}$  c), snow\_days = estimated number of days of snow cover from September to June, precip = precipitation, wks\_wilt = number of weeks in growing season until permanent wilting point was reached), ph = soil pH, om = soil % organic matter, p = soil phosphorous, n = soil nitrogen.

Model	Fixed Effects	BIC
full	elevation+gs_meanmin+ snow_days+av_precip+ph+om+n	-574
1	elevation+snow_days+av_precip+ph+om+n	-566
2	elevation+snow_days+av_precip+gs_meanmin+ph+n	-567
3	snow_days+av_precip+ph+om+n	-553
4	elevation+snow_days+ph+om+n	-284
5	elevation+av_precip+ph+om+n	-396
6	elevation+snow_days+av_precip+om+n	-562
7	elevation+snow_days+av_precip+ph+om	-565
8	elevation+snow_days+av_precip+ph+n	-571
9	elevation+snow_days+av_precip+n	-565
10	elevation+snow_days+av_precip+ph	-567
11	elevation+snow_days+av_precip+ph+n+wint_min	-574
12	elevation+snow_days+av_precip+ph+n+wint_meanmin	-567
13	Elevation+snow_days+av_precip+ph+n+wint_min+wint_frost	-574
14	Elevation+snow_days+av_precip+ph+n+wint_min+canopy closure	-574
15	elevation+snow_days+av_precip+ph+n+wint_min+bare ground	-574
elevation only	elevation	--



Station (683) YEAR=2010 (Daily) NRCS National Water and Climate Center - Provisional Data - subject to revision Tue Apr 03 07:15:37 PDT 2012



Station (683) YEAR=2011 (Daily) NRCS National Water and Climate Center - Provisional Data - subject to revision Tue Apr 03 07:16:06 PDT 2012

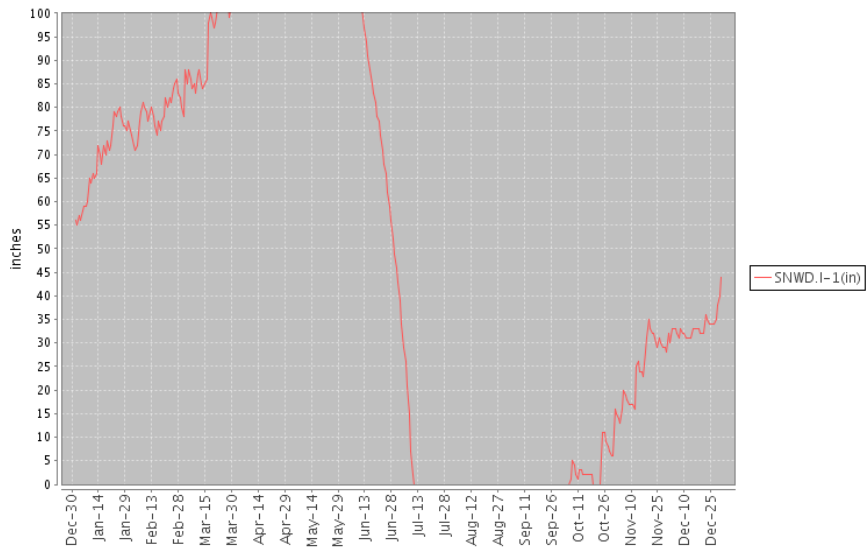


Figure B-5. Snotel data from Parker Peak Station, Wyoming, showing the increased snow cover in January– July 2011 as compared with the same time period in 2010.

APPENDIX C

LINARIA DALMATICA POPULATION MODEL

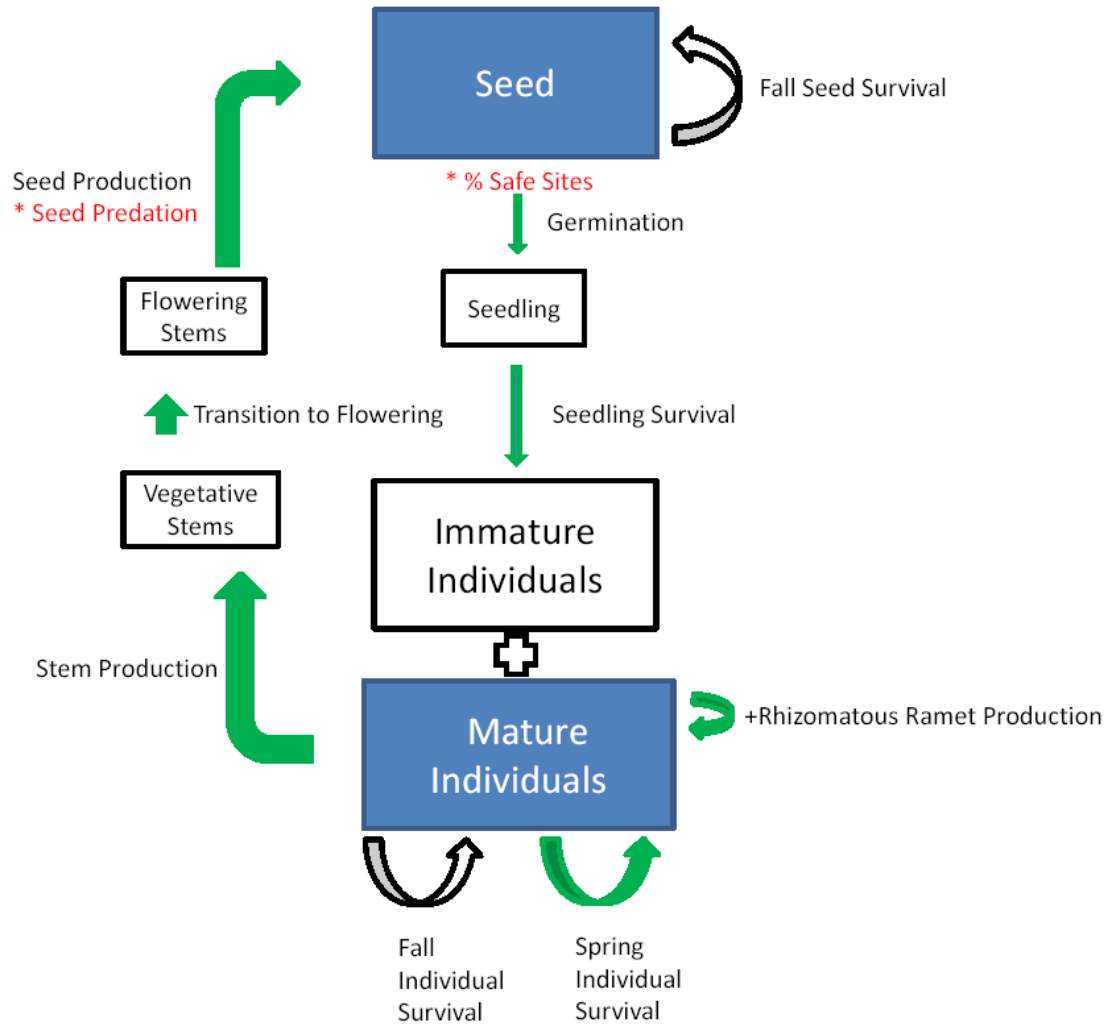


Figure C-1. Diagram of the population model used to estimate population growth of *L. dalmatica* at study sites. Shaded boxes represent stages propagated from year to year in the model. White boxes indicate temporary stages only present within each spring to fall transition. Shaded symbols indicate spring to fall transitions. Un-shaded symbols indicate fall to spring transitions. \* = rate was modified by indicated property.

```

#####
####this version of the model is for site 1 (elev 1737m). The code below runs the model out to 1000 generations
####for a successive (specified) number of iterations and creates a vector of length determined by
####the number of trials containing the final population level for each successive trial.
#####
#####
####this _sambyplot version differs from the others in that each plot is simulated individually (4 per site) and the vital
rates are
####drawn from a pool of vital rates differing by year.
####rates are drawn such that they are linked by a randomly drawn year identifier. For example, if the year
####identifier drawn is 1, then all vital rates for all plots come from year 1 values
#####
#####
####this section of code is used to run loop within loop and get the final pop
####level for 1000 iterations of a 1000 generation model
ITMAX=1000 #number of iterations of 1000 generation model
endpop1=vector() #establishes vector for final pop level output from 1000 generations for plot 1
endlam1=vector() #establishes vector for lambda output from 1000 generations for plot 1
endpop2=vector() #establishes vector for final pop level output from 1000 generations for plot_2
endlam2=vector() #establishes vector for lambda output from 1000 generations for plot_2
endpop3=vector() #establishes vector for final pop level output from 1000 generations for plot_3
endlam3=vector() #establishes vector for lambda output from 1000 generations for plot_3
endpop4=vector() #establishes vector for final pop level output from 1000 generations for plot_4
endlam4=vector() #establishes vector for lambda output from 1000 generations for plot_4
endpopsite=vector() #establishes vector for final pop level output from 1000 generations for site average
endlamsite=vector() #establishes vector for lambda output from 1000 generations for site average
for(i in 1:ITMAX){ ###starts outer loop
#####
ITMAX=30
stable=1
#####start code here for stability check
#c.....initialize state descriptions
##plot_1
  BSD1=25 #seed box
  BMS1=5 # mature ind box, started with average number of individuals/plot found in end summer 2009
##plot_2
  BSD2=25 #seed box
  BMS2=3 # mature ind box, started with average number of individuals/plot found in end summer 2009
##plot_3
  BSD3=25 #seed box
  BMS3=3 # mature ind box, started with average number of individuals/plot found in end summer 2009
##plot_4
  BSD4=25 #seed box
  BMS4=13 # mature ind box, started with average number of individuals/plot found in end summer 2009
#####defining rates for different sample years
year=c(1,2,3)###defines year levels for future draws
#####these variables have no year/year or plot/plot var and do not need to be re-drawn for each model or
iteration
#spring
  GVS=.225 #germinate to seedling, no year to year variability measured for this rate
#fall
  RPF= .613 #remain seed, this is product of equation % diff = x^2 from excel file for germination/viability
  UPF=1-RPF #seed mortality, no year to year variability measured for this rate
#seedling
  #spring
    USS = .99 #seedling mortality
    SSS = 1.0-USS #seedling survival
#Flowering Stems
  #spring
    P=.615 # seed predation adjustment
    Q = 0.71 #modifier of seed germ representing seeds which make it to suitable sites
#####these variables (below) have year to year variability and plot/plot variability, so
##### levels are specified below based on plot, and elements of string are years 1,2,and 3

```

```

###Plot_1
###mature individuals
UMS1= c(0.2,0,0) #mature individual mortality FOR YEARS 1,2, AND 3
SMS1= c(1.8,2,1.67) #mature individual veg stem production FOR YEARS 1,2, AND 3
TFS1= c(.22,0.5,0.2) #transition to flowering stem FOR YEARS 1,2, AND 3
ZMS1= c(0.5,0.25,0.25) #Rhizomatous production FOR YEARS 1,2, AND 3
UMF1= c(0.75,0.5,0.5) ##mature individual mortality(fall) FOR YEARS 1,2, AND 3
PFS1= c(0,419.79,62.19) ##seed production FOR YEARS 1,2, AND 3

#####
#####
###Plot_2
###mature individuals
UMS2= c(0,0.25,0.25) #mature individual mortality FOR YEARS 1,2, AND 3
SMS2= c(1,1.25,1) #mature individual veg stem production FOR YEARS 1,2, AND 3
TFS2= c(0.33,0.2,0) #transition to flowering stem FOR YEARS 1,2, AND 3
ZMS2= c(0.6,0.33,0.33) #Rhizomatous production FOR YEARS 1,2, AND 3
UMF2= c(0.2,0.5,0) ##mature individual mortality(fall) FOR YEARS 1,2, AND 3
PFS2= c(0,0,0) #####seed production FOR YEARS 1,2, AND 3

#####
#####
###Plot_3
###mature individuals
UMS3= c(0,1,1) #mature individual mortality FOR YEARS 1,2, AND 3
SMS3= c(0,0,0) #mature individual veg stem production FOR YEARS 1,2, AND 3
TFS3= c(0,0,0) #transition to flowering stem FOR YEARS 1,2, AND 3
ZMS3= c(0,0,0) #Rhizomatous production FOR YEARS 1,2, AND 3
UMF3= c(1,1,1) ##mature individual mortality(fall) FOR YEARS 1,2, AND 3
PFS3=c(0,0,0) ##seed production FOR YEARS 1,2, AND 3

#####
#####
###Plot_4
###mature individuals
UMS4= c(0,0,0.25) #mature individual mortality FOR YEARS 1,2, AND 3
SMS4= c(3.46,1.9,3.67) #mature individual veg stem production FOR YEARS 1,2, AND 3
TFS4= c(0.02,0,0.05) #transition to flowering stem FOR YEARS 1,2, AND 3
ZMS4= c(1.5,0.09,0.09) #Rhizomatous production FOR YEARS 1,2, AND 3
UMF4= c(0.7,0.5,0) ##mature individual mortality(fall) FOR YEARS 1,2, AND 3
PFS4=c(15.54,0,0) ##seed production FOR YEARS 1,2, AND 3

###C.....Clear shadow destination boxes
SBSD1=0.0
SBMS1=0.0
###C.....Clear shadow destination boxes
SBSD2=0.0
SBMS2=0.0
###C.....Clear shadow destination boxes
SBSD3=0.0
SBMS3=0.0
###C.....Clear shadow destination boxes
SBSD4=0.0
SBMS4=0.0

#####
#####this next section is the inner loop which simply runs the model for each plot
#####out to ITMAX generations
#####
#####
##
####plot_1
lambda1=vector() #####creates vector in which to store lambda values for each generation##
lambda2=vector() #####creates vector in which to store lambda values for each generation##
lambda3=vector() #####creates vector in which to store lambda values for each generation##
lambda4=vector() #####creates vector in which to store lambda values for each generation##
lambdasite=vector() #####creates vector in which to store lambda values (average of four sites) for each generation##
for (j in 1:ITMAX){
#####selecting year dependent parameter values

```

```

#####the code below sets the start of the population model so that gen 1 uses year 1 values, gen 2 uses year 2 values,
and gen 3 uses year
##### 3 values. After year 3, values are drawn randomly from y1, y2, or y3 for each successive generation
if(j==1)(y=1)
if(j==2)(y=2)
if(j==3)(y=3)
if(j>3)(y=sample(year,1,replace=T))
#Mature Individuals
#spring
#UMS,mature individual mortality
if(y==1)(UMS=UMS1[1])
if(y==2)(UMS=UMS1[2])
if(y==3)(UMS=UMS1[3])
#SMS, mature individual veg stem production
if(y==1)(SMS=SMS1[1])
if(y==2)(SMS=SMS1[2])
if(y==3)(SMS=SMS1[3])
#TFS, transition to flowering stem
if(y==1)(TFS=TFS1[1])
if(y==2)(TFS=TFS1[2])
if(y==3)(TFS=TFS1[3])
#ZMS, rhizomatous production #####only 2 years of data
if(y==1)(ZMS=ZMS1[1])
if(y==2)(ZMS=ZMS1[2])
if(y==3)(ZMS=ZMS1[3])
###PFS, seed production/stem
if(y==1)(PFS=PFS1[1])
if(y==2)(PFS=PFS1[2])
if(y==3)(PFS=PFS1[3])
#fall
#UMF, Mature ind mortality #####only 2 years of data
if(y==1)(UMF=UMF1[1])
if(y==2)(UMF=UMF1[2])
if(y==3)(UMF=UMF1[3])
RMF= 1.0-UMF #remain mature ind
#c.....accumulating process results in shadow state description
SUMORIG1=BMS1
#C seeds
SBMS1=SBMS1+(BSD1*Q*GVS*(1-USS))
SBSD1=SBSD1+BSD1*RPS
#c Mature Stems
SBMS1=SBMS1+(BMS1*(1-UMS))+(BMS1*(1-UMS))*ZMS #since the SBMS is not multiplied by zms here, that
effectively means that 1st year mature stems are not producing rhizomes
SBSD1=SBSD1+((BMS1+BMS1*ZMS)*SMS*TFS*PFS*P) #since the sbms is not part of this seed production equation,
that means that 1st year stems are not producing seeds
## the sbds equation above does not impose mortality on the mature stems in order to compensate for the way the
flowering ###transition and stem production
## rates were calculated. Stem pro was calculated based on t1 values (veg1/ind1). Flowering tran was calculated by
## dividing the number of flowering stems at t2 by the number of veg stems at t1(before any mature stem mortality would
have ##occurred). Imposing
## mortality in this equation would result in underestimating the number of stems produced and thus the number of
flowering stems. ##For example
## if 4 individuals produced 8 stems each at t1, and flow tran is .125, that results in 4 x 8 x .125 = 4 flowering stems. If
those 4 ##individuals experience 50%
## mortality, 2 individuals x 8 stems X .125 = 2 flowering stems, which is an underestimate.
#c.....load shadow into real state descriptions
BMS1=SBMS1
BSD1=SBSD1
#c.....done with spring dynamics
#C.....FALL DYNAMICS
#c.....clear shadow boxes again for fall
SBMS1=0.0
SBSD1=0.0
#C.....ACCUMULATE PROCESS RESULTS IN THE SHADOW STATE DESCRIPTION
SBSD1=SBSD1+BSD1*RPF
SBMS1=SBMS1+BMS1*(1-UMF)
#c.....load shadow into real state descriptions

```

```

BMS1=SBMS1
BSD1=SBSD1
NEWSUM1=BMS1
r1=NEWSUM1/SUMORIG1 #####this is lambda for each generation
#c.....Calculate total above ground pop size
pop1=BMS1
total1=BMS1+BSD1
prop_BMS1=BMS1/total1
prop_BSD1=BSD1/total1
#####
###prints proportions of pop for finding stable age dist
#write(c("iteration=",j,"prop_BMS1=",prop_BMS1,"prop_BSD1=",prop_BSD1),"",ncol=8)
#####
#####
##
###plot_2
#Mature Individuals
#spring
#UMS, mature individual mortality
if(y==1)(UMS=UMS2[1])
if(y==2)(UMS=UMS2[2])
if(y==3)(UMS=UMS2[3])
#SMS, mature individual veg stem production
if(y==1)(SMS=SMS2[1])
if(y==2)(SMS=SMS2[2])
if(y==3)(SMS=SMS2[3])
#TFS, transition to flowering stem
if(y==1)(TFS=TFS2[1])
if(y==2)(TFS=TFS2[2])
if(y==3)(TFS=TFS2[3])
#ZMS, rhizomatous production #####only 2 years of data
if(y==1)(ZMS=ZMS2[1])
if(y==2)(ZMS=ZMS2[2])
if(y==3)(ZMS=ZMS2[3])
###PFS, seed production/stem
if(y==1)(PFS=PFS2[1])
if(y==2)(PFS=PFS2[2])
if(y==3)(PFS=PFS2[3])
#fall
#UMF, Mature ind mortality #####only 2 years of data
if(y==1)(UMF=UMF2[1])
if(y==2)(UMF=UMF2[2])
if(y==3)(UMF=UMF2[3])
RMF= 1.0-UMF #remain mature ind
#c.....accumulating process results in shadow state description
SUMORIG2=BMS2
#C seeds
SBMS2=SBMS2+(BSD2*Q*GVS*(1-USS))
SBSD2=SBSD2+BSD2*RPS
#c Mature Stems
SBMS2=SBMS2+(BMS2*(1-UMS))+(BMS2*(1-UMS))*ZMS #since the SBMS is not multiplied by zms here, that
effectively means that 1st year mature stems are not producing rhizomes
SBSD2=SBSD2+((BMS2+BMS2*ZMS)*SMS*TFS*PFS*P) #since the sbms is not part of this seed production equation,
that means that 1st year stems are not producing seeds
#c.....load shadow into real state descriptions
BMS2=SBMS2
BSD2=SBSD2
#c.....done with spring dynamics
#C.....FALL DYNAMICS
#c.....clear shadow boxes again for fall
SBMS2=0.0
SBSD2=0.0
#C.....ACCUMULATE PROCESS RESULTS IN THE SHADOW STATE DESCRIPTION
SBSD2=SBSD2+BSD2*RPF
SBMS2=SBMS2+BMS2*(1-UMF)
#c.....load shadow into real state descriptions
BMS2=SBMS2

```

```

    BSD2=SBSD2
    NEWSUM2=BMS2
    r2=NEWSUM2/SUMORIG2 #####this is lambda for each generation
#c.....Calculate total above ground pop size
    pop2=BMS2
    total2=BMS2+BSD2
    prop_BMS2=BMS2/total2
    prop_BSD2=BSD2/total2
#C.....ONE YEAR HAS BEEN SIMULATED
#####
###prints proportions of pop for finding stable age dist
#write(c("iteration=",j,"prop_BMS2=",prop_BMS2,"prop_BSD2=",prop_BSD2),"",ncol=8)
#####
#####
#####
##
####plot_3
#Mature Individuals
    #spring
    #UMS,mature individual mortality
    if(y==1)(UMS=UMS3[1])
    if(y==2)(UMS=UMS3[2])
    if(y==3)(UMS=UMS3[3])
    #SMS, mature individual veg stem production
    if(y==1)(SMS=SMS3[1])
    if(y==2)(SMS=SMS3[2])
    if(y==3)(SMS=SMS3[3])
    #TFS, transition to flowering stem
    if(y==1)(TFS=TFS3[1])
    if(y==2)(TFS=TFS3[2])
    if(y==3)(TFS=TFS3[3])
    #ZMS, rhizomatous production #####only 2 years of data
    if(y==1)(ZMS=ZMS3[1])
    if(y==2)(ZMS=ZMS3[2])
    if(y==3)(ZMS=ZMS3[3])
    ###PFS, seed production/stem
    if(y==1)(PFS=PFS3[1])
    if(y==2)(PFS=PFS3[2])
    if(y==3)(PFS=PFS3[3])
    #fall
    #UMF, Mature ind mortality #####only 2 years of data
    if(y==1)(UMF=UMF3[1])
    if(y==2)(UMF=UMF3[2])
    if(y==3)(UMF=UMF3[3])
    RMF= 1.0-UMF #remain mature ind
#c.....accumulating process results in shadow state description
    SUMORIG3=BMS3
#C seeds
    SBMS3=SBMS3+(BSD3*Q*GVS*(1-USS))
    SBSD3=SBSD3+BSD3*RPS
#c Mature Stems
    SBMS3=SBMS3+(BMS3*(1-UMS))+BMS3*(1-UMS)*ZMS #since the SBMS is not multiplied by zms here, that
effectively means that 1st year mature stems are not producing rhizomes
    SBSD3=SBSD3+((BMS3+BMS3*ZMS)*SMS*TFS*PFS*P) #since the sbms is not part of this seed production equation,
that means that 1st year stems are not producing seeds
#c.....load shadow into real state descriptions
    BMS3=SBMS3
    BSD3=SBSD3
#c.....done with spring dynamics
#C.....FALL DYNAMICS
#c.....clear shadow boxes again for fall
    SBMS3=0.0
    SBSD3=0.0
#C.....ACCUMULATE PROCESS RESULTS IN THE SHADOW STATE DESCRIPTION
    SBSD3=SBSD3+BSD3*RPF
    SBMS3=SBMS3+BMS3*(1-UMF)
#c.....load shadow into real state descriptions

```



```

BMS3=SBMS3
BSD3=SBSD3
NEWSUM3=BMS3
r3=NEWSUM3/SUMORIG3 #####this is lambda for each generation
#c.....Calculate total above ground pop size
pop3=BMS3
total3=BMS3+BSD3
prop_BMS3=BMS3/total3
prop_BSD3=BSD3/total3
#C.....ONE YEAR HAS BEEN SIMULATED
#####
###prints proportions of pop for finding stable age dist
#write(c("iteration=",j,"prop_BMS3=",prop_BMS3,"prop_BSD3=",prop_BSD3),"",ncol=8)
#####
#####
#####
###
####plot_4
#Mature Individuals
#spring
#UMS, mature individual mortality
if(y==1)(UMS=UMS4[1])
if(y==2)(UMS=UMS4[2])
if(y==3)(UMS=UMS4[3])
#SMS, mature individual veg stem production
if(y==1)(SMS=SMS4[1])
if(y==2)(SMS=SMS4[2])
if(y==3)(SMS=SMS4[3])
#TFS, transition to flowering stem
if(y==1)(TFS=TFS4[1])
if(y==2)(TFS=TFS4[2])
if(y==3)(TFS=TFS4[3])
#ZMS, rhizomatous production #####only 2 years of data
if(y==1)(ZMS=ZMS4[1])
if(y==2)(ZMS=ZMS4[2])
if(y==3)(ZMS=ZMS4[3])
###PFS, seed production/stem
if(y==1)(PFS=PFS4[1])
if(y==2)(PFS=PFS4[2])
if(y==3)(PFS=PFS4[3])
#fall
#UMF, Mature ind mortality #####only 2 years of data
if(y==1)(UMF=UMF4[1])
if(y==2)(UMF=UMF4[2])
if(y==3)(UMF=UMF4[3])
RMF= 1.0-UMF #remain mature ind
#c.....accumulating process results in shadow state description
SUMORIG4=BMS4
#C seeds
SBMS4=SBMS4+(BSD4*Q*GVS*(1-USS))
SBSD4=SBSD4+BSD4*RPS
#c Mature Stems
SBMS4=SBMS4+(BMS4*(1-UMS))+(BMS4*(1-UMS))*ZMS #since the SBMS is not multiplied by zms here, that
effectively means that 1st year mature stems are not producing rhizomes
SBSD4=SBSD4+((BMS4+BMS4*ZMS)*SMS*TFS*PFS*P) #since the sbms is not part of this seed production equation,
that means that 1st year stems are not producing seeds
#c.....load shadow into real state descriptions
BMS4=SBMS4
BSD4=SBSD4
#c.....done with spring dynamics
#C.....FALL DYNAMICS
#c.....clear shadow boxes again for fall
SBMS4=0.0
SBSD4=0.0
#C.....ACCUMULATE PROCESS RESULTS IN THE SHADOW STATE DESCRIPTION
SBSD4=SBSD4+BSD4*RPF
SBMS4=SBMS4+BMS4*(1-UMF)

```

```

#c.....load shadow into real state descriptions
  BMS4=SBMS4
  BSD4=SBSD4
  NEWSUM4=BMS4
  r4=NEWSUM4/SUMORIG4 #####this is lambda for each generation
#c.....Calculate total above ground pop size
  pop4=BMS4
  total4=BMS4+BSD4
  prop_BMS4=BMS4/total4
  prop_BSD4=BSD4/total4
#write(c("iteration=",j,"prop_BMS4=",prop_BMS4,"prop_BSD4=",prop_BSD4),"",ncol=8)
#C.....ONE YEAR HAS BEEN SIMULATED
  r_allplots=as.vector(cbind(r1,r2,r3,r4))
  rsite=mean(r_allplots)
  pop_allplots=as.vector(cbind(pop1,pop2,pop3,pop4))
  popsite=mean(pop_allplots)
#####trying to evaluate stable age dist for total site

totalsite=mean(as.vector(cbind(total1,total2,total3,total4)))
BMSsite=mean(as.vector(cbind(BMS1,BMS2,BMS3,BMS4)))
BSDsite=mean(as.vector(cbind(BSD1,BSD2,BSD3,BSD4)))
prop_BMSsite=BMSsite/totalsite
prop_BSDsite=BSDsite/totalsite
#####
####prints proportions of pop for finding stable age dist
#if(stable=="true")(write(c("year=",y,"iteration=",j,"prop_BMSsite=",prop_BMSsite,"prop_BSDsite=",prop_BSDsite),"",ncol=
10))
if(stable=="true")(write(c("year=",y,"iteration=",j,pop1,pop2,pop3,pop4),"",ncol=8))
#write(c(j,y),"",ncol=2) ##diagnostic to see if sequential start for j=1:3 then random for j>3 works
#####
lambda1=append(lambda1,r1,after=length(lambda1)) ##adds each generation's lambda value to vector"lambda1"
lambda2=append(lambda2,r2,after=length(lambda2)) ##adds each generation's lambda value to vector"lambda2"
lambda3=append(lambda3,r3,after=length(lambda3)) ##adds each generation's lambda value to vector"lambda3"
lambda4=append(lambda4,r4,after=length(lambda4)) ##adds each generation's lambda value to vector"lambda4"
lambdasite=append(lambdasite,rsite,after=length(lambdasite)) ##adds each generation's lambda value to
vector"lambdasite"
} #####stop here for stability check
#####
#####this next code allows you to calculate geometric mean lambda for the n generations of the model##
#####
#####this next code allows you to calculate geometric mean lambda for the n generations of the model##
library(psych) ##loads library for calculating geometric mean
###plot 1
lambda1_frame=data.frame(lambda1)
lambda1a=ifelse(lambda1_frame$lambda1=="NaN",0,lambda1_frame$lambda1)# sets NaN to zero
lambda1a=data.frame(lambda1a)
lambda1a=ifelse(lambda1a$lambda1a=="Inf",NA,lambda1a$lambda1a) #sets Inf to NA
lambda1a=data.frame(lambda1a)
lambda1a=ifelse(lambda1a$lambda1a==0,0.0000001,lambda1a$lambda1a) # converts zero to small number for
calculating geometric mean
lambda1a=data.frame(lambda1a)
meanlam1=geometric.mean(lambda1a$lambda1a,na.rm=T)
meanlam1
###plot 2
lambda2_frame=data.frame(lambda2)
lambda2a=ifelse(lambda2_frame$lambda2=="NaN",0,lambda2_frame$lambda2)# sets NaN to zero
lambda2a=data.frame(lambda2a)
lambda2a=ifelse(lambda2a$lambda2a=="Inf",NA,lambda2a$lambda2a) #sets Inf to NA
lambda2a=data.frame(lambda2a)
lambda2a=ifelse(lambda2a$lambda2a==0,0.0000001,lambda2a$lambda2a) # converts zero to small number for
calculating geometric mean
lambda2a=data.frame(lambda2a)
meanlam2=geometric.mean(lambda2a$lambda2a,na.rm=T)
meanlam2

###plot 3
lambda3_frame=data.frame(lambda3)

```

```

lambda3a=ifelse(lambda3_frame$lambda3=="NaN",0,lambda3_frame$lambda3)# sets NaN to zero
lambda3a=data.frame(lambda3a)
lambda3a=ifelse(lambda3a$lambda3a=="Inf",NA,lambda3a$lambda3a) #sets Inf to NA
lambda3a=data.frame(lambda3a)
lambda3a=ifelse(lambda3a$lambda3a==0,0.0000001,lambda3a$lambda3a) # converts zero to small number for
calculating geometric mean
lambda3a=data.frame(lambda3a)
meanlam3=geometric.mean(lambda3a$lambda3a,na.rm=T)
meanlam3
####plot 4
lambda4_frame=data.frame(lambda4)
lambda4a=ifelse(lambda4_frame$lambda4=="NaN",0,lambda4_frame$lambda4)# sets NaN to zero
lambda4a=data.frame(lambda4a)
lambda4a=ifelse(lambda4a$lambda4a=="Inf",NA,lambda4a$lambda4a) #sets Inf to NA
lambda4a=data.frame(lambda4a)
lambda4a=ifelse(lambda4a$lambda4a==0,0.0000001,lambda4a$lambda4a) # converts zero to small number for
calculating geometric mean
lambda4a=data.frame(lambda4a)
meanlam4=geometric.mean(lambda4a$lambda4a,na.rm=T)
meanlam4
#### average by site
sitelam=as.vector(cbind(meanlam1,meanlam2,meanlam3,meanlam4))
meanlamsite=mean(sitelam)
#lambdasite_frame=data.frame(lambdasite)
#lambdasitea=ifelse(lambdasite_frame$lambdasite=="NaN",0,lambdasite_frame$lambdasite)# sets NaN to zero
#lambdasitea=data.frame(lambdasitea)
#lambdasitea=ifelse(lambdasitea$lambdasitea=="Inf",NA,lambdasitea$lambdasitea) #sets Inf to NA
#lambdasitea=data.frame(lambdasitea)
#lambdasitea=ifelse(lambdasitea$lambdasitea==0,0.0000001,lambdasitea$lambdasitea) # converts zero to small number
for calculating geometric mean
#lambdasitea=data.frame(lambdasitea)
#meanlamsite=mean(c(meanlam1,meanlam2,meanlam3,meanlam4))
#meanlamsite
#####
#####
#####this last section is used for the outer loop to add the final population size
#####to the vector "end" for each of the 1000 iterations
#####plot1
  endlam1=append(endlam1,meanlam1,after=length(endlam1))
  endpop1=append(endpop1,pop1,after=length(endpop1))#this adds the population level at t=ITMAX to the vector
#####plot2
  endlam2=append(endlam2,meanlam2,after=length(endlam2))
  endpop2=append(endpop2,pop2,after=length(endpop2))#this adds the population level at t=ITMAX to the vector
#####plot3
  endlam3=append(endlam3,meanlam3,after=length(endlam3))
  endpop3=append(endpop3,pop3,after=length(endpop3))#this adds the population level at t=ITMAX to the vector
#####plot4
  endlam4=append(endlam4,meanlam4,after=length(endlam4))
  endpop4=append(endpop4,pop4,after=length(endpop4))#this adds the population level at t=ITMAX to the vector
#####average of all sites
  endlamsite=append(endlamsite,meanlamsite,after=length(endlamsite))
  endpopsite=append(endpopsite,popsite,after=length(endpopsite))#this adds the population level at t=ITMAX to the
vector
}
#####plot1
#endpop1
#endlam1
simlam1=mean(endlam1) ####this is the mean of itmax geometric mean lambdas for this plot
write(endlam1,"clipboard",ncol=1)
simlam1

#####plot2
#endpop2
#endlam2
simlam2=mean(endlam2)

```

```
simlam2
####plot3
#endpop3
#endlam3
simlam3=mean(endlam3)
simlam3
####plot4
#endpop4
#endlam4
simlam4=mean(endlam4)
simlam4
####all plots average
#endpopsite
#endlamsite
mean(endlamsite)
#write(endlamsite,"clipboard",ncol=1)
meansimlam=mean(as.vector(c(simlam1,simlam2,simlam3,simlam4)))meansimlam ####this is the mean of the four
mean lambdas above (so site level mean lambda) for the itmax iterations
```

APPENDIX D

DATA PROCESSING AND R-CODE FOR TEMPERATURE DATA

Soil Temperature Data Collation for Lascar EL-USB 1 Temperature Probes

Temperature data gathered using Lascar EL-USB 1 temperature probes was collated in R. However, it was necessary to import the data from the text files (which are the format used by the lascar output software) into Microsoft Excel prior to collation in R to remove unnecessary fields and ensure that the data were consistent between sites. An example of the first two rows of a text file generated by the Lascar software is shown below.

```
site12,Time,Celsius(°C),Serial Number
1,02/06/2010 16:00:00,18.5,010025344
```

This format makes it impossible to use the raw text files in R since there is no heading for reading number or date (the first two entries in row 2) and the serial number is an unnecessary component for analysis. As such, data were imported into excel using the *import external data* option in the *Data* drop down menu. Within excel, a spreadsheet was made for each site which had the following column headings: *reading, date, time, temp, site, hour, month, day, and year*. Using the import feature in excel, data from the text files from each site were imported to the appropriate spreadsheet using the following procedure. After selecting the appropriate file to import, select the *delimited* option and specify to start importing at row 2 on the first screen. On the next screen, select *tab, comma, and space* as delimiters. On the next screen, highlight the column with the date data (column 2), and select *date, DMY* as the column data format. Then highlight the last column which has the probe serial number and select the *do not import column* option. Click on the *Finish* button and select the cell in which to paste the data. Once the data

are pasted into excel, it is necessary to manually input the site number in the *Site* data column. The *hour*, *month*, *day*, and *year* fields can be filled in by using functions in excel. For example, in row two, the appropriate functions and sources would be HOUR(D2), MONTH(C2), DAY(C2), and YEAR(C2) respectively. Below is an example of what the first few columns of the spreadsheet should look like.

site	reading	date	time	temp	hour	month	day	year
1	1	06/27/09	0:00:00	6	0	6	27	2009
1	2	06/27/09	1:00:00	5	1	6	27	2009
1	3	06/27/09	2:00:00	4	2	6	27	2009

After data from each site has been imported into excel in the appropriate spreadsheet, data from all sites must be combined into one spreadsheet. This is rather tedious and is done by cutting and pasting data into one spreadsheet, such that there is a master spreadsheet with temperature data from all sites. When this master spreadsheet is created, it is *imperative* that the date column be formatted so that the date data for each site in the same format shown above. If this is not the case (ie there are some 6/27/09 and 06/27/09 mixed) the r-code below will fail to work and hours may be spent trying to figure out why. Once the date column format has been checked (which can be done by simply selecting the column and formatting it appropriately), copy and paste the spreadsheet into the notepad program and save it as a text file using whatever naming convention you wish. At this point, the r-code below can be used to collate the data. The r-code below is an example of that was used to calculate the number of frost days and the mean minimum temperature for each site during the growing season (June- September).

```
#####linaria data#####

ld1=read.table('ld6.09_9.09.txt',header=T)###reading in temp data from june 09-sept 09###

#####for first time period jun-sept 09#####

mintemps1 = with(data=ld1,tapply(temp,list(date,site),min)) ###generates table of min temps

maxtemps1 = with(data=ld1,tapply(temp,list(date,site),max)) ###generates table of max temps

frost_days_growing=apply(mintemps1,2,function(mintemps1)sum(mintemps1<=0))###returns the
##number of days where temps were at or below freezing

frost_days_growing

growing_days1=apply(mintemps1,2,function(mintemps1)sum(mintemps1>0))###returns the
##number of days where temps were above freezing

growing_days1

mean.min_growing=apply(mintemps1,2,mean)#####gives mean minimum temp for
##growing season

mean.min_growing

###use code below to paste tables into excel if want to combine time periods in one
###spreadsheet

write.table(mintemps1,"clipboard",sep="\t",col.names=NA)

###go to excel and paste table before proceeding to next line

write.table(maxtemps1,"clipboard",sep="\t",col.names=NA)
```

In order to use this code for your own purposes, some things will obviously need to be changed. For example, the file naming convention, 'ld6.09\_9.09.txt', was what I used for my temperature data, but some other name would have worked just as well.



APPENDIX E

PLOT LOCATION INFORMATION

The following information is provided in the event that there is any desire to relocate the sites and/or plots used in this study. The coordinates provided in the table below were collected using a Trimble GeoXT 2008 series GPS unit. Coordinates are UTM based on WGS 1984.

Table E-1. Coordinates for study plot locations

Northing	Easting	Plot Number	Site	Species	Transect
4982123.124	524072.452	1	1	LD	1
4982117.802	524067.737	2	1	LD	1
4982113.306	524071.677	3	1	LD	1
4982121.739	524066.654	4	1	LD	1
4982097.812	524036.03	5	1	LD	1
4982093.855	524037.631	6	1	LD	1
4982091.588	524037.234	7	1	LD	1
4982094.62	524034.182	8	1	LD	1
4982122.471	524070.234	9	1	LD	1
4982119.107	524068.628	10	1	LD	1
4979011.991	524518.848	11	2	LD	1
4979006.127	524511.599	12	2	LD	1
4979007.87	524507.082	13	2	LD	1
4979036.766	524546.59	14	2	LD	1
4979035.57	524543.337	15	2	LD	1
4979032.788	524537.681	16	2	LD	1
4978952.819	524530.676	17	2	LD	1
4978964.262	524537.828	18	2	LD	1
4978963.429	524533.77	19	2	LD	1
4978941.53	524537.195	20	2	LD	1
4977130.384	527346.94	21	3	LD	1
4977131.187	527349.042	22	3	LD	1
4977122.026	527304.317	23	3	LD	1
4977122.893	527305.765	24	3	LD	1
4977120.159	527304.333	25	3	LD	1
4977116.336	527304.454	26	3	LD	1
4977114.858	527304.184	27	3	LD	1
4977115.258	527306.143	28	3	LD	1
4977115.66	527303.48	29	3	LD	1
4977115.359	527302.451	30	3	LD	1
4976536.051	528782.397	31	4	LD	1
4976537.658	528782.371	32	4	LD	1
4976538.614	528781.515	33	4	LD	1
4976540.142	528780.147	34	4	LD	1
4976538.773	528780.488	35	4	LD	1
4976537.313	528780.333	36	4	LD	1

Northing	Easting	Plot Number	Site	Species	Transect
4976556.183	528759.336	37	4	LD	1
4976555.309	528761.354	38	4	LD	1
4976555.732	528759.818	39	4	LD	1
4976565.202	528752.989	40	4	LD	1
4978755.567	534570.022	41	5	LD	1
4978752.238	534561.929	42	5	LD	1
4978749.133	534565.847	43	5	LD	1
4978745.085	534559.015	44	5	LD	1
4978752.241	534569.314	45	5	LD	1
4978739.043	534545.098	46	5	LD	1
4978742.03	534550.263	47	5	LD	1
4978746.375	534549.61	48	5	LD	1
4978740.222	534548.082	49	5	LD	1
4978737.996	534547.257	50	5	LD	1
4977858.766	537122.013	51	6	CM	1
4977857.054	537121.159	52	6	CM	1
4977850.395	537122.446	53	6	CM	1
4977848.22	537129.2	54	6	CM	1
4977839.048	537123.272	55	6	CM	1
4977836.239	537118.707	56	6	CM	1
4977825.159	537123.275	57	6	CM	1
4977822.26	537126.182	58	6	CM	1
4977818.394	537129.604	59	6	CM	1
4977819.359	537133.616	60	6	CM	1
4977209.094	538706.732	61	7	LD	1
4977224.891	538693.764	62	7	LD	1
4977246.139	538699.927	63	7	LD	1
4977231.622	538705.067	64	7	LD	1
4977220.727	538711.819	65	7	LD	1
4977208.023	538741.504	66	7	LD	1
4977204.58	538771.299	67	7	LD	1
4977213.168	538790.151	68	7	LD	1
4977215.438	538793.703	69	7	LD	1
4977200.058	538796.11	70	7	LD	1
4975148.926	541326.97	71	8	CM	1
4975147.05	541328.216	72	8	CM	1
4975146.725	541327.608	73	8	CM	1
4975163.695	541333.503	74	8	CM	1
4975167.426	541336.722	75	8	CM	1
4975168.359	541335.999	76	8	CM	1
4975167.793	541334.835	77	8	CM	1
4975169.556	541335.942	78	8	CM	1
4975168.307	541336.857	79	8	CM	1
4975169.359	541338.112	80	8	CM	1
4963284.739	543889.525	101	9	CM	1
4963284.629	543889.486	102	9	CM	1
4963285.832	543889.381	103	9	CM	1

Northing	Easting	Plot Number	Site	Species	Transect
4963285.76	543890.597	104	9	CM	1
4963285.54	543891.196	105	9	CM	1
4963289.926	543890.806	106	9	CM	1
4963284.945	543892.196	107	9	CM	1
4963287.719	543892.155	108	9	CM	1
4963288.406	543893.742	109	9	CM	1
4963289.074	543894.809	110	9	CM	1
4961943.295	544750.147	321	10	CM	1
4961942.968	544752.619	322	10	CM	1
4961945.409	544747.204	323	10	CM	1
4961945.404	544744.903	324	10	CM	1
4961949.124	544738.518	325	10	CM	1
4961953.595	544743.795	326	10	CM	1
4961950.836	544745.167	327	10	CM	1
4961950.283	544748.656	328	10	CM	1
4961950.881	544752.002	329	10	CM	1
4961960.459	544741.992	330	10	CM	1
4961894.712	544806.109	111	11	CM	1
4961909.483	544803.585	112	11	CM	1
4961901.642	544810.308	113	11	CM	1
4961900.043	544868.262	114	11	CM	1
4961903.893	544896.563	115	11	CM	1
4961914.624	544865.98	116	11	CM	1
4961933.156	544854.098	117	11	CM	1
4961921.902	544834.166	118	11	CM	1
4961919.032	544802.249	119	11	CM	1
4961915.68	544831.539	120	11	CM	1
4968679.149	548522.055	81	12	CM	1
4968680.794	548525.251	82	12	CM	1
4968686.082	548528.71	83	12	CM	1
4968677.07	548523.326	84	12	CM	1
4968671.385	548533.305	85	12	CM	1
4968670.5	548536.184	86	12	CM	1
4968670.894	548538.182	87	12	CM	1
4968617.835	548476.454	88	12	CM	1
4968618.247	548474.507	89	12	CM	1
4968621.08	548469.416	90	12	CM	1
4959442.43	544063.056	341	33	CM	1
4959426.451	544057.967	342	33	CM	1
4959427.259	544060.177	343	33	CM	1
4959422.619	544054.313	344	33	CM	1
4959413.617	544052.101	345	33	CM	1
4959410.057	544028.218	346	33	CM	1
4959397.553	544027.675	347	33	CM	1
4959396.328	544028.436	348	33	CM	1
4959392.136	544026.049	349	33	CM	1
4959388.575	544022.369	350	33	CM	1

Northing	Easting	Plot Number	Site	Species	Transect
4993701.16	531412.97	221	23	CM	2
4993703.497	531417.683	222	23	CM	2
4993701.288	531418.683	223	23	CM	2
4993701.535	531419.988	224	23	CM	2
4993688.824	531426.926	225	23	CM	2
4993680.68	531424.085	226	23	CM	2
4993676.057	531420.754	227	23	CM	2
4993677.24	531423.903	228	23	CM	2
4993675.311	531424.951	229	23	CM	2
4993684.811	531427.943	230	23	CM	2
4993292.82	530627.828	231	24	CM	2
4993295.619	530627.257	232	24	CM	2
4993294.138	530626.862	233	24	CM	2
4993285.422	530625.542	234	24	CM	2
4993301.045	530621.286	235	24	CM	2
4993324.871	530613.432	236	24	CM	2
4993326.305	530611.252	237	24	CM	2
4993324.883	530609.55	238	24	CM	2
4993321.669	530611.757	239	24	CM	2
4993322.206	530606.796	240	24	CM	2
4993259.708	530376.261	241	25	CM	2
4993269.049	530369.048	242	25	CM	2
4993271.015	530366.768	243	25	CM	2
4993260.08	530367.118	244	25	CM	2
4993259.704	530362.535	245	25	CM	2
4993248.711	530365.749	246	25	CM	2
4993243.325	530365.018	247	25	CM	2
4993261.173	530378.402	248	25	CM	2
4993253.7	530383.183	249	25	CM	2
4993251.933	530384.215	250	25	CM	2
4992853.964	529975.094	251	26	CM	2
4992854.614	529977.799	252	26	CM	2
4992803.236	529962.964	253	26	CM	2
4992805.979	529964.513	254	26	CM	2
4992798.395	529962.133	255	26	CM	2
4992794.118	529960.889	256	26	CM	2
4992793.358	529961.926	257	26	CM	2
4992793.211	529962.21	258	26	CM	2
4992791.504	529963.335	259	26	CM	2
4992790.803	529964.855	260	26	CM	2
4991735.648	529685.625	261	27	LD	2
4991736.831	529689.79	262	27	LD	2
4991740.139	529690.161	263	27	LD	2
4991736.209	529693.23	264	27	LD	2
4991735.047	529697.185	265	27	LD	2
4991723.789	529716.452	266	27	LD	2
4991724.425	529719.935	267	27	LD	2

Northing	Easting	Plot Number	Site	Species	Transect
4991721.762	529722.229	268	27	LD	2
4991721.616	529733.609	269	27	LD	2
4991725.248	529736.969	270	27	LD	2
4988912.793	527104.512	271	28	LD	2
4988934.389	527120.555	272	28	LD	2
4988914.726	527098.338	273	28	LD	2
4988927.635	527094.813	274	28	LD	2
4988909.126	527073.615	275	28	LD	2
4988903.348	527089.882	276	28	LD	2
4988922.287	527115.883	277	28	LD	2
4988916.906	527085.936	278	28	LD	2
4988917.193	527097.408	279	28	LD	2
4988906.841	527103.104	280	28	LD	2
4987844.115	525726.78	281	29	LD	2
4987837.888	525738.719	282	29	LD	2
4987819.062	525749.905	283	29	LD	2
4987838.311	525760.206	284	29	LD	2
4987823.863	525732.064	285	29	LD	2
4987831.531	525743.534	286	29	LD	2
4987839.871	525742.17	287	29	LD	2
4987833.139	525721.012	288	29	LD	2
4987828.481	525755.5	289	29	LD	2
4987833.323	525768.89	290	29	LD	2
4987555.781	525092.07	291	30	LD	2
4987551.891	525095.415	292	30	LD	2
4987545.825	525092.78	293	30	LD	2
4987555.53	525095.188	294	30	LD	2
4987564.038	525096.518	295	30	LD	2
4987560.56	525091.982	296	30	LD	2
4987559.359	525097.341	297	30	LD	2
4987563.964	525094.314	298	30	LD	2
4987550.382	525095.539	299	30	LD	2
4987550.782	525096.667	300	30	LD	2
4987102.329	524527.447	301	31	LD	2
4987101.415	524532.334	302	31	LD	2
4987100.092	524532.39	303	31	LD	2
4987098.678	524535.676	304	31	LD	2
4987096.238	524533.897	305	31	LD	2
4987099.781	524551.626	306	31	LD	2
4987089.395	524556.447	307	31	LD	2
4987077.706	524579.226	308	31	LD	2
4987074.726	524583.784	309	31	LD	2
4987076.844	524587.9	310	31	LD	2
4987422.983	523454.058	311	32	LD	2
4987474.82	523460.03	312	32	LD	2
4987474.708	523437.147	313	32	LD	2
4987486.399	523450.439	314	32	LD	2

Northing	Easting	Plot Number	Site	Species	Transect
4987486.293	523448.581	315	32	LD	2
4987475.615	523435.625	316	32	LD	2
4987478.063	523436.714	317	32	LD	2
4987484.789	523438.019	318	32	LD	2
4987483.265	523440.607	319	32	LD	2
4987478.411	523446.545	320	32	LD	2
4990745.539	525059.733	151	13	CM	3
4990739.511	525048.005	152	13	CM	3
4990745.22	525044.727	153	13	CM	3
4990749.924	525037.078	154	13	CM	3
4990742.416	525028.632	155	13	CM	3
4990734.242	525021.542	156	13	CM	3
4990722.974	525022.7	157	13	CM	3
4990715.272	525032.817	158	13	CM	3
4990720.191	525040.849	159	13	CM	3
4990725.989	525056.216	160	13	CM	3
4990764.435	526104.49	171	14	LD	3
4990765.762	526095.107	172	14	LD	3
4990769.619	526100.414	173	14	LD	3
4990777.2	526098.968	174	14	LD	3
4990749.811	526112.861	175	14	LD	3
4990757.882	526111.01	176	14	LD	3
4990774.896	526091.83	177	14	LD	3
4990767.487	526103.356	178	14	LD	3
4990758.37	526104.057	179	14	LD	3
4990762.709	526099.531	180	14	LD	3
4990953.737	525311.721	161	15	LD	3
4990949.427	525301.627	162	15	LD	3
4990943.798	525300.029	163	15	LD	3
4990947.65	525295.963	164	15	LD	3
4990944.013	525307.81	165	15	LD	3
4990944.063	525293.192	166	15	LD	3
4990938.891	525298.51	167	15	LD	3
4990964.814	525328.575	168	15	LD	3
4990963.623	525327.487	169	15	LD	3
4990961.409	525330.217	170	15	LD	3
4987930.995	525597.227	121	16	LD	3
4987913.977	525615.4	122	16	LD	3
4987915.791	525602.049	123	16	LD	3
4987935.532	525604.507	124	16	LD	3
4987936.939	525607.396	125	16	LD	3
4987943.928	525653.611	126	16	LD	3
4987949.676	525672.334	127	16	LD	3
4987976.081	525648.651	128	16	LD	3
4987966.306	525623.986	129	16	LD	3
4987945.209	525642.458	130	16	LD	3
4988666.555	525081.139	131	17	LD	3

Northing	Eastng	Plot Number	Site	Species	Transect
4988664.323	525080.776	132	17	LD	3
4988666.503	525085.683	133	17	LD	3
4988665.236	525082.947	134	17	LD	3
4988676.589	525093.227	135	17	LD	3
4988678.71	525094.742	136	17	LD	3
4988682.497	525096.956	137	17	LD	3
4988696.14	525089.048	138	17	LD	3
4988697.308	525085.018	139	17	LD	3
4988694.286	525086.138	140	17	LD	3
4988809.252	524707.328	141	18	LD	3
4988814.319	524696.537	142	18	LD	3
4988808.709	524687.432	143	18	LD	3
4988813.459	524707.327	144	18	LD	3
4988813.653	524713.054	145	18	LD	3
4988818.033	524717.03	146	18	LD	3
4988824.609	524728.985	147	18	LD	3
4988824.673	524738.799	148	18	LD	3
4988826.57	524750.971	149	18	LD	3
4988823.816	524745.366	150	18	LD	3
4993642.72	527306.312	201	19	CM	3
4993653.982	527295.442	202	19	CM	3
4993648.561	527291.746	203	19	CM	3
4993644.339	527293.281	204	19	CM	3
4993642.36	527301.669	205	19	CM	3
4993653.264	527307.109	206	19	CM	3
4993650.218	527300.812	207	19	CM	3
4993660.57	527296.893	208	19	CM	3
4993656.072	527300.313	209	19	CM	3
4993636.661	527304.557	210	19	CM	3
4992996.64	527395.16	211	20	CM	3
4992997.31	527390.084	212	20	CM	3
4992993.376	527388.137	213	20	CM	3
4992988.666	527394.104	214	20	CM	3
4992994.272	527392.955	215	20	CM	3
4993002.985	527394.77	216	20	CM	3
4993001.408	527388.893	217	20	CM	3
4992989.189	527389.282	218	20	CM	3
4992989.491	527382.785	219	20	CM	3
4992997.557	527391.751	220	20	CM	3
4992249.632	527066.033	191	21	CM	3
4992254.615	527062.706	192	21	CM	3
4992253.564	527062.297	193	21	CM	3
4992257.407	527064.06	194	21	CM	3
4992280.553	527084.364	195	21	CM	3
4992283.827	527083.553	196	21	CM	3
4992283.961	527084.312	197	21	CM	3
4992231.913	527043.181	198	21	CM	3



Northing	Easting	Plot Number	Site	Species	Transect
4992230.122	527041.435	199	21	CM	3
4992229.416	527038.406	200	21	CM	3
4992029.351	526498.814	181	22	LD	3
4992029.071	526495.761	182	22	LD	3
4992028.222	526495.429	183	22	LD	3
4992027.283	526499.318	184	22	LD	3
4992027.938	526500.14	185	22	LD	3
4992029.084	526500.725	186	22	LD	3
4992029.443	526502.299	187	22	LD	3
4992030.933	526502.563	188	22	LD	3
4992032.961	526504.597	189	22	LD	3
4992033.906	526505.143	190	22	LD	3

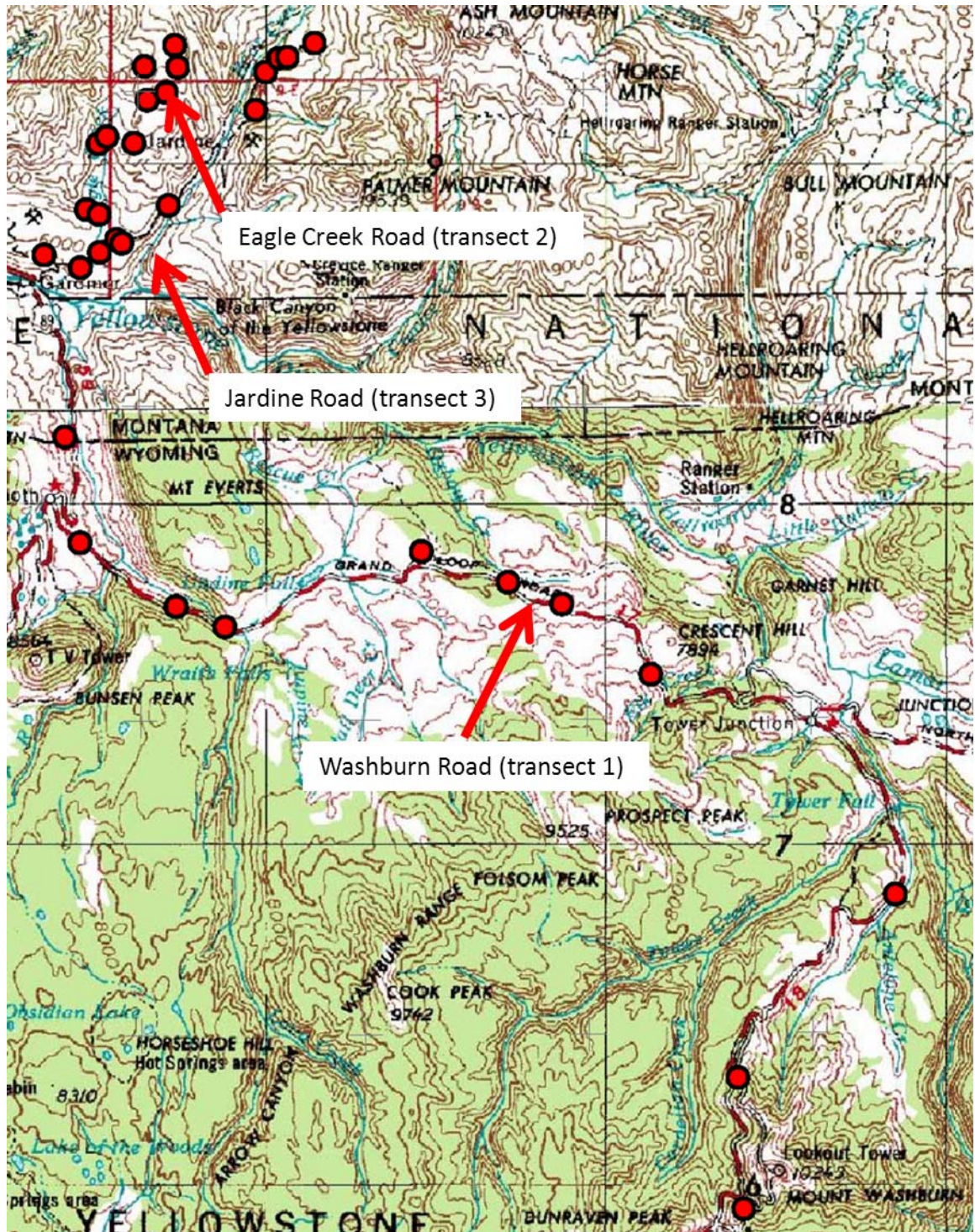


Figure E-1. Map of study area. Circles indicate study sites.