INVASIVENESS OF YELLOW TOADFLAX (*LINARIA VULGARIS*) RESULTING FROM DISTURBANCE AND ENVIRONMENTAL CONDITIONS

by

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ABSTRACT

Invasive plant species are considered to be one of the greatest threats to ecosystems and biological diversity throughout the world, and are thus often aggressively managed. The degree of plant invasiveness, however, varies both with environment and with type of landscape disturbance. This research was designed to understand how the factors of environment and disturbance affect the invasiveness of *Linaria vulgaris* (yellow toadflax) in southwest Montana and to quantify the varying degrees of invasiveness resulting from each factor. Data were obtained through four separate projects.

The effects of disturbance size and propagule pressure on *L. vulgaris* establishment were evaluated through a series of experiments in both disturbed and undisturbed plots. *L. vulgaris* establishment and survival were low in all plots, but followed the general trend of more successful establishment in larger disturbed plots and in disturbed plots with a higher seeding density.

An invasiveness index was developed that quantified invasiveness between -4 and +4 based on changes in population density and plant occupancy within permanent monitoring grids. This index was applied to *L. vulgaris* populations in three distinct environments, and invasiveness was found to range from -1.9 (declining population) to 1.8 (invasive population), indicating that invasiveness varied widely based on environment.

The effects of the disturbances of herbicide, digging, burning and vegetation clipping on established *L. vulgaris* populations were evaluated in four environments. In the first year after treatment, herbicide reduced invasiveness of *L. vulgaris* in all environments, while digging and burning increased invasiveness and clipping had no effect. In the second year, herbicide resulted in increased *L. vulgaris* invasiveness at the three sites dominated by forbs, while it still reduced invasiveness at the grass-dominated site. The other treatments had minimal effects.

Finally, effects of the above disturbances on the whole plant community were assessed using relative species abundance, richness and diversity metrics. Treatments generally decreased these metrics initially, but values recovered over time, with the exception of the herbicide treatment.

The results demonstrated that *L. vulgaris* population invasiveness and treatment effectiveness varies with environment, suggesting that prioritizing management on an environment basis may be appropriate.

PROLOGUE: A SHIFT TOWARD ECOLOGICALLY-BASED MANAGEMENT OF NON-INDIGENOUS PLANT SPECIES

"And this I believe: that the free, exploring mind of the individual human is the most valuable thing in the world…" – John Steinbeck

"The free, unhampered exchange of ideas and scientific conclusions is necessary for the sound development of science, as it is in all spheres of life." – Albert Einstein

Much work has been done in the past to attempt to characterize invasive plant species by biological traits (Gray 1986; Lodge 1993; Baker 1974). While this work has been useful in establishing some generalities regarding plant invasiveness (e.g., rapid vegetative growth facilitates invasion), predicting which species from a newly introduced group will ultimately become invasive is still not possible. An abundance of studies, stemming from the "biotic resistance" principle (Elton 1958), have also attempted to define characteristics of plant communities that are more readily invaded (Tilman et al. 1997; Shea and Chesson 2002; van Ruijven et al. 2003). Results indicate that environment plays an important role in invasions, with species poor and/or disturbed communities generally being more readily invaded (but see Fridley 2007 and references therein for exceptions). Nonetheless, the focus on species rather than environment has remained, and the current paradigm for non-indigenous plant species (NIS) management is to attempt wholesale control of a species. That is, the assumption is often made that a NIS, because of some biological property, will be invasive. Moreover, NIS are assumed to be equally invasive in all environments, and the same degree of management is often prescribed without consideration of the potential for differing levels of invasiveness.

The work presented in this thesis evaluates the invasiveness of *Linaria vulgaris*, not on any particular biological properties of the species, but across different environments and as a function of external system inputs (i.e., disturbances). The ultimate goal of this thesis is an attempt to present data and methodology to facilitate a paradigm shift from managing NIS on a species level, to managing NIS based on their degrees of invasiveness resulting from environmental variation. Four main questions related to *L. vulgaris*, or more broadly to all NIS, are explored. First is the issue of NIS colonization. It is known that both soil disturbance and increased seed rain (propagule pressure) positively correlate with colonization of many NIS, but how specifically does size of soil disturbance and seed density affect *L. vulgaris* colonization? To answer this question, *L. vulgaris* seeds were planted in a range of different sized plots and at a range of densities, and colonization rates were determined (Chapter 2). Second, I was interested in how invasiveness of NIS varies across environments, and the specific question was, does *L. vulgaris* invasiveness vary in different environments, and if so, how can it be quantified? Six populations of *L. vulgaris*, in three distinct environments, were monitored for five years, and calculations of invasiveness were made based on changes in population density and area (Chapter 3). The third question related to the effects of disturbance on *L. vulgaris* invasiveness in different environments. Past research has shown that plant invasions are strongly related to disturbance (see Lozon and MacIsaac for review). I tested the response of *L. vulgaris* to soil disturbance (digging), burning, grazing (clipping) and herbicide over two years and in four environments (Chapter 4). The final question departed from analysis of environment and

disturbance effects on *L. vulgaris*, and examined these effects on the plant communities as a whole. Using the same disturbances as described above, the extant plant community was monitored for three years and changes in species richness, diversity and community composition were assessed. The impacts of *L. vulgaris* on the plant communities were also explored (Chapter 5).

This work is not intended to be a theoretical study of the effects of environment and disturbance on NIS or plant communities – rather it is meant to be applied. Practical applications of this work are fourfold. First, Chapter 2 presents data on the colonization success of *L. vulgaris* related to disturbance size and propagule pressure. This information will be particularly useful to land managers in assessing how soil disturbance associated with certain activities (e.g., logging) may affect the expansion of existing *L. vulgaris* populations (which act as the propagule source). Second, data presented in Chapter 3 show differing levels of *L. vulgaris* invasiveness across environments and methodology for calculating invasiveness is presented. It is hoped that such methodology will be used by land managers to quantify invasiveness of the NIS they are charged with managing in different environments, and that management will then be prioritized by levels of invasiveness. This will allow managers to utilize their limited budgets to target the most invasive populations, while avoiding treating NIS in areas where they are not invasive and likely having no impacts. Third, Chapter 4 provides data on the effects of different disturbances, and potential management techniques, on *L. vulgaris*. These data show how *L. vulgaris* responds to the disturbances in different environments, and will facilitate informed decision making when planning management. Finally, the data

presented in Chapter 5 regarding *L. vulgaris* impact on plant communities and community response to disturbances will inform managers about the relative impacts of the NIS versus those of the proposed treatment, and will again, lead to better, ecologically-based management.

CHAPTER 1

INTRODUCTION AND REVIEW OF LITERATURE

Introduction

Invasions by non-indigenous plant species (NIS) are reportedly having serious ecological, economic and social consequences around the world (Vitousek et al. 1996; Dukes and Mooney 1999; Williamson 1999; Pimentel et al. 2005). A few of the many issues associated with NIS include a breakdown of regional distinctiveness of Earth's flora (Olden et al. 2004), loss of native biological diversity, species extinctions and threats to human welfare in terms of both health and wealth (Vitousek et al. 1997; Wilcove et al. 1998). These invasions are generally facilitated by humans (Vitousek et al. 1997), but are certainly not limited to human population centers or even areas directly disturbed by human activity. Even natural areas are susceptible to invasion; it seems that no nature reserve outside Antarctica is free from introduced species (Usher 1988; Lonsdale 1999).

Nations and organizations around the world are greatly concerned with the problem of NIS. For example, the Convention for Biodiversity (CBD), Scientific Committee on Problems of the Environment (SCOPE), United Nations Environment Programme (UNEP), World Conservation Union (IUCN) and others all have programs to research or control NIS (Williamson 1999). In the United States, the economic cost of NIS, including lost revenue from crops and forage as well as the cost of management, is

estimated to be $33 billion per year (Pimentel et al. 2005). The U. S. Department of Agriculture's annual budget for NIS programs exceeds $500 million (Powell 2004).

Despite the international concern, and the amount of money spent on research and management of NIS, there is still debate about the extent of the problem. Numerous authors report that NIS increase rather than reduce community richness and biodiversity (PlantyTabacchi et al. 1996; Wiser et al. 1998; Lonsdale 1999; Stohlgren 1999; Levine 2000; Rosenzweig 2001; Espinosa-Garcia et al. 2004), and that communities are not homogenized by NIS (McKinney 2004). Additionally, there is little empirical evidence that competition from NIS limits or suppresses growth of native species (Hager and McCoy 1998; Houlahan and Findlay 2004) or has any measurable effect on native species (Bruno et al. 2005). Theory (Davis 2003) and literature review (Sax et al. 2002; Gurevitch and Padilla 2004) have also shown that NIS invasions are not likely major causes of plant extinctions or even community change (MacDougall and Turkington 2005). Rather habitat disturbance and destruction may be the leading cause of community change and species loss (Gurevitch and Padilla 2004; MacDougall and Turkington 2005).

Regardless of the much debated environmental costs, the magnitude of economic costs of NIS necessitates that we learn more about the processes involved in NIS invasion. It is crucial to understand what environmental and anthropogenic factors lead to the establishment of new populations and their subsequent expansion. Also, with limited funds and labor directed toward management of NIS, and with potential negative

impacts from management, developing a method of determining NIS invasiveness and prioritizing management is imperative.

This research attempted to address a number of these issues through the study of the NIS *Linaria vulgaris* Mill. (yellow toadflax) in the area of West Yellowstone, Montana. The goals of the research were (1) to evaluate *L. vulgaris* colonization with respect to size of soil disturbance and magnitude of propagule pressure, (2) to evaluate the dynamics of *L. vulgaris* populations in different environments and quantify invasiveness, (3) to quantify the effects of different disturbances (herbicide, digging, burning and clipping) on *L. vulgaris* distribution within and around existing populations in different environments, and (4) to evaluate the impacts of disturbance and *L. vulgaris* on native plants. This chapter presents a review of the literature on plant invasions and *L. vulgaris*, and discusses the primary objectives of the research.

Plant Invasions

Plant invasions can occur when species are transported, either naturally or through facilitation by humans, from their home range to new locations, and they subsequently proliferate, spread and persist (Elton 1958; Mack et al. 2000). Invasions have occurred throughout time, but the magnitude in number, geographic scope and frequency have increased drastically and in direct proportion with expanding transport and commerce (Wells et al. 1986; di Castri 1989; Mooney and Cleland 2001). Most plants that arrive in a new range do not survive to become invaders (Mack et al. 2000; Mooney and Cleland 2001), but those that do are having tremendous ecological and economic consequences

(Heywood 1989; Vitousek et al. 1996; Vitousek et al. 1997; Dukes and Mooney 1999; Williamson 1999; Pimentel et al. 2005). The following sections discuss the numerous, and sometimes conflicting, theories of how generally plant communities are assembled and how specifically plant invasions occur, as well as the economic and ecological impacts of invasions.

Community Assembly Theory

Before explicitly discussing plant invasions, it is appropriate to examine various theories of how plant communities are assembled, and in particular, the factors controlling the number and identity of species that inhabit a community. There are two general schools of thought on community formation. The "niche assembly" perspective argues that communities are groups of interacting species, whose presence, absence and relative abundance are determined by assembly rules based on ecological niches or functional roles of each species (Levin 1970; MacArthur 1970; Diamond 1975; Weiher and Keddy 1999). In contrast, "dispersal assembly" argues that communities are open, nonequilibrium assemblages of species arranged by chance, history and random dispersal (Hubbell 2001). Species are transient, with presence or absence dictated by random dispersal and stochastic extinction (Hubbell 2001). Additionally, there are theories regarding the effects of competition, disturbance and the environment on plant communities. The following subsections present a brief overview of these and other important theories, as well as how they are related to invasion ecology.

Niche Assembly Theory. The concept of the "niche" has been used in ecology for many years to define the habitat of a particular species (Real and Levin 1991). Grinnell (1917) first defined niche as a species' place or location in the environment and subsequently narrowed the definition to the "ultimate distributional unit within which each species is held by its structural and functional limitations" (Grinnell 1928). Elton (1927) emphasized a species' function rather than location within the environment by defining niche as "the status of an animal in its community." Gause (1934) furthered Elton's definition by including competitive interactions among species. He stated, "a niche indicates what place the given species occupies in a community, i.e. what are its habits, food, and mode of life." Gause (1934) used this definition of niche to formulate his competitive exclusion principle, which states that two similar species cannot coexist if they have identical needs for a limited resource (i.e., one species will exclude the other such that the niche is only occupied by a single species). Hutchinson (1957, 1959) combined ideas from Elton's and Gause's niche concepts to form his idea of the "fundamental niche". This is essentially a multi-dimensional space defined by the limiting values of resources required by a species (i.e., minimum amounts of light, nutrients, and water) needed for survival and reproduction. In this theory, large assemblages of species can occur in a given area because of niche differentiation. That is, species with different niche requirements inhabit parts of the environment with slightly different niche characteristics, thus creating diverse communities. The underlying implication of these theories is that a niche space can only be occupied by one species at a time, and if a species is better suited to a particular niche than the species

currently occupying that niche, then the former species can "invade" and replace the latter (Hutchinson 1959).

Dispersal Assembly Theory. In 1967, the theory of island biogeography (MacArthur and Wilson 1967) was introduced in an attempt to explain, among other things, how islands become populated. The number of species on a given island, within a specific biogeographic region, is a function primarily of the island's size, and, to a lesser degree, its distance from a mainland source. The authors proposed that the number of species on an island was determined through the balancing processes of immigration of new species from outside sources and local extinction. Larger islands closer to a mainland source would receive more immigration than smaller islands farther away, and thus would have a greater complement of species. The model is neutral in the respect that all species have equal probability of immigrating into the system or going extinct. This theory says that, at least on a broad scale, communities are functions of random colonization and extinction, rather than competition and niche partitioning (MacArthur and Wilson 1967).

Unified Neutral Theory. Hubbell (2001), with the unified neutral theory of biodiversity and biogeography, attempted to unite the niche assembly and dispersal assembly perspectives. He modified MacArthur and Wilson's (1967) theory by allowing for speciation, assuming neutrality at the individual rather than species level (i.e., all organisms are equal in their per capita probabilities of giving birth, dying, immigrating and speciating), and assuming that the environment is biologically saturated (i.e., no

species in a community can increase in abundance without a corresponding decrease of another species). This theory proposes that communities are assembled largely by chance, but with species relative abundance based on the number of individuals in the immigration pool (Hubbell 2001). In terms of invasion ecology, this means that propagule pressure (i.e., the number of seeds or vegetative parts arriving at a site) is more important than relative competitive ability for an invading species.

Competition Theory. From aspects of niche assembly theory, it is assumed that competition among species for limited resources can explain much about how communities are assembled. Tilman (1976, 1977, 1982) built upon Gause's (1934) competitive exclusion principle to develop the R* concept of competition for limiting resources. In this theory, R* represents the resource concentration required for the growth rate of a species to be exactly offset by the species' mortality rate. If a limiting resource for a species falls below the concentration of R* in a particular habitat, then the species will eventually become extinct in that habitat. If multiple species are competing for one limiting resource, then the species that can tolerate the lowest concentration of the resource (i.e., lowest R* value) should displace all other species from the habitat (Tilman 1976, 1977). In this sense, the better competitor is not necessarily the one that can obtain most of the resource, but rather the one that requires the least of it.

This theory was tested in a nitrogen limiting environment where five species were grown in garden plots with three different starting conditions: seed competing against seed, seed competing against established plants, and established plants competing against each other. In all cases, the species with a significantly lower R* displaced the other

species (Wedin and Tilman 1993). This has serious implications for invasion ecology, as it suggests that invasion of any community is possible as long as the invading species is a better competitor (has a lower R* value).

Disturbance. Disturbance has long been recognized as an important factor shaping plant communities (Connell 1978; Grime 1979; Huston 1979; Pickett and White 1985). Pickett and White (1985) define disturbance as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment." Natural processes such as fire, flooding, herbivory, tree-fall, and animal burrowing are disturbances that structure communities, at least partially, by creating conditions favorable to certain plant species (Pickett and White 1985). These disturbances create patches of either open ground, or increased resource availability, often by the removal of the existing plant community (Hobbs 1989). Many plant communities are dependent on disturbance for regeneration (Pickett and White 1985). For example, prairie fires generally do not kill individual grasses, but rather stimulate them (Hobbs 1989). Anthropogenic disturbances such as agriculture, roads, logging, and fire suppression activities similarly shape plant communities, often leading to a change in species composition (Hobbs 1989; Hobbs and Huenneke 1992; Burke and Grime 1996; D'Antonio et al. 1999; Davis et al. 2000).

There are three important characteristics of disturbance: frequency, intensity and spatial extent (Pickett and White 1985). Frequent disturbance, if intense enough to eliminate the existing vegetation, will keep the plant community in an early successional state. Ruderal species (i.e., high reproductive effort and growth rate) adapted to high-

resource environments tend to dominate this environment. Longer inter-disturbance periods allow the community to mature, with competitive species (i.e., efficient use of resources and low reproductive effort) replacing ruderal species (Grime 1979). Long-term lack of disturbance allows the community to mature to a late successional stage, considered to be biotically stressful (Grace 1991). The spatial extent of disturbance is important for plant community structuring not only in terms of how much area is affected, but also in the sense of the pattern formed (e.g., mosaic landscapes formed by patchy burns) (Turner 1987). Mosaic patterns allow for areas with different successional states, thereby creating an overall more diverse community. Connell (1978), with the intermediate disturbance hypothesis, has proposed that intermediate levels of disturbance, in terms of frequency, intensity and size, will lead to the most diverse plant community.

Other Factors Shaping Plant Communities. The abiotic environment (e.g., resources, climate), biotic environment (e.g., competitors, herbivores), and the interaction between the two are also important factors structuring plant communities. The interaction between year and the above factors is also important, as temporal variation in one factor will affect the others (Crawley 1997) (e.g., higher mean temperature in one year will affect the number of plant enemies, which in turn affects plant populations).

Plant Invasion Theory

The study of invasion ecology began with Elton's (1958) book, *The Ecology of Invasions by Animals and Plants*. While the evidence presented by Elton is anecdotal rather experimental-based, and his predictions regarding invasions are based on such

empirical evidence, most hold true today (Simberloff in the Forward to the 2000 edition of Elton (1958)). These include predictions about the general lack of success of most invaders, increasing number of invasions, susceptibility of islands to invasion, patterns of spatial spread of invaders, impacts, and generally low level of predictability of invasions. The primary theory from Elton's work is that of ecological resistance – i.e., diverse communities better resist invasion by non-native species. Elton (1958) makes the point that most alien plants live in habitats greatly simplified by man – arable land, waste dumps, railroad tracks, etc., and these same plants are unable to invade rich native communities.

While much ecological research conducted since Elton has focused on the idea that diverse systems are less invasible, with the assumptions that niche space is limiting and communities are strongly structured by competition, the theory of ecological resistance has not been proven. On the contrary, while theoretical models continue to support the negative relationship between native species diversity and invasibility (e.g., (Case 1990; Drake 1990; Law and Morton 1996)), reviews of empirical and experimental studies (Levine and D'Antonio 1999; Levine et al. 2004) show mixed results. Knops (1999) showed that experimental reduction in grassland plant richness increased ecosystem vulnerability to plant invasions. Similarly, in an experiment where seeds were added to plots of varying native plant richness, Tilman (1977) found that invasibility declined with increasing richness. Many other studies show opposite results, indicating that species rich communities may be more susceptible to invasion (Robinson 1995; PlantyTabacchi et al. 1996; Stohlgren et al. 1998; Wiser et al. 1998; Stohlgren 1999;

Levine 2000; Symstad 2000; Stohlgren et al. 2001; Stohlgren et al. 2003). Native species richness in a given area is controlled by habitat heterogeneity and available resources (Lonsdale 1999), seed supply (Tilman 1997), and other factors such as disturbance, land use, species migration and turnover, herbivory, competition, diseases and pathogens (Stohlgren 1999), and it is hypothesized that NIS respond to these same factors, explaining the positive relationship between native species richness and invasibility (Stohlgren 2002). Levine and D'Antonio (1999) in their review paper, concur with this notion, stating that the factors known to influence diversity (i.e., competition, disturbance, resource availability and propagule pressure) are the same factors that influence invasions. Fridley et al. (2007) offer an explanation to this debate by acknowledging that a simple theory to the diversity-invasiveness relationship is not realistic, and agreeing that natively rich ecosystems are likely to be highly invaded by exotic species, but that the reduction of local species richness can further accelerate invasion.

Two hypotheses often invoked when explaining the success of NIS are the "enemy-release" and "novel weapons" hypotheses. In the former, it is believed that species colonizing a new environment have an advantage because they arrive unaccompanied by their co-evolved predators and pathogens (Darwin 1859; Lake and Leishman 2004). This allows NIS to allocate more resources to growth than to defense and thus to evolve genotypes with increased competitive ability (Blossey and Notzold 1995). The concept of the novel weapons hypothesis is that root exudates (e.g., allelopathic or antimicrobial compounds) from a plant may have negligible effects

against its natural neighbors, but they may be highly inhibitory to plants or microbes encountered in the new environment that have not evolved in the presence of the NIS (Callaway and Ridenour 2004).

Of all the factors influencing invasion, disturbance may be the most important because it potentially frees up resources, reduces competition and creates empty niches that invaders can occupy (Elton 1958; Hobbs 1989; Rejmanek 1989; Hobbs and Huenneke 1992; Burke and Grime 1996). It is generally accepted that many weed species have evolved through selection and adaptation to continuous habitat disturbance (Radosevich et al. 1997). In a review by Lozon and MacIsaac (1997) of 133 papers on invasions, it was found that disturbance was required for plant establishment in 86% of cases and for range expansion 58% of the time. Numerous other studies, a few examples of which are presented below, have also shown the importance of disturbance relative to invasion. In an empirical study, Larson (2003) found that the disturbances of prairie dog towns, roads and trails were all positively correlated with NIS. Thompson et al. (2001) experimentally showed that invasion of a grassland increases along a soil disturbance gradient. Similarly, Duggin and Gentle (1998) showed that invasion of a dry rainforest – open forest ecotone, was invaded along a disturbance (fire and livestock grazing) gradient. Finally, it has been known for centuries that agricultural systems, with their repeated disturbances, are susceptible to invasion (Crawley 1987; Cousens and Mortimer 1995; Radosevich et al. 1997).

Impacts of NIS

The impacts of NIS are widespread, including both economic (Pimentel et al. 2005) and environmental damage (Wilcove et al. 1998). The economic cost associated with NIS in the United States, including lost revenue from crops and forage as well as the cost of management, is estimated to be $33 billion per year (Pimentel et al. 2005). Environmental or ecosystem damage includes loss of native species diversity and alteration of environmental processes (Wilcove et al. 1998; Dukes and Mooney 2004). Indeed, NIS invasions are purportedly one of the most serious environmental threats, with NIS already having caused alteration of the earth's biota, disruption of evolutionary processes, and change in species abundance, including extinctions (Cronk and Fuller 1995; Rhymer and Simberloff 1996). Additionally, these alterations are a threat to global biodiversity, second in impact only to direct habitat destruction (Walker and Steffen 1997). Specific examples of impacts, many of which come from a review by Dukes and Mooney (2004), are discussed below, focusing on environmental damage rather than impacts in agricultural systems.

Non indigenous species can alter geomorphology and hydrology. On the west coast of the United States, introduced beach grasses (*Ammophilla* spp.) have stabilized sand dunes to the point where natural movement of sand in some areas has ceased (Seabloom and Wiedemann 1994; Wiedemann and Pickart 1996). Also on the west coast, introduced species of cordgrass (*Spartina* spp.) have replaced native cordgrass, causing excess sedimentation in estuaries and blocked tidal channels and waterways (Asher 1991 in Dukes and Mooney 2004). Other species such as giant reed (*Arundo donax*), salt cedar

(*Tamarix ramosissima*) and bermudagrass (*Cynodon dactylon*) may stabilize sediment in riparian areas, thereby altering stream morphology, while spotted knapweed (*Centaurea maculosa*) and others can increase erosion by creating more bare ground (Dukes and Mooney 2004). Salt cedar and *Centaurea* spp., as well as *Eucalyptus* spp., tend to use more water than the native species they replace, thereby drawing down the water table (Dukes and Mooney 2004).

Non-native grasses such as cheatgrass (*Bromus tectorum*) have replaced native vegetation and altered the fire cycle in western United States deserts and shrublands (D'Antonio and Vitousek 1992). These grasses provide a continuous path of fine fuels that promote the spread and increase the frequency of fires. The grass populations tend to recover quickly after fire, but the increased fires may decimate shrubs and other native perennials (Dukes and Mooney 2004).

Rare or endangered plants may be affected by NIS. Thompson (2005) showed that seedling recruitment of a California endemic, Antioch Dunes evening primrose (*Oenothera deltoids*), was limited by the presence of a non-native grass. Similarly, Huenneke and Thompson (1995) found that seedlings and rosettes of the NIS teasel (*Dipsacus sylvestris*) had negative effects on the growth of the rare Mescalero thistle (*Cirsium vinaceum*).

Loss of biodiversity after NIS invasion is also of concern, and several recent studies have documented this. In a Mediterranean-type shrubland in California, invasion by jubata grass (*Cortaderia jubata*) created a structurally less complex perennial grassland that was depauperate of native shrub species (Lambrinos 2000). Likewise, Sri

Lankan privet (*Ligustrum robustum*) has invaded human-disturbed rainforests on the island of La Réunion, displaced native species, and formed monocultures (Lavergne et al. 1999). A problematic wetland species is purple loosestrife (*Lythrum salicaria*). Schooler et al. (2006) found that wetlands with high densities of *Lythrum salicaria* had lower native plant diversity. Others, however found no negative effects of *Lythrum salicaria* on native vegetation (Hager and McCoy 1998; Farnsworth 2004; Houlahan and Findlay 2004), and in the broader sense, several authors have shown that NIS do not have a major impact on biodiversity (PlantyTabacchi et al. 1996; Lonsdale 1999; Sax et al. 2002; Gurevitch and Padilla 2004).

While all of these environmental effects of NIS are important, NIS effects that have direct economic consequences are often the ones that receive the most attention from landowners or land managers. In agricultural settings, weeds reduce crop yields and may damage the value of the product (Cousens and Mortimer 1995). Where timber production is the goal, weeds are of concern because they compete with tree seedlings and hamper forest regeneration (Radosevich et al. 1997). In rangeland situations, NIS such as Canada thistle (C*irsium arvense*), *Centaurea maculosa*, yellow starthistle (*Centaurea solstitialis*) and *L. vulgaris* are of concern because they may limit forage production and may be toxic to some livestock (Lajeunesse 1999; Morishita 1999; Sheley et al. 1999; Sheley et al. 1999). Note that in the case of agricultural, forest, and sometimes rangeland weeds, many of the problematic species are actually native rather than NIS (e.g., larkspur (*Delphinium* spp.) in rangelands grazed by cattle). In such cases

the species are defined as weeds simply because they are growing where they are unwanted or they interfere with human activities or goals.

Impact of Weed Management

When NIS are deemed to pose a threat to human activities or land manager goals, they may be managed, often through the use of chemical herbicides. Unfortunately, management of NIS may have off-target effects that are worse than the effects of the NIS themselves (Civeyrel and Simberloff 1996; Matarczyk et al. 2002). Undesirable effects of management may include environmental degradation by herbicides (NRC 2000), development of herbicide resistance by the target plant (Maxwell and Mortimer 1994; Clements et al. 2004), loss of native species diversity and re-invasion by other NIS (Ogden and Rejmanek 2005), and herbicide drift leading to mortality of adjacent plants (Matarczyk et al. 2002).

Linaria vulgaris

The following sections provide information about the history, range, economic and ecological problems associated with *L. vulgaris*, as well as details pertinent to understanding its growth, potential invasiveness and control. Where possible, references are strictly for *L. vulgaris*. However, in many cases peer reviewed references are not available for this species but they are for the closely related Dalmatian toadflax (*L. genistifolia spp. dalmatica* (*L.*)). For example, little or no information is available regarding the response of *L. vulgaris* to fire or grazing, but several papers discuss the response of *L. dalmatica*. This lack of peer-reviewed literature highlights the importance

of the research that was conducted as part of this project and presented in the following chapters.

Origin and Distribution

L. vulgaris, also known as common toadflax or "butter-and-eggs", is native to the steppes of southeastern Europe and southwestern Asia (Meusel et al. 1978 in Saner et al. 1995) and is now naturalized throughout much of this area (Reed and Hughes 1970). A Welsh Quaker who immigrated to Delaware first introduced it to the United States (Mitich 1993) sometime before 1672 (Saner et al. 1995). Today, the plant is found throughout the United States, Canada and Mexico (Lajeunesse et al. 2000), and has also been introduced to Japan, Australia, New Zealand, South Africa, Jamaica and Chile (Saner et al. 1995). In the United States and Canada, *L. vulgaris* most commonly occurs in the northeastern states and eastern provinces, respectively, and localized populations also exist in western states and provinces (Lajeunesse 1999). The northern limit of its range is approximately 55 – 60° North (Saner et al. 1995).

In the Gallatin National Forest around West Yellowstone, Montana, where this research was conducted, *L. vulgaris* was introduced in the 1800's as an ornamental at homesteads and stage stops (Lamont pers. comm.). It has since been observed in both disturbed and undisturbed lands at elevations ranging from 1900 m to 2200 m. In other areas of the Rocky Mountains, it has been found at elevations up to 3000 m (Pauchard et al. 2003).

Reason for Concern

L. vulgaris is a perennial weed in both agricultural and rangeland environments, and is designated a noxious weed in nine states (Alaska, Colorado, Idaho, Montana, New Mexico, Nevada, Oregon, Washington and Wyoming) and four Canadian provinces (Alberta, British Columbia, Manitoba and Saskatchewan) (Figure 1.1). In the Gallatin National Forest, Montana, *L. vulgaris* occupies lands heavily disturbed by fire and logging as well as areas not directly disturbed by human activities (Pauchard et al. 2003). It is also believed to be expanding its range in the adjacent Yellowstone National Park (Oliff et al. 2001; Whipple 2001) where it is considered a Priority II species on the Yellowstone National Park Exotic Plant Priority List (Yellowstone National Park 2005), indicating that it is an aggressive invader and well established in some localities, making eradication impractical. Containment is the primary goal in established infestations.

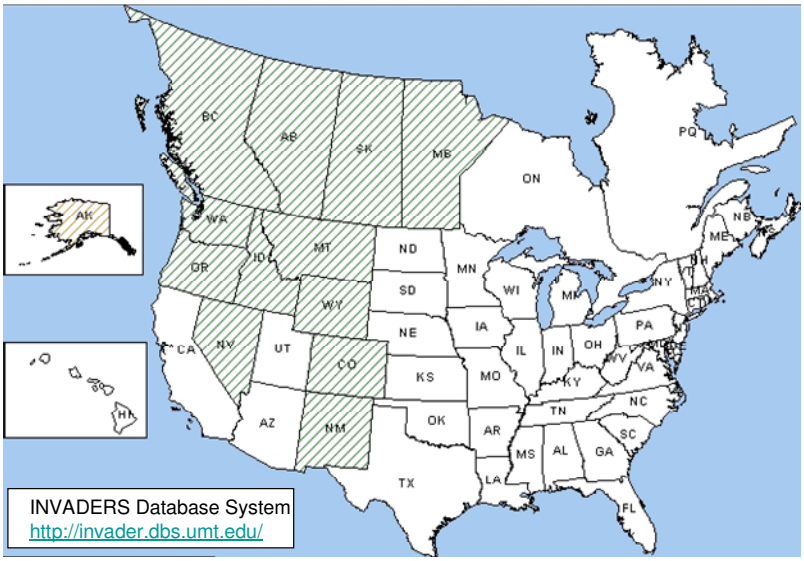

Figure 1.1. States and provinces listing *Linaria vulgaris* as a noxious weed as indicated by hatching.

Individual plants or small infestations away from core infestation areas are a high priority for aggressive control. Control efforts reportedly have a high probability of successfully limiting the spread (Yellowstone National Park 2005).

Historical and Beneficial Uses

For centuries *L. vulgaris* has been used for many beneficial purposes, including medicinal and ornamental (Mitich 1993). During the Middle Ages, in Europe and Asia, it was commonly prescribed as a remedy for throat ailments such scrofula (enlargement of the lymph glands in the neck), and for figs or piles (hemorrhoids), hence its inclusion in the family Scrophulariaceae or Figwort (Mitich 1993). In the 16th century it was used to relieve hot swellings, treat ulcers, and cure ailments of the liver and spleen. Water distilled from the plant was used as a remedy for redness and inflammation of the eyes (Mitich 1993). In the Elizabethan period (late 1500's), *L. vulgaris* was a popular garden plant of England, which the herbalist John Gerard (1928) called "a most glorious and goodly flower". Farmers in Sussex, England in the 17th century called the plant gallwort and added it to the drinking water of poultry to rid them of galls (Culpeper 1802).

During the early history of the United States, *L. vulgaris* was cultivated in gardens for use by settlers who valued it as a dye, a salve for insect bites, treatment for liver ailments, and numerous other medicinal uses (Mitich 1993). It was also boiled in milk and set out in saucers to poison flies that were problematic to settlers (Haughton 1978). *L. vulgaris*, with its two active constituents, the glycosides linarin and pectolinarian, is still prescribed to treat jaundice, liver problems, and various skin diseases (LeStange 1977).

Habitat

L. vulgaris evolved in Eurasia in plant communities that were grazed moderately to intensely by sheep, goats, and to a lesser extent, cattle. Thus, many populations are adapted to the periodic disturbances of agriculture (Lajeunesse 1999). In its native region, *L. vulgaris* is typically found in vineyards, woodland clearings and clearcuts, and its preferred substrates are dry to moderately humid sandy loam soils that are moderate to rich in nutrients (Saner et al. 1995).

In the United States and Canada, *L. vulgaris* is typically found in cultivated fields, roadsides, railways, "waste areas", clearcuts, overgrazed pastures and rangeland, and in plant communities that are open or disturbed (Arnold 1982). It is also common on well-drained rocky or gravelly river banks (Lajeunesse 1999), although it cannot tolerate saturated conditions (Zilke 1954 in Saner et al. 1995). Its growth is also limited by lack of sunlight, and therefore does not compete well under closed canopies (Saner et al. 1995; Pauchard et al. 2003). There is not a typical vegetation type that *L. vulgaris* colonizes. Rather, it is able to thrive in locations where disturbance has removed or suppressed existing vegetation (Arnold 1982).

Morphology

L. vulgaris is an herbaceous perennial of the Scrophulariaceae family. In a literature review on *L. vulgaris*, Saner et al. (1995) report that it typically forms colonies by means of adventitious buds from a creeping root system. Individual plants develop taproots that may be more than 1 m deep. Stems are 25-80 cm tall, glabrous or glandular hairy above, and often branched in the upper part. Leaves are alternate and linear to

narrowly lanceolate with a tapering petiolate base. Inflorescences are numerously flowered terminal racemes at the ends of branches. Flowers have five sepals and the corolla is 2-3 cm long with five united petals (Hitchcock and Cronquist 1973). The upper lip is yellow and two-lobed. The lower lip is yellow and three-lobed with an orange spot and a conical spur. The seed capsule is 8-12 mm long and has two cells. Seeds dehisce through two or three pores or slits at the apex. Seed are flattened, approximately circular, 1.4-2.1 mm in diameter and 0.5 mm thick, dark-brown or black, and are surrounded by a chartaceous wing (Saner et al. 1995).

The habit of *L. vulgaris* is highly variable depending on environmental factors such as shading, grazing or soil type (Saner, pers. obs.). Morphological variability is demonstrated through floral abnormalities, particularly peloric flowers, variability in the size and fertility of pollen grains, and frequent irregular meiotic divisions (Saner et al. 1995).

Comparison and Possible Hybridization with *Linaria dalmatica*

L. vulgaris and *L. dalmatica* are easily distinguished from one another, primarily by the leaves. In contrast to *L. vulgaris* leaves that are typically narrow and lanceolate, leaves of *L. dalmatica* are usually broad and somewhat heart-shaped (Hitchcock and Cronquist 1973). The bases of the leaves tend to wrap around the stem. Both leaves and stems of *L. dalmatica* are waxy and have a whitish or bluish hue, while *L. vulgaris* leaves are not waxy and are pale green (Saner et al. 1995).

Hybrids between *L. vulgaris* and striped toadflax (*L. repens* (L.) Miller) commonly occur (Dillemann 1953 in Saner et al. 1995). Hybrids between *L. vulgaris* and

L. dalmatica have been produced in the laboratory (Bruun 1937 in Saner et al. 1995, Ward pers. comm.), and such hybrids have been identified at a few sites in Montana (Ward pers. comm.).

Floral Biology and Seed Production

L. vulgaris plants are self-incompatible, although according to Darwin (1892), a small proportion of seeds can develop without cross-pollination. Typically the plant is insect pollinated and depends primarily on bumblebees (*Bombus* spp., *Psithyrus* spp.) and halictid bees (*Dialictus* spp., *Halictus* spp.) for pollination (Arnold 1982).

Seed production is highly variable. Numerous authors (in Saner et al. 1995) have reported seed production ranging from 1,500 to 30,000 seeds per plant. Nadeau and King (1991) reported that 210,000 seeds fell within a 0.5 m radius around the parent plant (a single transplanted root and shoot). It is difficult, however, to compare per plant seed counts from the literature because the definition of what constitutes an individual plant was unclear in these studies.

Seed Dispersal

L. vulgaris seeds may be dispersed by wind, water, ants, birds and rodents (Saner et al. 1995). The seeds have thin, papery wings that may facilitate dispersal by wind (Brenchley 1920). Nadeau and King (1991), however, found that approximately 90% of seeds fell within 0.5 m of the parent plant and the remaining seeds fell within a 1.5 m radius. Wind may play a greater role in secondary seed dispersal if seeds fall onto a snow crust in the winter (Saner et al. 1995). Water dispersal is possible because the seeds are

oily and can float (Lewis 1954 in Saner et al. 1995). Zilke (1954) (in Saner et al. 1995) reports the migration of *L. vulgaris* along watercourses. Ants, birds and rodents eat *L. vulgaris* seeds, providing a possible mechanism for dispersal (Saner et al. 1995). Zilke and Coupland (1954) (in Saner et al. 1995) report that seed dispersal via farm operations is likely an important mode of dispersal in agricultural land.

Germination and Seedling Establishment

Most seeds produced are either dormant or non-viable (Nadeau and King 1991) and reproduction by seed is rare. Seeds are innately dormant and require stratification, which leads to increased levels of gibberellic acid. This is likely the physiological mechanism that triggers germination (Bielefeld 1987 in Saner 1995). Nadeau and King (1991) found that germination was maximized in a laboratory experiment following a wet stratification at 5°C for a period of at least 8 weeks. Seed viability (from tetrazolium test) was as low as 40%, and seedling emergence varied from 0.13% to 0.23%.

Seedling emergence begins in early to mid-May in Alberta, Canada (Nadeau and King 1991) and earlier in warmer regions of the United States (Lajeunesse 1999). Most seedlings emerge in the spring, but emergence may also occur in the fall. Seedlings that do emerge are vulnerable to dehydration and competition from other species, especially in areas with good ground cover (Lajeunesse 1999).

Vegetative Reproduction

L. vulgaris plants can reproduce vegetatively by the formation of adventitious shoots from both the taproot and lateral roots (Bakshi and Coupland 1960). Early spring

regeneration of shoots from vegetative buds on the perennial root stock may provide *L. vulgaris* with a competitive advantage over other species (Lajeunesse 1999). Early production of vegetative shoots from new genets may provide an additional competitive advantage. Nadeau et al. (1992) report that new plants produce shoots only three weeks after cotyledon appearance. Mature plants are prolific producers of new shoots, with 90 to 100 shoots generated in the first year and 200 to 250 in the second year (Salisbury 1929, Rauh 1937, Zilke 1954 and Hartl 1974 in Saner et al. 1995).

Rapid spread of the population is possible through vegetative reproduction. Nadeau et al. (1991) found that a 20 cm long clipping could spread up to a radius of 1 or 2 m, and produce 75 or 694 shoots, in barley or on fallow land, respectively in one year. Zilke (1954 in Saner et al. 1995) reported that a seedling can produce a patch with a radius of 1 m in the first year, and subsequent year increases average 1.2 m in the patch diameter.

L. vulgaris is capable of forming dense stands in both disturbed agricultural systems and undisturbed natural settings. Nadeau et al. (1991) report maximum average densities of 300 and 700 shoots m^{-2} in barley and on fallow land, respectively. Clements and Cavers (1990) found densities of 94 to 160 shoots m^{-2} for five urban populations of *L. vulgaris* in southern Ontario. Shoot density in a population varies with precipitation and competition, with increased precipitation and decreased competition leading to greater *L. vulgaris* density (Nadeau et al. 1991).

The success of *L. vulgaris* is attributed to vegetative growth in hostile environments such as subarctic areas (Staniforth and Scott 1991) or in pastures and

orchards where fire and herbicide are regularly used to control weeds (Saner et al. 1995). Even in less hostile environments, vegetative reproduction is important because of the generally low rate of seedling establishment (Nadeau and King 1991; Nadeau et al. 1992). Salisbury (1942) concisely summarizes the importance of vegetative reproduction as follows: "The distribution of the species and its local abundance suggest rather poor dispersal but efficient multiplication, once colonization has taken place, and this is probably an example of a species whose maintenance in the northern and western extremes of its range has depended rather on successful vegetative multiplication than upon seed production".

Phenology

The phenology of *L. vulgaris* is highly variable and dependent upon environment. Kock (1966 in Saner et al. 1995) provides a detailed description of its phenology in northern Germany, which should be reasonably similar to that in the northwestern United States and Canada. Ramet growth begins in early to mid April when soil temperatures are between 5 and 10°C. Branching of the stems begins in early June when stems are between 40 and 60 cm. Flower buds appear in late June and flowering begins in mid-July with its peak at the end of July. Fruit capsules begin to open in September and are typically all open by the end of the month. Ramets die with the first hard freeze, but stems may remain erect and some seeds may remain in the capsules until strong winds dislodge them or the stems fall over (Saner et al. 1995).

Invasive Potential

L. vulgaris has many characteristics that make it a good potential invader, especially of disturbed sites. It can quickly colonize open areas because of high seed production (Nadeau and King 1991) and early vegetative reproduction (Nadeau et al. 1991). It has the ability to quickly spread via long roots and new shoots produced from adventitious buds (Nadeau et al. 1991). Finally, the deep, perennial root system and long-lived seeds (Saner 1995) allow it to persist once established.

Large-scale invasion of *L. vulgaris* in Saskatchewan, Canada was observed by Coupland et al. (1963) through a series of surveys and re-surveys of quarter-sections of land in the early 1950's. They found 57,749 ha in 4,993 quarter-sections were infested with *L. vulgaris*, with 86% of the infested area under cultivation, 5% abandoned cultivation, and 8% native plant communities. Results from 14 re-surveys of quarter-sections found a 47% average increase in number of hectares infested by *L. vulgaris*, with the percent change ranging from -67% to +186%. Coupland et al. (1963) note, however, that during the time period of 1944 to 1955, studies of natural grasslands of the region showed a doubling of grass cover apparently associated with above-average precipitation. Increases in *L. vulgaris* may have been related to this increased precipitation as well.

In Europe, large populations have been observed where competing vegetation has been suppressed by grazing, fire, or the regular application of non-selective herbicides (Saner, pers. obs.). Invasions have also been documented in agricultural settings (especially no tillage); (Saner et al. 1995) and many other disturbed settings including roadsides, gravel pits, pastures, clearcuts, vacant lots and railroad yards (Arnold 1982).

L. vulgaris can even invade rangeland in pristine condition via small-scale, naturally occurring disturbances (Lajeunesse 1999). Lajeunesse (1999) also states that even rangeland in pristine condition will do little to slow expansion once highly competitive vegetative growth has begun. These speculative statements by Lajeunesse (1999), however, are not documented with any references, and may not be consistent with other observations. Harris (1984 in Saner et al. 1995) states that *L. vulgaris* may perform well in moist, highly fertile areas, but is likely to be replaced by other species in less favorable conditions.

Impacts

Ecological. Lajeunesse (1999) reports that *L. vulgaris* can displace existing plant communities and associated animal life. She also states that where *L. vulgaris* replaces native sod-forming or bunch brass communities, soil erosion, surface runoff and sediment yield may be increased. Data to document these statements are, however, not provided.

Economic. In rangelands, economic impacts resulting from *L. vulgaris* infestation are from loss or reduced value of grazing land for livestock and loss of carrying capacity (Lacey and Olsen 1991). *L. vulgaris* is reported to be mildly poisonous to cattle (Mitich 1993), presumably because of its secondary compounds, and while cattle may occasionally browse flowering shoots (Harris and Carder in Lajeunesse 1999), they generally avoid the plant. Toxic compounds in the plant include alkaloids (e.g., peganin and choline) and iridoid glycosides (e.g., antirrhinoside and glycosylaucubin) in the foliage, flavonoids in the flowers and saponins in the seeds (Saner et al. 1995). These

compounds, however, do not negatively affect domestic sheep and goats because these animals can neutralize the phytochemicals that are toxic to other animals, and thus can use *L. vulgaris* as a food source (Walker 1994).

While previously only a problem in rangelands, railroad corridors and waste areas, the adoption of reduced tillage practices in agriculture have allowed *L. vulgaris* to establish in many horticultural and agronomic crops (Darwent 1975). Here, economic impacts occur as the result of yield losses. Darwent (1975) found that yields of forage crops such as creeping red fescue (*Festuca rubra* L.) may be reduced by 33 % at *L. vulgaris* densities of 180 stems m^{-2}, however, in most observed areas densities were less than 20 stems m^{-2}. In Alberta, in canola and cereal crops, yields were reduced by 20% at densities of 12 and 74 stems m^{-2}, respectively (O'Donovan and McClay 1987; O'Donovan and Newman 1989). More recently, *L. vulgaris* has become a serious problem in mint production in Wisconsin, where approximately 50% of the hectarage is infested (Eagen et al. 1992 in Volenberg et al. (1999)). An additional problem is that *L. vulgaris* provides over-wintering sites for the crop pests cucumber mosaic virus and broad bean wilt virus in New York (Saner et al. 1995).

In Alberta, *L. vulgaris* is considered a serious perennial broad-leaved weed. From 1971 to 1973, a survey of the Peace River region of northwestern Alberta assessed 4,189 ha as moderately or heavily infested. A 1987 survey of Alberta found 28,000 ha to be infested (30% annual crops, 30% forages, 20% pasture and 20% non-agricultural land) and cost of treatment was \$360,000 yr^{-1} (Saner et al. 1995). No economic costs of *L.*

vulgaris are reported in Montana, but one Montana ranch, with 129 ha severely infested with *L. dalmatica* in 1992 showed that control averaged \$99 ha^{-1} (Lajeunesse 1999).

Response to Disturbance

Fire. The above ground portion of *L. vulgaris* plants is typically killed by fire, but regeneration occurs via vegetative buds on its extensive root system, which is likely to survive (Lehnhoff, pers. obs.). Reports on the effects of fire on *L. vulgaris* populations are mixed. One study in south-central New York showed that there was no significant difference in toadflax cover between burned and unburned sites (Swan 1966). Others report that toadflax responds negatively to fire (Nermberg 1994), but experimental data are lacking.

Linaria species are well adapted to dry, open areas with little plant competition. This may give it a competitive advantage in burned areas and allow for establishment of new populations (Sackett and Haase 1993; Sackett and Haase 1996; Phillips 2000). In two cases near Flagstaff, AZ where prescribed fire was implemented to reduce fuel loads, *L. dalmatica* was a dominant species after the fires (Sackett and Haase 1993, 1996). In another study in Arizona, it was found that *L. dalmatica* was among several NIS that dominated sites that had been burned by large-scale, high-severity fires over the previous four decades (Kyle 2000). In all of these studies, however, no data are available regarding the presence of *L. dalmatica* before the fires. In a study of the effects of prescribed fire, Jacobs and Sheley (2003) found increased biomass and seed production from *L. dalmatica* after the burn.

Linaria spp. may respond positively to fire suppression activities, as well as to the fire itself. In Glacier National Park, *L. dalmatica* was found after a wildfire in bulldozed areas, but not in areas that had burned (Benson and Kurth 1993).

Soil Disturbance. Within agricultural systems where tillage occurs, physical disturbance of soil and spread of root pieces may result in significant spread of *L. vulgaris* infestations through new ramet production (Nadeau et al. 1992). Bakshi and Coupland (1960) reported, however, that in cultivated soil, there was an average of 53 *L. vulgaris* lateral roots per 15 cm length of main root, as compared to 67 lateral roots per 15 cm of main root in undisturbed soil. Also, shallow tillage in the spring can kill seedlings, especially those less than 3 weeks old, although deep-rooted plants will not be killed (Nadeau et al. 1992; Saner et al. 1995). Outside of agricultural systems, literature regarding the direct effects of soil disturbance on *L. vulgaris* is not available. There are, however, numerous sources (Arnold 1982, Lajeunesse 1999, Saner 1995) that state that the species typically populates disturbed areas.

Grazing. Cattle generally will not graze toadflax (Mitich 1993), but sheep and goats have been shown to preferentially choose *L. dalmatica* in situations where its cover was 25% to 100% of existing vegetation (Lajeunesse 1999). Compensatory growth of individual *Linaria* plants has not been demonstrated, but overgrazing of *Linaria* infested pastures or rangelands can lead to population increases as seedlings can better compete with grazed plants for soil moisture and other resources (Lajeunesse 1999).

Management

Biological. Biological control of NIS is based on the philosophy that the NIS have an advantage in their new range because they have left behind natural enemies which would limit their growth (enemy release hypothesis (Darwin 1859)). Under this theory, without these natural enemies, NIS often grow as solid extensive stands in the areas where they have been introduced, whereas in their home range the pattern is typically more patchy or clumped as a result of attack by their enemies (Radosevich et al. 1997). Biological control, therefore, involves introducing one or more of the plants' natural enemies for control purposes. The objective of biological control is not eradication of a NIS, but rather to lower its population level or competitive ability. Some of the NIS population should remain to maintain a population of the natural enemy, making the control measure permanent once the NIS and natural enemy populations are in equilibrium (Radosevich et al. 1997).

There are approximately 100 species of arthropods that attack *L. vulgaris* in Europe (Saner 1995). Several of these have been released, either intentionally or accidentally, in the United States and Canada. The released species include a defoliating moth (*Calophasia lunula* Hufnagel), a root-mining moth (*Eteobalea serratella* Treitschke), two seed capsule-feeding weevils (*Gymnaetron antirrhini* Paykull) and *Gymnaetron netum* (Germar)), an ovary-feeding beetle (*Brachypterolus pulicarius* L.) and a stem-boring weevil (*Mecinus janthinus* Germar) (Lajeunesse 1999; Volenberg et al. 1999).

Two species (*B. pulicarius* and *G. antirrhini*) are partially credited with reduction of *L. vulgaris* populations in Canada in the 1950's (Harris and Carder in Volenberg et al. 1999). *B. pulicarius* and *G. antirrhini* larvae develop inside the ovaries and fruit, respectively, and limit seed production and the quantity of viable seeds produced. Harris and Carder (1971 in Saner et al. 1995) found that seed production was reduced by over 90%, and McClay (1992) observed that flowering was delayed and the number of viable seeds declined by 74% in populations affected by *B. pulicarius*. Harris (1961 in Saner et al. 1995) concluded that *G. antirrhini* is the species most responsible for the decline and control of *L. vulgaris* in Canada's eastern provinces, British Columbia, and the northwestern United States. *G. netum* apparently has little impact on *L. vulgaris* (Lajeunesse 2000).

The leaf-feeding moth, *C. lunula*, was introduced to several areas of Canada in 1962 (Harris 1963 in Saner et al. 1995). Most releases failed (Saner 1995), probably because of intolerance to cold (McClay and Hughes 1995), but the species is now present throughout Ontario and in some areas of northern Idaho and Montana (Lajeunesse 2000). This moth defoliates up to 20% of the attacked plants (Harris 1963 in Saner et al. 1995).

M. janthinus is a weevil that is established on *L. dalmatica* in British Columbia and Alberta. Larvae of this species bore in stems and adults feed on shoots. In greenhouse studies, attack by *M. janthinus* reduced stem biomass (Saner 1995). Survival of this species may also be negatively affected by cold temperatures, but despite high winter mortality, rate of attack on *L. dalmatica* has increased with time since its release (De Clerck-Floate and Miller 2002). At this time, *M. janthinus* establishment on *L.*

vulgaris is unknown, but this weevil has been recommended for the control of *L. vulgaris* (Jeanneret and Schroeder 1992 in Saner et al. 1995).

The root-mining moth *E. serratella* has recently been considered as a control mechanism for *L. vulgaris* in mint production in Wisconsin. In laboratory tests, this species reduced plant biomass by an average of 20% (Volenberg et al. 1999). Saner and Mullerscharer (1994) found that attacked plants had a shorter flowering season and produced seeds of lower weight, but mining by the insect throughout the winter produced double the number of stems in the spring, while total biomass was unaffected.

While biological control has shown some success in controlling populations of *L. vulgaris*, there are concerns. Risks associated with the introduction of biological control agents fall into two main categories: (1) when the agent causes unintended and deleterious impacts to non-target species and (2) when the agent fails to reduce populations of, or causes undesired impacts on, the target NIS (Sing et al. 2005). Hansen and Gassmann (2002 in Sing et al. 2005) illustrate an example of the former by showing that the native Scrophulariaceae, *Sairocarpus virga* (Gray), which is found only in one region of California, may be attacked by *M. janthinus*. Additional examples of non-target feeding include *C. lunula*, in its larval stage, feeding on the naturalized ornamental plants *Antirrhinum majus*, *Cymbalaria muralis*, and *Linaria maroccana* (Sing et al. 2005). An example of undesired impacts of the biocontrol agent on the target species is illustrated by Saner (1994), showing increased vegetative growth of *L. vulgaris* in response to biological attack. In this situation, the competitive ability of the plant may have actually

increased in terms of the limiting resource of space, at no apparent cost in moisture and nutrient capture because the plant did non lose biomass or size (Sing et al. 2005).

Chemical. Herbicides used against *Linaria* spp. include 2,4-D with dichlorprop, amitrole, chlorthal-dimethyl, chlorsulfuron, dicamba, diquat, glyphosate and picloram (Saner et al. 1995; Baig et al. 1999; Lajeunesse 1999; Lajeunesse et al. 2000). Sebastian and Beck (1989) (in Lajeunesse 1999) reported on herbicide effectiveness against toadflax in several studies. Fall application of picloram (1.12 kg ai/ha) provided up to 98% control of *L. dalmatica* on some sites. In other studies, dicamba applied pre-bloom (4.83 kg ai/ha) and a tank mix of picloram plus 2,4-D (0.56 kg + 1.12 kg ai/ha) applied pre-bloom or in the fall provided excellent control. Fair to good control of *L. vulgaris* for one year was achieved using high rates of picloram plus fluroxypyr (1.12 kg + 0.89 kg ai/ha) applied pre-bloom. Others have had limited or no success with these herbicides (Ferrell and Whitson 1989; Hansen et al. 1989 in Lajeunesse 1999). Glyphosate applied early bloom at 1, 2, and 4 kg ai/ha provided 40, 70, and 90% current season control in barley, but abundant regrowth occurred early the next spring (Saner 1995). Baig et al. (1999) found the pre-harvest application of glyphosate reduced *L. vulgaris* by more than 80% in barley, canola and flax fields in Alberta. Triclopyr, fluroxypry, 2,4-D, MCPA, 2,4-DB, MCPB and mecoprop are reportedly ineffective against toadflax (Saner et al. 1995).

Effectiveness of chemical control is highly variable, in part because of the plant's high genetic variability (Lajeunesse 1999). Even when chemical treatment appears effective, long-term control may not be achieved and reinvasion may occur via seeds

from the seedbank. It may be necessary to treat infestations every 3 or 4 years for up to 12 years to achieve complete eradication (Lajeunesse 1999).

Ineffectiveness of herbicide treatment may be related to timing of application and soil type. Picloram, one of the most effective herbicides against *L. dalmatica* and *L. vulgaris*, and the herbicide of choice in the study area of this project, should be applied just before a rainfall so that it is moved into the soil (Lamont pers. comm.). If it remains on the soil surface, it will significantly degrade in the sunlight in 3 to 4 weeks (Lajeunesse 1999). If the soil is too coarse or lacks sufficient organic matter, as is often the case in areas where toadflax thrives, the herbicide may leach below the root zone (Lajeunesse 1999).

An additional problem with herbicide application is the potential for off-target effects. For example, application of picloram at the high rate necessary to be effective against *Linaria* species will kill many broadleaf species and possibly alter the plant community (Lajeunesse 1999). It has also been reported (Lange 1958 and Duncan 1992 in Lajeunesse 1999) that removal of plants such as *Centaurea maculosa* and St. Johnswort (*Hypericum perforatum*) from plant communities that also contain *Linaria* results in sudden germination of *Linaria* seeds, and thus the need for even higher herbicide rates.

<u>Physical/Mechanical/Cultural</u>. The keys to controlling *L. vulgaris* in cropping systems are the prevention of seed production and "root starvation" according to Alberta Agriculture (1988 in Saner et al. 1995). It is recommended that tillage begin on summer fallow in June with cultivations repeated every 3 to 4 weeks. In post-seedling cultivation,

tillage should be very shallow to keep from spreading roots. In the fall, tillage should begin immediately after crop harvest and continue every 3 to 4 weeks until top growth is killed by frost. Morishita (1991) concurs with these recommendations and adds that this type of intensive clean cultivation requires at least 2 years with 8 to 10 cultivations in the first year and 4 to 5 in the second. Warren (1957 in Saner et al. 1995) reports that best control is obtained when cultivation occurs when toadflax plants have 7 to 10 days of green growth. Seedlings less than 2 to 3 weeks old are very susceptible to tillage because vegetative growth has not yet started (Nadeau et al. 1992).

There are some concerns with such an intensive tillage program. First, excessive tillage can lead to erosion problems. In such areas, Alberta Agriculture (1988 in Saner et al. 1995) recommends strips of crop and fallow or the combination of cultivation and herbicides. Another concern is that tillage could possible spread toadflax to other fields if machinery is not cleaned properly, because root pieces as small as 1 cm can produce new shoots and create new infestations (Nadeau et al. 1992). Finally, tillage is generally not appropriate for pasture or rangeland situations.

Cutting, mowing and hand pulling *L. vulgaris* can be effective in removing seedlings and limiting patch spread, but these techniques will not kill the plants. Removal for 5 or 6 years may be necessary to deplete the plants root reserves, and it may take 10 to 15 years to remove all seedlings produced from dormant seeds. Hand pulling is most effective in moist, sandy soil where a greater proportion of the root system may be removed (Saner et al. 1995; Lajeunesse 1999).

Perhaps the best way to control *L. vulgaris* populations is to maintain a vigorous, healthy plant community (Lajeunesse 1999). Such a community may by able to outcompete *L. vulgaris* seedlings and prevent their establishment, or prevent the spread of small populations. Many grasses compete well with *L. vulgaris* (Carder 1963; Saner et al. 1995), and seeding disturbed sites with well-adapted grasses may help control *L. vulgaris* populations (Lajeunesse 1999).

Fire. Burning is not an effective means of controlling *L. vulgaris*. Roots and buds are typically unharmed by fire, and fire can increase the competitive ability of *L. vulgaris* by removing desirable plants. However, scorching individual plants with a propane torch can be an effective method of preventing seed production in small infestations (Lajeunesse 1999).

Grazing. There are no reports in the literature of domestic animals being used to control *L. vulgaris*. However, sheep have been used on *L. dalmatica* infestations (Lajeunesse 1999). In field trials in Montana, 1000 ewes and lambs were placed in hilly rangelands that were moderately to heavily infested (25% to 100% vegetative cover). Approximately 35% to 45% of the *L. dalmatica* vegetation was stripped, including the terminal 6 to 10 inches of the stems (Lajeunesse 1999). As with mechanical methods for cutting or mowing toadflax, grazing will not kill the plants, but may prevent flowering and seed production if the timing is correct.

Integrated Management. The successful management of *L. vulgaris* will likely require an integration of two or more of the above control techniques, and management

programs need to be site-specific. This is because of the high genetic variability (Ward pers. comm.) of *L. vulgaris* that results in localized populations that respond differently to the same treatments (Lajeunesse 1999). A successful program should place primary emphasis on reducing vegetative spread with secondary emphasis on the prevention of seed production (Lajeunesse 1999).

Primary Objectives of Research

L. vulgaris is widespread throughout disturbed areas of the study site near West Yellowstone, Montana. It is a Category I noxious weed in the state of Montana, meaning it can spread rapidly and generally limit beneficial uses of the land (Montana Department of Agriculture 2003). It is also a Priority II species on the Yellowstone National Park Exotic Plant Priority List, indicating that it is an aggressive, well-established invader that is impractical to eradicate (Yellowstone National Park 2005).

The multiple objectives of this project all serve to provide a better understanding of *L. vulgaris* growth patterns and facilitate its management in the West Yellowstone area. In a broader sense, the objectives are to contribute to the body of literature regarding the establishment and spread of NIS and to develop methodology that can be used to promote site-specific management of NIS populations. It is hoped that accomplishment of this latter objective will allow management personnel to target the most problematic NIS populations, while minimizing the use of potentially environmentally harmful management techniques by avoiding treatment of populations that are not invasive.

The specific objectives of the project were (1) to quantify the effects of propagule pressure and disturbance on *L. vulgaris* colonization; (2) to evaluate the population dynamics of *L. vulgaris* in different environments and develop a method to quantify its invasiveness; (3) to quantify the effects of different disturbances (burning, clipping, digging and herbicide) and environment on *L. vulgaris* invasiveness; and (4) to determine impacts of disturbance and *L. vulgaris* on native vegetation in different environments.

Objective 1: Effects of Size of Soil Disturbance and Propagule Pressure on *L. vulgaris* Colonization

Disturbance and propagule pressure are widely recognized as important factors in the establishment of NIS (Hobbs and Huenneke 1992; Burke and Grime 1996; D'Antonio et al. 1999; Kellogg and Bridgham 2004; Maron 2006). Disturbance generally serves to make resources more available by removing or suppressing the existing species and providing suitable microsites for germination (Hobbs and Huenneke 1992), and higher levels of seed rain increase the probability of successful population establishment. Few experiments, however, have been conducted to determine threshold levels of either disturbance size or seed number for the establishment of new populations of NIS (for exceptions see Burke and Grime (1996) and Maron (2006)). This research was conducted in an attempt to determine these threshold levels for *L. vulgaris*, and is discussed in Chapter 2.

Objective 2: Population Dynamics
and Invasiveness

To assess the threat of any population of NIS, it is important to understand the dynamics of the population. Not only is it important to know if the overall population is increasing or decreasing, it is useful to quantify birth rates, death rates, immigration and emigration, as well as survival through different life stages. Demographic models are valuable tools for organizing biological information, examining population dynamics and for assessing the effectiveness of different management strategies (Maxwell et al. 1988; Thomson 2005).

Matrix models are used for studying plant populations and evaluating conservation or management alternatives (Caswell 2001). Input to matrix models consists of information on each life stage transition for the species being studied (e.g., proportion of seeds that survive to produce seedlings or proportion of seedlings that survive from to rosette stage). Although originally used to study animal populations, such a stage based matrix model was first developed by (Lefkovitch 1965). Sarukhan and Gadgil (1974) adapted this approach to model a plant species that had two modes of reproduction (seed and vegetative).

More recently, matrix models have been used for a variety of NIS management and plant conservation applications (Maxwell et al. 1988; Griffith and Forseth 2005; Thomson 2005). Maxwell et al. (1988) developed a matrix model for leafy spurge (*Euphorbia esula*) using the transition values between the life stages of seeds, root buds, seedlings, vegetative shoots and flowering shoots, and results were used to test the effects of management options, including herbicide application and herbivory by livestock, on

the population growth rate. A population model developed by Griffith and Forseth (2005), in combination with life table response experiments (LTRE), was used to explore conservation issues regarding the rare plant sensitive joint vetch (*Aeschynomene virginica*). Through this approach, the effects of interspecific competition and environment on the vital parameters of fecundity, seedling establishment and survival were assessed. Thompson (2005) used matrix models, parameterized by four years of field data, to assess the impacts of the NIS ripgut brome (*Bromus diandrus*) on a rare endemic plant, the Antioch Dunes evening primrose (*Oenothera deltoids* subsp. *Howellii*). The study sought to determine how the NIS may cause population decline of the endemic species, and found that seedling establishment was the most crucial stage in the life cycle of the Antioch Dunes evening primrose, and seed germination was significantly reduced by litter production from the NIS (Thomson 2005).

While matrix models of population dynamics are excellent tools for modeling population growth (Caswell 2001), they do not incorporate any information on change in spatial structure of the patch, or actual invasiveness of the species. Also, matrix models are considerably less useful for species that reproduce primarily vegetatively because the transition values for seed production, seed survival in the seedbank, seed germination and seedling survival are irrelevant if any parameter is very near zero (as was the case with *L. vulgaris* seed germination in the area of West Yellowstone during the course of the study). Therefore, a goal of this part of the research was not only to understand *L. vulgaris* population dynamics, but also to develop a tool for quantifying NIS population

invasiveness based on both change in population numbers and area occupied by the NIS. This method is presented in Chapter 3, and used again is Chapter 4.

A further purpose of the research was to investigate differences in the relative invasiveness of *L. vulgaris* in different environments. It has generally been assumed that NIS are equally invasive in all environments, although it is widely accepted that a given species has varying levels of vigor along a habitat suitability gradient (Grinnell 1928; Gause 1934; Hutchinson 1957; Hutchinson 1959). Based on this, and the belief that invasiveness should vary with habitat suitability for the NIS, the method to assess invasiveness was to be used to quantify invasiveness in different environments. These results are also presented in Chapter 3.

Objective 3: Effects of Disturbance and Habitat on *L. vulgaris* Population Invasiveness

While disturbance is well documented as promoting invasion by NIS, the relative invasibility of NIS in different environments has not been well studied, nor has NIS response to disturbance in different environments. Rather it has been assumed that NIS respond equally to disturbance in all environments. This part of the research, presented in Chapter 4, examined both how *L. vulgaris* populations responded to different types of disturbance and how the responses differed by environment.

Objective 4: Impacts of Disturbance and *L. vulgaris* on Native Vegetation

NIS are often cited as a major cause of plant extinctions (Mack et al. 2000; Mooney and Cleland 2001; Hooper et al. 2005). There is still debate, however, about the

relative importance of NIS compared to anthropogenic factors (Gurevitch and Padilla 2004; MacDougall and Turkington 2005). Even if species extinction is not the end result, some NIS can locally replace existing species, creating a structurally less complex plant community (Huenneke et al. 1990; Lavergne et al. 1999; Lambrinos 2000), although this is not always the case (Houlahan and Findlay 2004; McKinney 2004). This research sought to understand how native, and existing non-native vegetation at the study sites, was affected by the presence of *L. vulgaris* in different environments as well as by different types of disturbances. Results for this part of the study are presented in Chapter 5.

CHAPTER 2

EFFECTS OF DISTURBANCE SIZE AND PROPAGULE PRESSURE ON *LINARIA VULGARIS* COLONIZATION SUCCESS

Introduction

Disturbance and propagule pressure are important factors structuring plant communities (Pickett and White 1985; Crawley 1997; Hubbell 2001; Jongejans et al. 2006). Niche (Gause 1934) and disturbance theory (Pickett and White 1985; Hobbs 1989; Davis et al. 2000), predict that disturbances facilitate invasions by non-indigenous plant species (NIS) (Burke and Grime 1996; D'Antonio et al. 1999; Lake and Leishman 2004; MacDougall and Turkington 2005). Neutral theory promotes the idea that, regardless of disturbance, plant communities are structured based on the relative abundance of propagules arriving at the site (Hubbell 2001; Colautti et al. 2006). Hence, if a NIS contributes enough propagules to a given area, then that NIS will be able to establish and possibly dominate.

One purpose of this research was to examine the role of disturbance on the colonization success of the NIS *Linaria vulgaris* (yellow toadflax). The study area – the Gallatin National Forest near West Yellowstone, Montana – has been subject to large-scale disturbances including logging, road construction and grazing since the late 1800's (Pauchard et al. 2003). Soil disturbance by pocket gophers (*Thomomys* spp.) is of more relevance, on a finer scale. These animals create soil disturbances (gaps) up to 50 cm in diameter (Hobbs and Mooney 1991) that are readily colonized by plants (Goldberg 1987; Hobbs and Mooney 1991; Wolfe-Bellin and Moloney 2000). Goldberg (1987) also

showed that seedling emergence and survival was greater in disturbed gaps than adjacent undisturbed areas in mid-successional old fields. The research described in this chapter tested the hypothesis that *L. vulgaris* colonization success would be greater in disturbed gaps than in undisturbed areas and also in larger areas of disturbance (ranging from 0.01 to 1 m^2). This is based on the idea that greater areas of soil disturbance will provide more suitable microsites for colonization (Eriksson and Ehrlen 1992; Crawley 1997).

A second part of this research tested the hypothesis that there is a threshold level of seed necessary for *L. vulgaris* colonization. This is based, in part, on the lack of seedling establishment observed at the study sites (Lehnhoff, pers. obs.), the very low germination and viability rates of *L. vulgaris* seed, and on the annual quantity of seed that the species is capable of producing. Nadeau and King (1991) reported that while 210,000 seeds were deposited within 0.5 m of the parent plant, seedling emergence was less than 0.25% and seed viability was as low as 40%. The threshold hypothesis is also based on the neutral theory concept of local community structure being a function of the propagules supplied by the greater community, in this case everything outside of the disturbed gap (Hubbell 2001). In this respect, the number of seed added to a disturbed area may be important because the seed are competing for germination sites with all other propagules supplied by the community (Zeiter et al. 2006). Likewise, to successfully colonize a disturbance, seedlings of all species must compete with each other for available resources, so the species with the most seedlings to emerge may have an advantage in colonization (Zeiter et al. 2006).

Materials and Methods

Site Descriptions

Four sites, representing different environments and management conditions within the Gallatin National Forest near West Yellowstone, MT, were selected for this research (Table 2.1). The sites included an area that was logged in the mid 1980s (Clearcut Site), formerly forested land that burned in a wildfire in 1988 (Wildfire Site), a low-lying area adjacent to a riparian system (Riparian Site) and a sagebrush (*Artemesia tridentata)* / grassland meadow (Meadow Site). The locations of all sites are shown on Figure 2.1.

Table 2.1. Summary of study sites.

Site	Slope	Elevation (m)	Geology	Dominant Vegetation	Management History
Clearcut	flat	2021	glacial outwash	*Pinus contorta* / forbs	clearcut in mid-1980's
Wildfire	flat	1999	glacial outwash	*Pinus contorta* / forbs	burned by wildfire in 1988
Riparian	flat	1996	glacial outwash	grasses and forbs	some grazing
Meadow	~15° North	2029-2042	glacial drift	shrubs and grasses	rangeland improvement

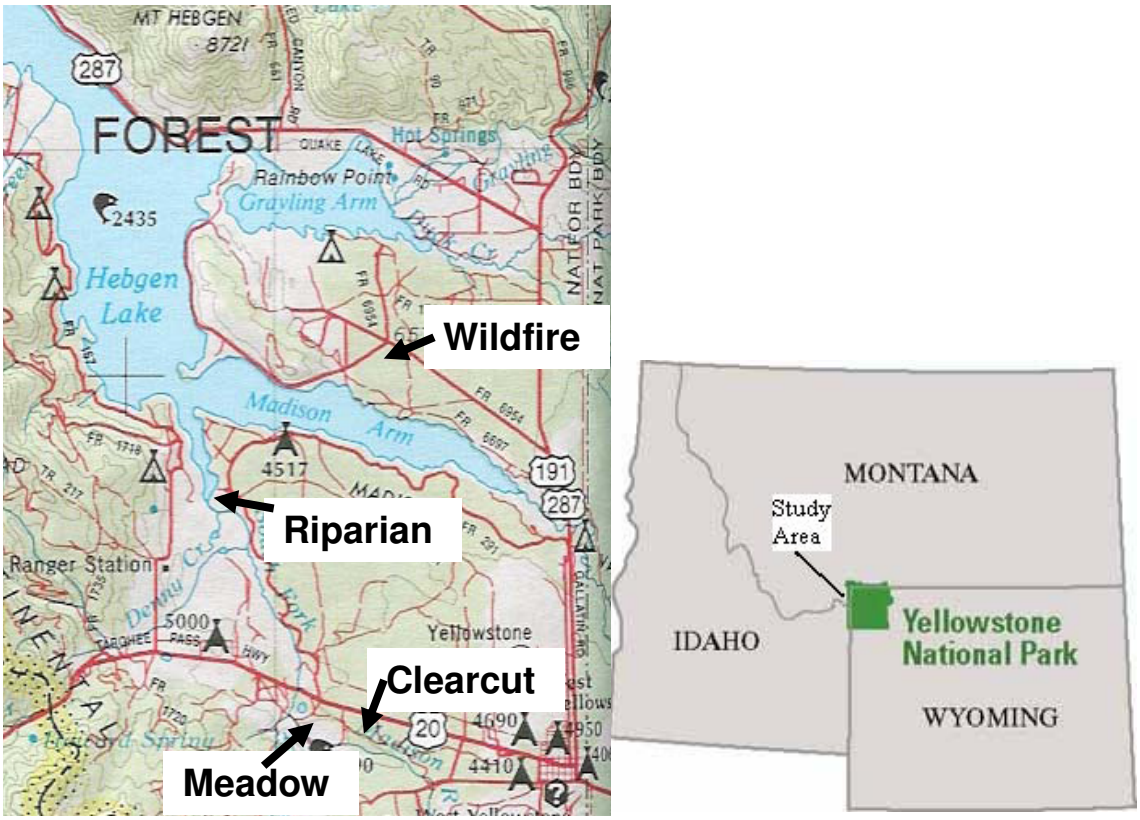

Figure 2.1 Site locations. Gallatin National Forest, Montana.

Clearcut Sites. Two clearcut logged sites were selected from the numerous cuts within the *L. vulgaris* invaded portion of the Gallatin National Forest. These sites were located off of a Forest Service road approximately 6 kilometers west of West Yellowstone, MT and just south of Highway 20 (Figure 2.1). The clearcuts were within an area commonly referred to as the "flats" because it is a glacial outwash plain and there is little topographic relief. The elevation is approximately 2021 meters. Soils of the area were typic cryochrepts with an obsidian sand substratum. Soils were formed on glacial outwash and alluvial deposits weathered from obsidian and rhyolite. The alluvium was coarse textured and contained rounded pebbles and cobbles (USDA, 1996).

The Clearcut Sites were populated by lodgepole pines (*Pinus contortus*) prior to being logged, and the dominant habitat type in unlogged areas was *P. contorta* / bitterbrush (*Purshia tridentata*) (Pfister et al. 1977). Tree re-growth has been sparse, and low foliage cover is now dominated by a grassland community including bluebunch wheatgrass (*Psuedoroegneria spicatum*), Idaho fescue (*Festuca idahoensis*) and associated herbaceous species. *L. vulgaris* infestations were frequently present within clearcuts throughout this portion of the Gallatin National Forest.

Wildfire Site. This site was located approximately 6.5 kilometers west of Highway 191 on the south side of the road to Rainbow Point (Figure 2.1). The Wildfire Site was also on the "flats" (at 1999 meters) and had the same typic cryochrept soil type as the Clearcut Site. Vegetation characteristics were similar to that of the Clearcut, although *P. contorta* recovery in burned areas was progressing faster than at the logged sites. While there were still areas without trees, there is a mosaic pattern of new tree growth. Several *L. vulgaris* patches of varying sizes were scattered throughout the burned area. The habitat type for this area is also *P. contorta / P. tridentata* (Pfister et al. 1977).

Riparian Site. The Riparian Site was located near the confluence of the South Fork of the Madison River with the South Arm of Hebgen Lake (Figure 2.1). Soil and geology at the site were somewhat similar to the Clearcut and Wildfire Sites in that soils were formed on glacial outwash. However, this site was at an elevation of 1996 meters,

and within the flood plain of the river. It is occasionally flooded during spring snowmelt, and may contain additional deposits of alluvial sand and silt (USDA 1996).

The vegetation of the site was dominated by sedges and grasses with Kentucky bluegrass (*Poa pratensis*) being the most common. Common herbaceous species included wild strawberry (*Fragaria virginiana*), Western yarrow (*Achillea millefolium*) and several *Asteraceae* species. *L. vulgaris* densely populated the upper edges of this site, especially in the well drained gravelly soil along the roadside. Very few *L. vulgaris* plants extend into the wetter riparian area.

Meadow Site. The Meadow Site was located approximately 1.5 kilometers west of the Clearcut Sites. This site (~2040 m) was slightly higher in elevation than the other three sites and was situated on a north-northeast facing slope. Soil here was a typic cryochrept formed on glacial drift weathered from granitic rock. The soil was medium textured with a high water-holding capacity (USDA 1996).

Vegetation at the Meadow Site was dominated by big sagebrush (*Artemesia tridentata*) and *P. pratensis*. Also present was a diverse array of herbs including many *Asteraceae* species, clover (*Trifolium* spp.) and sticky geranium (*Geranium viscosissimum*). The Meadow Site has been the subject of "range improvement" in the past as evidenced by the lack of native grasses, the paucity of *A. tridentata*, and the dominance of the introduced species *P. pratensis* and *Bromus inermus* (Pechanec et al. 1954; Plummer et al. 1955).

Study Area Climate Data

Climate information for the study area was obtained from the West Yellowstone weather station (station number 248859) with data compiled by the Western Regional Climate Center (2006). Mean annual precipitation, based on an 80-year average, is approximately 52 cm, with approximately half of the precipitation falling as snow in the months from October to March. The highest monthly amount of precipitation typically occurs in June (6 cm) and the lowest in August (3.5 cm). Cumulative precipitation (June to May) is shown on Figure 2.2. The mean maximum and minimum annual temperatures are 10°C and -7°C, respectively. Monthly mean temperatures ranged from a low of -11°C in January to a high of 15°C in July.

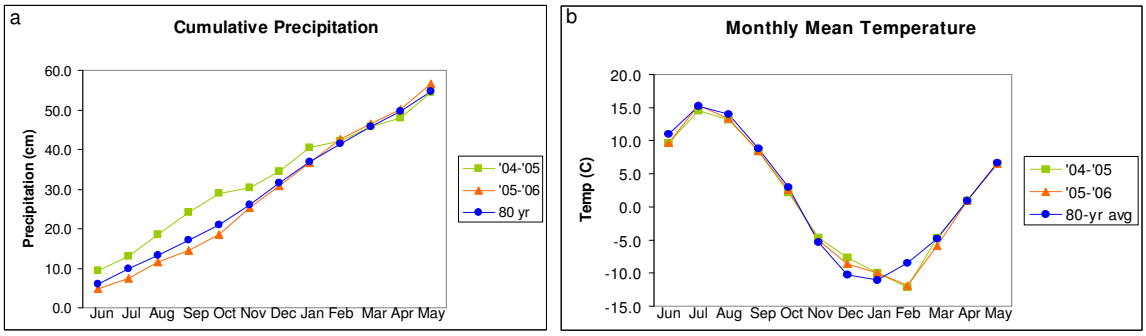

Figure 2.2. (a) Cumulative annual precipitation at study sites from June – May. Growing season is assumed to begin in June, so cumulative precipitation represents the amount received from one growing season to the next. (b) Monthly mean temperatures at study sites. All data from West Yellowstone weather station (station number 248859).

Seed Collection, Weighing and Counting

L. vulgaris seeds were collected from the sites in September 2004 and 2005. In 2004, no seeds were produced at the Meadow Site, and very few were produced at the

Wildfire Site. Seeds were collected from plants at the Riparian and Clearcut Sites at locations outside of the study plots. These seeds were collected from within randomly placed 1/16th m^2 frames after recording the number of stems per frame and number of seed capsules per plant. In 2005, no seeds were produced at any site, but there was abundant seed production along the edge of the road adjacent to the Riparian Site. Some of this seed was harvested for use in the experimental treatments, but number of stems and seed capsules was not recorded.

For seeds collected in 2004, individual seeds were counted in each capsule to obtain the total number of seeds produced per stem. The number of seed capsules in which the seedhead boring weevil (*Gymnaetron antirrhini*) was present was also recorded to determine the percentage of infestation by this biocontrol insect. These data were not recorded in 2005 because there was no seed production on any of the study sites, and all seeds were collected from an offsite location. For both years, several samples with different numbers of seeds (already removed from the capsules) were weighed and linear regression used to determine the relationship between seed sample weight and number of seeds. This regression equation was then used to determine weight of seeds needed to equal a specific number of seeds for the planting experiments described in the next section. The appropriate weight of seeds for each seed number was then packed into individual envelopes and stored for planting.

Experimental Treatments

Two different types of experiments were conducted to study *L. vulgaris* germination and establishment: varying size of soil disturbance with constant rate of *L.*

vulgaris seed addition, and varying *L. vulgaris* seeding rate over constant soil disturbance size. Experiments were conducted in both 2005 and 2006, although the methodology differed slightly between years. All *L. vulgaris* seeds for the experiment were collected from the roadside near the Riparian Site in 2005.

Varying Size of Soil Disturbance. In May 2005, disturbances of different sizes were created on each site to simulate natural disturbances by deer or elk hooves or by pocket gophers (*Thomomys* spp.). Disturbance sizes were 0.01 m^2, 0.1 m^2, 0.4 m^2 and 1 m^2. To create the disturbances, vegetation was removed from plots with a pulaski and soil was then excavated to a depth of 7 cm, which was determined to be the average depth of disturbance by *Thomomys* spp. at the Meadow Site. Soil that was excavated was passed through a 1.6 cm sieve to remove large rhizomes, roots or other plant fragments. Soil and other matter retained on the sieve was discarded and soil passing through was spread evenly back into the disturbed area. Each disturbed area was then seeded at a constant rate of 1,000 seeds m^{-2} with the previously counted *L. vulgaris* seeds. The seeds had been kept in cold storage (5°C) at Montana State University throughout the winter to achieve optimal stratification (Nadeau 1991). Seeds were spread evenly over the surfaces of the prepared plots and smoothed in by hand. Each disturbed area was paired with a non-disturbed area of the same size that was seeded in the same manner. The set of plots (both disturbed and undisturbed) was replicated three times at each of the four sites (Figure 2.3).

In 2006, the experiment was repeated, with some variations, at the Meadow Site only. For this experiment, plots were created, as described above, in October 2005.

These plots were immediately seeded, with *L. vulgaris* seed collected that fall, at a constant rate of 10,000 seeds m^{-2}, and seeds wintered on the site so that they received natural cold stratification rather than cold stratification in the laboratory as in the previous experiment. For this experiment, three sets of disturbed plots were created, but there was only one set of undisturbed plots (Figure 2.4).

Varying Propagule Pressure. The propagule pressure experiment was established in May 2005 by creating five disturbances of 0.1 m^2 each, all paired with undisturbed plots of the same size at each of the four sites. The plots were individually seeded with *L. vulgaris* seed (collected the previous fall and stored at 5°C throughout the winter at Montana State University) at rates of 50, 100, 250, 500 and 1,000 seeds m^{-2}. This experiment was replicated four times at each of the sites (Figure 2.5).

This experiment was repeated in 2006 at the Meadow Site, with some variation. Three repetitions (five plots each) of 0.1 m^2 disturbed plots were created and paired with one repetition of undisturbed plots. The plots were seeded in October 2005 with *L. vulgaris* seed collected that fall to allow natural versus laboratory based stratification. Seeding densities were 500, 1,000, 5,000, 10,000 and 20,000 seeds m^{-2} (Figure 2.6).

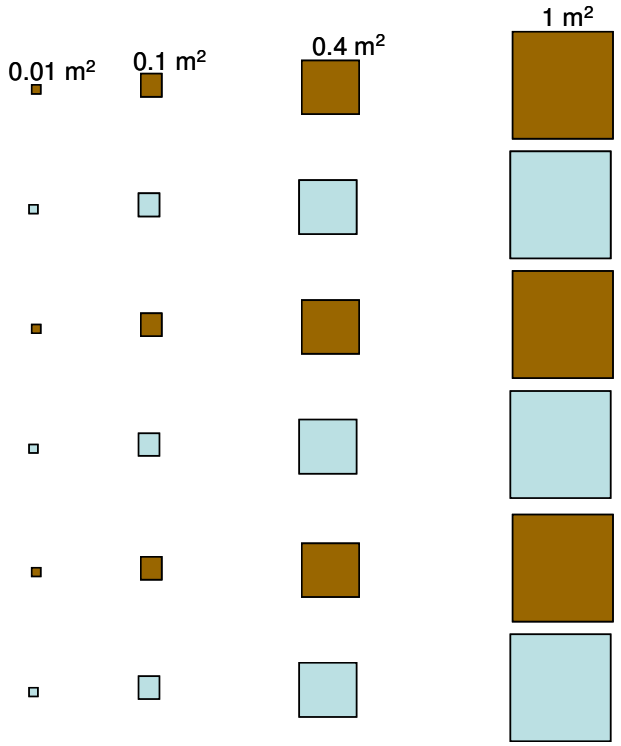

Figure 2.3. Plot layout for varying disturbance size plots in 2005. All plots seeded with *Linaria vulgaris* at rate of 1,000 seeds m^{-2}. Dark plots were disturbed and light plots were undisturbed.

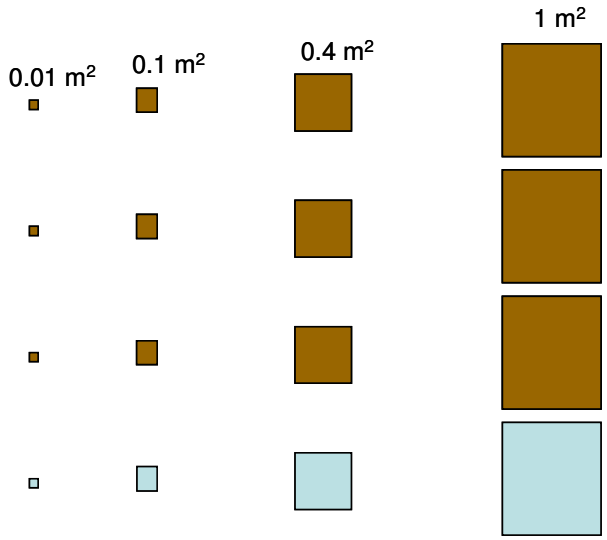

Figure 2.4. Plot layout for varying disturbance size plots in 2006. All plots seeded with *Linaria vulgaris* at rate of 10,000 seeds m^{-2}. Dark plots were disturbed and light plots were undisturbed.

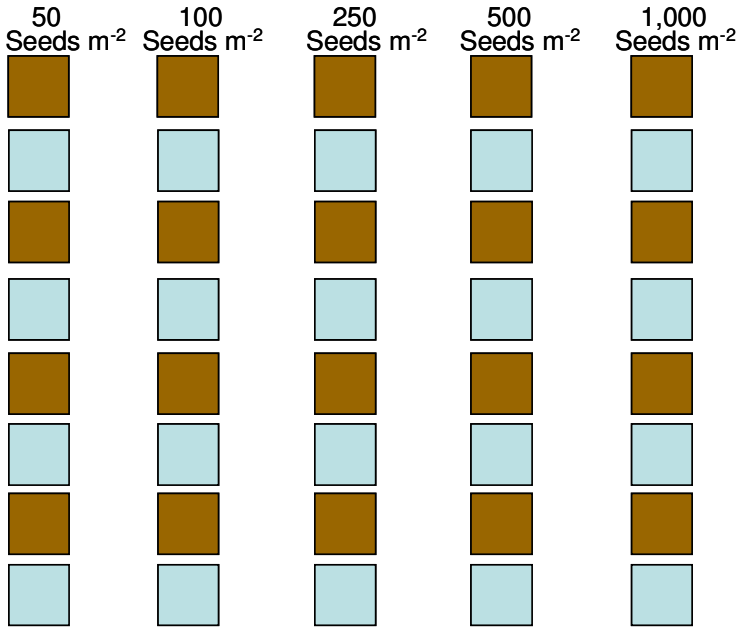

Figure 2.5. Plot layout for varying seed density plots in 2005. All plots were 0.1 m^2. Dark plots were disturbed and light plots were undisturbed.

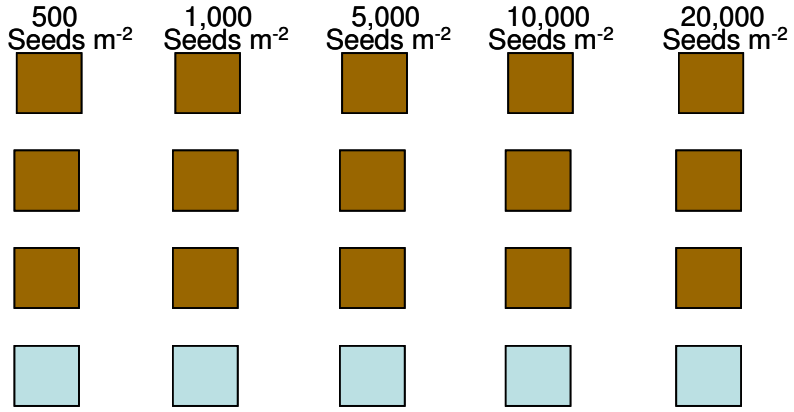

Figure 2.6. Plot layout for varying seed density plots in 2006. All plots were 0.1 m^2. Dark plots were disturbed and light plots were undisturbed.

Plot Monitoring

In 2005, plots were checked weekly for *L. vulgaris* seedling emergence from mid-May through June (May 18 – June 29) and periodically thereafter. In all plots with *L.*

vulgaris seedlings present, seedlings were counted and percent cover was visually estimated to the nearest 1%. Number of individuals and percent cover of all other species was also recorded. Periodic monitoring of all plots continued in the spring and summer of 2006, with number and percent cover of all species recorded for plots containing *L. vulgaris*.

For the 2006 experiment conducted at the Meadow Site, plots were monitored for *L. vulgaris* seedling emergence weekly in June (beginning June 5), with number and percent cover of *L. vulgaris* recorded. Number and percent cover of other species, as well as amount of bare ground, was also recorded. Plots were monitored twice more with the same data recorded, in July and September, to track the survival of *L. vulgaris* seedlings previously identified.

Data Analysis

For the 2005 experiments, *L. vulgaris* colonization success was evaluated by site both as the proportion of plots colonized for each disturbance size or seeding rate, and as the number of *L. vulgaris* ramets (individual stems) occurring within the plots. To determine the proportion of plots colonized, any presence of *L. vulgaris* stems at any time during the monitoring period was considered a successful colonization. Linear regression was employed to determine whether significant relationships existed between the proportion of plots colonized and disturbance size (log transformed) and seeding density (log transformed).

Stem count data tended to be non-normally distributed, so the Kruskal-Wallis rank sum test was used to test for significant differences in stem counts by the different

sites, disturbance size or seeding density. Where differences were identified, the Tukey-Kramer method of multiple comparisons was employed to determine which sites, sizes or seeding densities resulted in the differences. Regression analysis was also used, as it tends to be fairly robust against non-normality of data, and given the small number of data points, non-normality is difficult to test for accurately. Therefore, results from both regression and non-normality comparison tests are provided. Data for 2006 were evaluated in the same manner, except without consideration of site differences, as this experiment was only conducted at the Meadow Site. All analyses were performed in S-Plus 2000, Mathsoft Inc.

Results

Seed Production

In 2004 at the Clearcut Site, the mean *L. vulgaris* stem density in the area where seeds were collected was 6 stems 1/16th m^{-2} (96 stems m^{-2}). There was a mean of 2.63 seed capsules stem^{-1} with a mean seed production of 22 seeds capsule^{-1}, for a total seed production of 58 seeds stem^{-1} (5,555 seed m^{-2}). Of the seed capsules collected, 60% were infested with *Gymnaetron antirrhini* (Table 2.2). *L. vulgaris* stem density in 2004 at the Riparian Site was 16 stems 1/16 m^{-2} (256 stems m^{-2}), with a mean of 0.84 capsules stem^{-1} and seed production of 50 seed capsule^{-1} for a total seed production of 42 seeds stem^{-1} (10,752 seed m^{-2}). Approximately 37% of seed capsules were infested with *G. antirrhini* (Table 2.2). Minimal seed was produced at the Wildfire Site and none was produced at the Meadow Site in 2004. In 2005 seed was not produced at any site.

Table 2.2. Summary of seed produced at each site in 2004. Standard deviations are in parentheses.

Site	Stems m^{-2}	Seed Capsules $Stem^{-1}$	Seed $Capsule^{-1}$	Seed m^{-2}	% *Gymnaetron antirrhini* infestation
Clearcut	87 (56)	2.63 (0.83)	22 (19)	5,555	60
Wildfire	NR[1]	NR	NR	NR	NR
Riparian	256 (126)	0.84 (0.88)	50 (54)	10,752	37
Meadow	NR	NR	0	0	NR

[1]NR = Not recorded.

2005 Experiment – All Sites

Disturbance Size Differences in *L. vulgaris* Colonization. With the exception of plots at the Meadow Site, colonization by *L. vulgaris* on plots of any size was rare. The number of plots colonized in the Clearcut, Wildfire, Riparian and Meadow Sites was, 0, 1, 2 and 7, respectively (Figure 2.7). This represents 0%, 4%, 8% and 29% of all plots at the respective sites. All of these plots had received the soil disturbance treatment (i.e., none of the undisturbed plots were colonized), so 0%, 8%, 16% and 58% of disturbed plots were colonized at the Clearcut, Wildfire, Riparian and Meadow Sites, respectively (Table 2.3). Regression analysis indicated that the proportion of disturbed plots colonized was a function of site and disturbance size ($P=0.006$, $R^2=0.70$). Analysis by site indicated that disturbance size was not a significant predictor at the Wildfire Site ($P=0.349$) or the Riparian Site ($P=0.137$), but it was significant at the Meadow Site ($P=0.042$), where colonization increased with disturbance size ($R^2=0.918$). Specifically, the 0.01 m^2 plots had no colonizations, the 0.1 m^2 plots had one colonization (33% of disturbed plots), and the 0.4 m^2 and 1 m^2 plots each had 3 colonizations (100% of disturbed plots had at least one *L. vulgaris* plant).

Disturbance Size Differences in *L. vulgaris* Stem Number. Only plots at the Meadow Site showed significant differences (Kruskal-Wallis P=0.032) in *L. vulgaris* stem number as a function of disturbance size. Regression analysis also showed an increasing number of stems with greater disturbance size (P=0.001, R^2=0.67). The mean number of stems in the 0.01 m^2, 0.1 m^2, 0.04 m^2 and 1 m^2 plots was 0, 1.7, 4.3 and 17.7, respectively. Tukey-Kramer multiple comparisons indicated that the 1 m^2 plots had significantly more stems than the 0.01 m^2 or 0.1 m^2 plots (Figure 2.8).

Propagule Pressure Differences in *L. vulgaris* Colonization. There were no plots colonized by *L. vulgaris* in the constant plot size experiment where propagule number varied at the Clearcut, Wildfire or Riparian Sites in 2005. However, at the Meadow Site ten plots, all of which were disturbed, were colonized (Table 2.3). For the seeding densities of 50, 100, 250, 500 and 1000 seeds m^{-2}, the number of plots colonized was 0, 2 (50% of disturbed plots), 1 (25% of disturbed plots), 3 (75% of disturbed plots) and 4 (100% of disturbed plots), respectively (Figure 2.9). Regression analysis indicated a positive trend of plot colonization with increasing seeding density (P=0.052, R^2=0.77).

Propagule Pressure Differences in *L. vulgaris* Stem Number. Linear regression analysis indicated increased stem counts with greater seeding rate (P=0.002, R^2=0.41). For the seeding densities of 50, 100, 250, 500 and 1000 seeds m^{-2}, the mean number of stems in the disturbed plots was 0, 0.75, 0.5, 2 and 3, respectively. Results of the Kruskal-Wallis rank sum test indicated that there were differences in *L. vulgaris* stem

number as a function of seeding rate (P=0.050), however these differences did not carry through to the Tukey-Kramer multiple comparisons test (Figure 2.10).

Effects of Soil Disturbance on *L. vulgaris* Colonization. Soil disturbance positively affected plot colonization by *L. vulgaris*. None of the 128 undisturbed plots were colonized while 10 (7.8%) of the 128 disturbed plots were colonized.

2006 Experiment – Meadow Site

Disturbance Size Differences in *L. vulgaris* Colonization. For the 0.01 m^2, 0.1 m^2, 0.4 m^2 and 1 m^2 plots, there were 1, 1, 2 and 3 plots colonized, respectively (Figure 2.11). For each respective size, this represents 25%, 25%, 50% and 75% of the plots. The 0.01 m^2 plot was undisturbed while all others were disturbed. Thus, for the disturbed plots, the 0.01 m^2, 0.1 m^2, 0.4 m^2 and 1 m^2 sizes had 0%, 33%, 75% and 100% colonization, respectively, and 50% of all disturbed plots were colonized while 25% of undisturbed plots were colonized (Table 2.3). Regression analysis indicated that colonization increased with increasing plots size (P=0.021, R^2=0.96).

Disturbance Size Differences in *L. vulgaris* Stem Number. Kruskal-Wallis analysis indicated that there were no differences in the number of *L. vulgaris* stems present in plots as a function of disturbance size (P=0.384). Regression analysis also showed that stem number was not related to disturbance size (P=0.101, R^2=0.18). The mean number of *L. vulgaris* stems in the 0.01 m^2, 0.1 m^2, 0.4 m^2 and 1 m^2 plots was 0.25,

3.5, 3.3 and 6.8, respectively. The maximum number of stems recorded in any plot was 14, with this number occurring in a 0.1 m^2 and 1 m^2 plot (Figure 2.12).

Propagule Pressure Differences in *L. vulgaris* Colonization. For the seeding densities of 500, 1,000, 5,000, 10,000 and 20,000 seeds m^{-2}, the number of plots colonized was 0, 0, 2, 3 and 0, respectively (Figure 2.13). All of the colonizations occurred in disturbed plots, so the percentage of disturbed plots colonized for each size was 0%, 0%, 67%, 100% and 0%, respectively, with 33% of all disturbed plots colonized (Table 2.3). Regression analysis of proportion of plots colonized as a function of propagule pressure indicated that there was not a significant relationship (P=0.452).

Propagule Pressure Differences in *L. vulgaris* Stem Number. Kruskal-Wallis rank sum test results indicated that there were differences in *L. vulgaris* stem number as a function of propagule pressure (P=0.033). Tukey-Kramer multiple comparisons indicated that the seeding density of 10,000 seed m^{-2} produced significantly more stems than the seeding rates of 50, 100 or 20,000 seed m^{-2} (Figure 2.14). Linear regression analysis did not indicate increasing stem counts with greater seeding rate (P=0.670). For the seeding densities of 500, 1,000, 5,000, 10,000 and 20,000 seeds m^{-2}, the mean number of stems in the disturbed plots was 0, 0, 0.7, 2.7 and 0, respectively.

Effects of Soil Disturbance on *L. vulgaris* Colonization. Soil disturbance was positively related to *L. vulgaris* colonization. Eleven of 27 (41%) disturbed plots were colonized while only one of nine (11%) undisturbed plots was colonized.

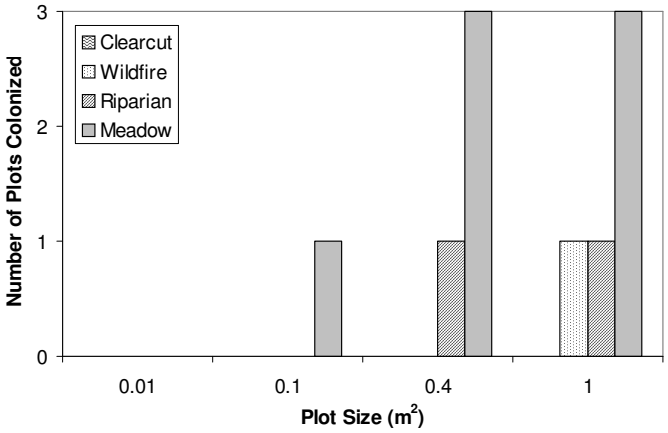

Figure 2.7. Number of plots colonized by *Linaria vulgaris* in 2005 in different size plots with constant seeding density of 1,000 seeds m^{-2}. Only disturbed plots shown. N=3 for each size plot at each site.

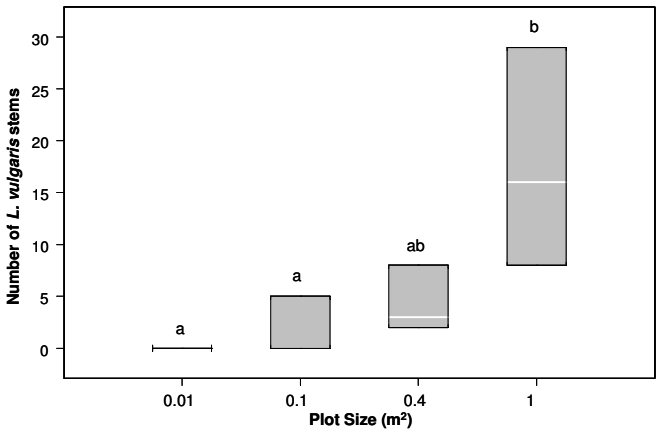

Figure 2.8. Number of *Linaria vulgaris* stems observed in 2005 at the Meadow Site in different size plots with constant seeding density of 1,000 seeds m^{-2}. Only disturbed plots only. N=3 for each size plot. Grey boxes contain 100% of the data. White lines represent medians. Letters indicate significant differences in stem numbers.

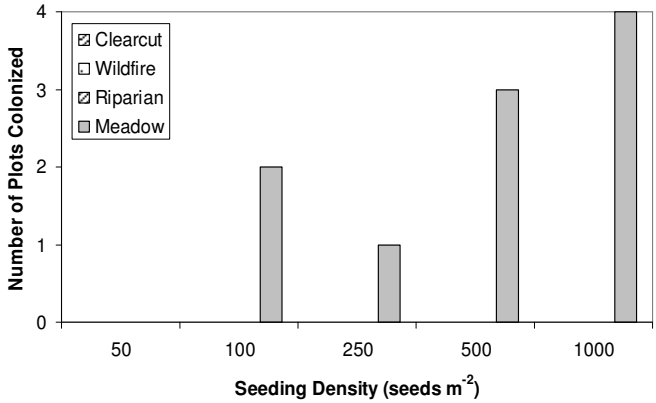

Figure 2.9. Number of 0.1 m^2 plots colonized by *Linaria vulgaris* in 2005 in plots seeded at different densities. Only disturbed plots shown. N=4 for each seeding density.

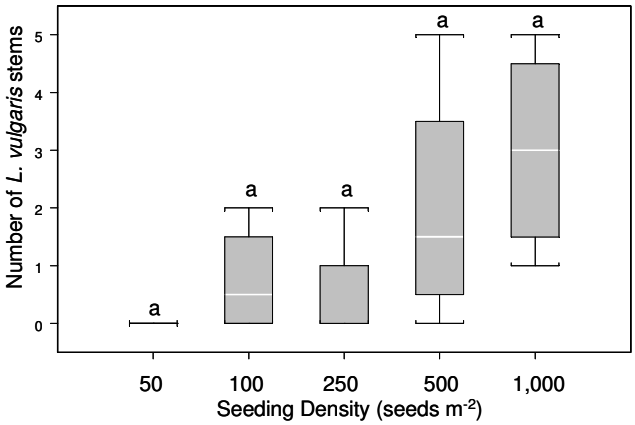

Figure 2.10. Number of *Linaria vulgaris* stems observed in 2005 at the Meadow Site in 0.1 m^2 plots seeded at different densities. Disturbed plots only. Grey boxes contain 50% of the data. White lines represent medians. Bars contain 95% of the data. Letters indicate significant differences in stem numbers.

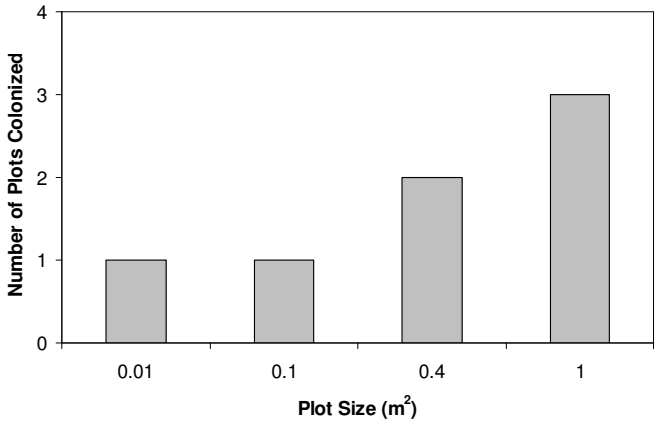

Figure 2.11. Number of plots colonized by *Linaria vulgaris* in 2006 at Meadow Site in different size plots with constant seed density of 10,000 seeds m^{-2}. The 0.01 m^2 plot was undisturbed. All other plots were disturbed. N=3 disturbed and N=1 undisturbed plots for each size.

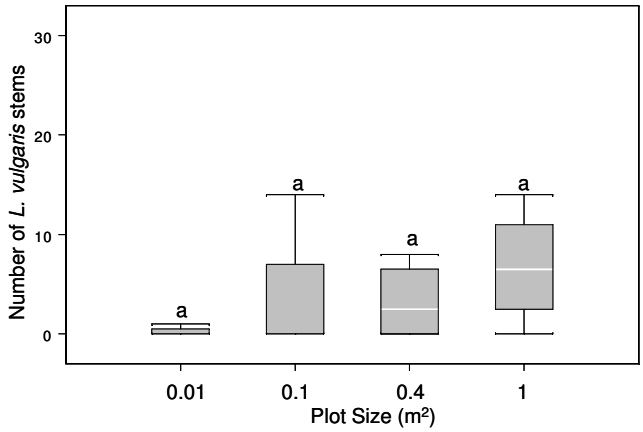

Figure 2.12. Number of *Linaria vulgaris* stems observed in 2006 at Meadow Site in different size plots with constant seed density of 10,000 seeds m^{-2}. N=3 disturbed and N=1 undisturbed plots for each size. Grey boxes contain 50% of the data. White lines represent medians. Bars contain 95% of the data. Letters indicate significant differences in stem numbers.

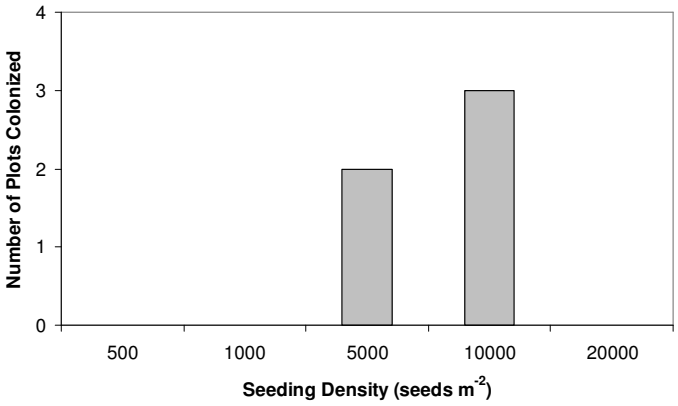

Figure 2.13. Number of plots colonized by *Linaria vulgaris* in 2006 at Meadow Site in 0.1 m^2 plots seeded at different densities. Only disturbed plots shown. N=3 for each seeding density.

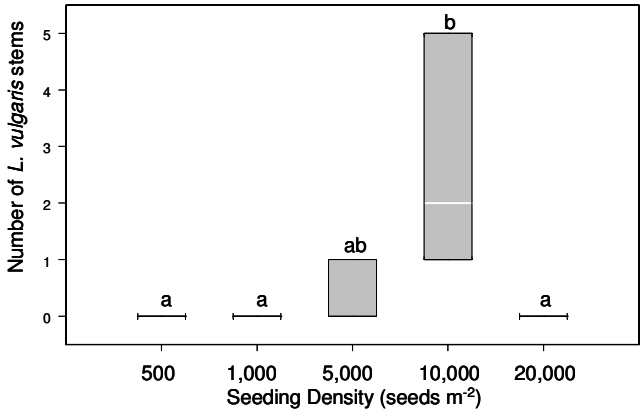

Figure 2.14. Number of *Linaria vulgaris* stems observed in 2006 at Meadow Site in 0.1 m^2 plots seeded at different densities. Only disturbed plots shown. N=3 for each seeding density. Grey boxes contain 100% of the data. White lines represent medians. Letters indicate significant differences in stem numbers.

Table 2.3. Percentage of plots colonized in 2005 and 2006 at each site.

Site	2005				2006 (Meadow Only)			
	Different Size Plots		Different Propagule Pressure Plots		Different Size Plots		Different Propagule Pressure Plots	
	D[1,2]	ND[2,3]	D[4]	ND[4]	D[5]	ND[6]	D[7]	ND[8]
Clearcut	0	0	0	0	--	--	--	--
Wildfire	8	0	0	0	--	--	--	--
Riparian	16	0	0	0	--	--	--	--
Meadow	58	0	50	0	50	25	33	0

[1]D=disturbed plots. [2]N=12 per site. [3]ND=Undisturbed plots. [4]N=20 per site. [5]N=12. [6]N=4. [7]N=15. [8]N=5.

Discussion

Seed Production

L. vulgaris seed production at all sites was limited. In 2004, only the Clearcut and Riparian Sites produced any significant amount of seed, and in 2005 seed was not produced at any site. Seed production for the Clearcut and Riparian Sites was 5,568 and 10,752 seed m^{-2}, respectively. This is in the low to mid range of the values of 1,500 to 30,000 seed m^{-2} reported by numerous authors in Saner et al. (1995), and is considerably lower than the value of 210,000 seeds falling within 0.5 m of the parent plant reported by Nadeau and King (1991). Low seed production in 2004 at the Clearcut and Riparian Sites could be partially attributed to the presence of the seedhead boring weevil *G. antirrhini*, which was present in 60% and 37% of seed capsules at the respective sites. This insect has been linked to lack of *L. vulgaris* seed production or the production of "grey" seeds with very low viability (Saner et al. 1995). However, this does not explain the lack of *L. vulgaris* seed production at other sites or in other years when the plant failed to produce seed capsules or when capsules did not complete development. Lack of

seed production may be explained by late summer or early fall frosts in August or September which are not uncommon in the area of West Yellowstone (Lehnhoff, pers. obs.).

L. vulgaris Colonization

General. *L. vulgaris* establishment from seed was rare in the study plots. In 2005, 20 of 256 plots (8%) were colonized (defined as at least one plant) by *L. vulgaris*. Evaluating the data by site shows that no plots (0%) were colonized at the Clearcut Site, one (2%) at the Wildfire Site and two (3%) at the Riparian Site. Colonization was more successful at the Meadow Site with *L. vulgaris* establishing in 17 plots (27%). In 2006 at the Meadow Site, 12 plots (33%) were colonized. Where *L. vulgaris* did establish, stem counts were low. The maximum number of *L. vulgaris* stems recorded in any plot was 29 in a 1 m^2 plot at the Meadow Site.

The lack of *L. vulgaris* establishment at the Clearcut, Wildfire and Riparian Sites, which are all currently heavily infested by the species, points to the importance of temporal variation and episodic events in the initiation of new colonies (Davis et al. 2000; Gray et al. 2006; James et al. 2006). These sites were obviously colonized by *L. vulgaris* at some point in the past, and are suitable for its continued growth, but it may be that conditions (e.g., temperature and soil moisture) were not suitable for *L. vulgaris* establishment at these sites during the study period. The greater colonization at the Meadow Site during this same time period may be a function of different soil conditions

– specifically increased soil moisture relative to the other sites (see Chapter 4 for more information on site soil differences).

Effects of Disturbance Size on *L. vulgaris* Colonization and Stem Number. Disturbance size was not an important predictor of *L. vulgaris* colonization at the Clearcut, Wildfire or Riparian Sites; this is likely because colonization was minimal at these sites, with 0, 1 and 2 plots being colonized, respectively. Only larger plots were colonized at these sites (either 0.4 m^2 or 1 m^2), but the high number of uncolonized plots made the regression relationship insignificant.

At the Meadow Site, larger areas of disturbance were colonized more often, with disturbance size explaining 92% of the variation in colonization. A possible mechanism for increased colonization with larger disturbance size is the freeing of *L. vulgaris* seedlings from competition from other species that might quickly recolonize smaller disturbances vegetatively.

The strong correlation of plot colonization with disturbance size may be a result of the confounding factor of increased number of *L. vulgaris* seed with increasing disturbance size. This confounding factor was necessary to provide an equal density of seeds in each disturbance size (i.e., 1,000 seeds m^{-2} in 2005 and 10,000 seeds m^{-2} in 2006). Alternatively, the experiment could have been performed using an equal number rather than an equal density of seed in each plot, but implicit in this design would have been the unrealistic assumption that larger areas of disturbance do not collect more propagules. The way that the experiment was designed assumed that, in addition to the

possibility of escape from native vegetative competition in large plots, disturbance size is important because larger areas receive more propagules, and high numbers of propagules may be important for the establishment of *L. vulgaris* which has a very low germination rate (Nadeau and King 1991).

Effects of Propagule Pressure on *L. vulgaris* Colonization and Stem Number. Propagule pressure generally had a positive effect on *L. vulgaris* colonization and stem number. In 2005, at the Meadow Site, 77% and 41% of the variation in colonization and number, respectively, was explained by the number of *L. vulgaris* seed added to plots. In 2006, number of seed added was not a significant predictor of colonization or recruitment. The analysis, however, was highly influenced by the fact that the seeding rate of 20,000 seeds m^{-2} did not produce any successful colonizations. When this outlier point was removed, the relationship between propagule pressure and colonization was significant (P=0.023) with a R^2 value of 0.95. For *L. vulgaris* stem number, the relationship also became significant (P=0.009) with a R^2 value of 0.40. The mechanism causing a decline in *L. vulgaris* colonization at the 20,000 seed m^{-2} density is unknown, but density dependent seed predation (Reichman 1979; Hulme 1994; Cromar et al. 1999) or chemical inhibition could offer an explanation. In such a case, predators would be attracted to plots with higher density of seeds whereas they may not be attracted to the plots with lower seed densities. Thus, predation in the 20,000 seed m^{-2} plots may have reduced seed numbers sufficiently to prevent colonization.

Effects of Soil Disturbance on *L. vulgaris* Colonization. *L. vulgaris* established better in plots with disturbed soil than in undisturbed plots. There was only one colonization by *L. vulgaris* in the 137 undisturbed plots (0.7%) while 21 of 155 disturbed plots (13.5%) were colonized. This is consistent with the literature that reports soil disturbance as often being an essential component for plant invasions (Goldberg 1987; Burke and Grime 1996; Huston 2004; Lake and Leishman 2004).

Population Longevity / Seedbank Survival

L. vulgaris stems that established in 2005 persisted through 2006. The survival of plants establishing in the new Meadow plots in 2006 is yet uncertain. By September 2006, *L. vulgaris* plants remained in only one of the 12 newly colonized plots, and this population consisted of only 3 individuals. The uncertainty lies in the fact that it is unknown whether or not the plants survived long enough to establish sufficient root reserves for vegetative regrowth in 2007. This is currently being assessed.

L. vulgaris seeds in the soil seedbank (i.e., those seeds that did not germinate during the time of the experiments) may lead to additional colonization of the plots in the future. Initial germination is typically very low (Nadeau and King 1991) and Carder (1963) reported that *L. vulgaris* seed can remain dormant for eight years. These studies, however, do not provide any information regarding seed decay rates. Seed viability loss over time can generally be described with a negative exponential model (Chambers and MacMahon 1994). This means, with initial low seed viability (40% – 60%), a very small percentage of *L. vulgaris* seeds would be viable after just two years, making the establishment of additional populations unlikely.

General Conclusions

The data do not allow the definitive assignment of threshold levels of disturbance size or propagule pressure necessary for *L. vulgaris* colonization. In fact, definitive threshold levels of disturbance size or propagule pressure which lead to NIS colonization cannot be defined. Colonization is possible, given ideal conditions, from one seed regardless of the disturbance size. The above results, however, address the general trends of increasing colonization success with increasing disturbance size up to 1 m^2 and propagule pressure up to 10,000 seeds m^{-2}. Disturbed plots had a much greater chance of being colonized by *L. vulgaris* than non-disturbed plots, and disturbances 0.1 m^2 and larger were colonized at a greater rate than smaller sized disturbances. Likewise, plots receiving 1,000 or more seeds m^{-2} were generally more likely to be colonized.

CHAPTER 3

QUANTIFYING *LINARIA VULGARIS* INVASIVENESS

Introduction

Invasive plant species (hereafter non-indigenous species or NIS) cause both economic (Pimentel et al. 2005) and environmental damage (Wilcove et al. 1998). The economic cost of NIS in the United States, including lost revenue from crops and forage as well as the cost of management, is estimated to be $33 billion per year (Pimentel et al. 2005). Environmental or ecosystem damage includes loss of native species diversity and alteration of environmental processes (Wilcove et al. 1998; Dukes and Mooney 2004).

As a result of the high costs of NIS management, especially in rangelands or wildlands where control costs are approximately $5 billion per year (Pimentel et al. 2005), land management agencies such as the U.S. Forest Service (USFS) and the Bureau of Land Management generally have insufficient budgets for addressing the entire problem. For example, the proposed USFS budget for 2007 includes only $94 million for the management of invasive species, which include animals and fungal pathogens as well as plants (USDA 2006). Thus, managers must choose areas in which management of NIS is most critical.

Where NIS are managed, there are concerns beyond simply controlling the plants. Off-target effects of the management may be worse than the NIS themselves (Civeyrel and Simberloff 1996; Matarczyk et al. 2002). Undesirable effects of management may include environmental degradation by herbicides (NRC 2000), development of herbicide

resistance by the target plant (Maxwell and Mortimer 1994; Clements et al. 2004), loss of native species diversity and re-invasion by other NIS (Ogden and Rejmanek 2005), and herbicide drift leading to mortality of adjacent plants (Matarczyk et al. 2002).

The working null hypothesis in the field of invasive plant management is that all plants labeled as "invasive" or "noxious" are rapidly increasing in population size. The reality is that this is not true, and indeed all populations of NIS may not merit management. A first principle of ecology is that any plant species that persists in a community must be capable of increasing when rare. Thus, any such species, either native or NIS, has the potential to be invasive given optimum environmental conditions (Crawley 1997). However, population growth rates can vary both temporally as resource availability fluctuates, and spatially as a function of heterogeneity (Davis et al. 2000; Parker 2000; Hansen and Wilson 2006). Therefore, invasiveness of a NIS can be expected to vary with time and also along a habitat suitability gradient in accordance with classical niche assembly theory (Grinnell 1928; Gause 1934; Hutchinson 1957, 1959; Hubbell 2001). This theory assumes that for any species there is a fundamental niche (a multi-dimensional space defined by the limiting values of resources required by a species) where a species is able to survive and reproduce (Hutchinson 1959). In accordance with such theory, one would expect to find variability in the vigor of NIS within different environments as niche suitability and availability varies. This theory further implies that a niche space can only be occupied by one species at a time, and if a species is better suited to a particular niche than the species currently occupying that niche, then that newer species can "invade" and displace the established species

(Hutchinson 1959). A large body of literature, however, supports the idea that some type of disturbance is needed to facilitate invasion (see review by Lozon and MacIsaac 1997). Disturbance alters and often increases resource availability, reduces the intensity of competition and creates empty niches that new species can occupy (Elton 1958; Hobbs 1989; Rejmanek 1989; Hobbs and Huenneke 1992; Burke and Grime 1996). In fact, many of the so-called weed species have evolved through selection and adaptation to continuous habitat disturbance (Radosevich et al. 1997).

These aspects of the niche and disturbance solidify the belief that NIS proliferation should be viewed as a local phenomenon rather than a species characteristic, and thus management of NIS should be site-specific. Hence, effective management should be focused on local populations at the landscape level and their response to the environment and disturbance, as evaluated by monitoring over multiple years. Rarely, however, has long-term monitoring of individual NIS populations been conducted (for exceptions see Woitke and Dietz 2002; Buckley et al. 2003; Jacquemyn et al. 2005; Dodson and Fiedler 2006).

The large scope of the NIS problem, the under-funding of NIS programs, varying degrees of invasiveness of different species and populations, and the potential negative off-target effects of management necessitate the development of a method to determine which populations of NIS are likely to be the most invasive. While we are interested in the driving processes of invasions, we also recognize the need to develop a quick, tractable and accurate assessment tool for managers. Therefore, we propose a method to quantify the invasiveness of NIS populations of herbaceous annuals or perennials that are

established, but still rare. It is envisioned that such a method would be applied to several discrete populations of an herbaceous NIS located in distinct environments. The end result of the methodology would be a quantification of population invasiveness (*I*), which could be used to rank populations on a continuum from not (or minimally) invasive to very invasive. This method would allow land managers to prioritize populations for management. For any such method to be practicable, it should require minimal field monitoring of NIS populations to detect trends in population change while being computationally simple. The method proposed herein fits these criteria, requiring NIS density counts in permanent plots only once a year and performing calculations based on these recorded density values. Here we describe the method, present results of a case study using yellow toadflax (*Linaria vulgaris* Mill.) as the test NIS, compare results with traditional population growth rate estimates, bootstrap the data to increase the statistical power, and discuss the utility of the method in different situations.

Materials and Methods

Linaria vulgaris

L. vulgaris is a perennial species that reproduces both vegetatively and by seed (Saner et al. 1995). It is common in western and northeastern United States and in western Canada, usually being found in drier open rangelands and along roadsides or other disturbed areas (Lajeunesse et al. 2000). *L. vulgaris* was chosen for this work because of its purported invasiveness (Saner et al. 1995; Pauchard et al. 2003) and

because, through its clonal growth form and short dispersal distance, it tends to form discrete patches (Nadeau and King 1991; Saner et al. 1995).

Site Descriptions

Populations of *L. vulgaris* were studied at sites representing three different habitats within the Gallatin National Forest in southwestern Montana, United States. Site 1 (Ridge) is located at an elevation of 2200 m on a steep south facing slope (approximately 33°) at 44°48'N, 111°12'W. The habitat type is big sagebrush (*Artemesia tridentata*)/Idaho fescue (*Festuca idahoensis*) (Despain 1990). Soils are limestone-derived loams of the family Typic Calciboroll. Surface horizons are basic and contain 30 to 60 percent rock fragments (USDA 1996). Range productivity in this area is limited by moisture stress (USDA 1996). The site is undisturbed by human actions, but has small-scale disturbances from natural slope movement, elk grazing and trampling, and small mammal burrowing.

Site 2 (Valley) is located on the valley floor where the topography is very flat at an elevation of 1851 m (44°37'N, 111°00'W). The plant community is similar to that of Site 1, but the soil is derived from rhyolite-obsidian sand on a glacio-fluvial outwash plain (USDA 1996). The soil is of the family Typic Argiboroll or Aridic Argiboroll and the texture is silt loam to sandy loam with some clay in lower horizons. Surface soils are mildly acidic and contain 5 to 35 percent rock fragments (USDA 1996). In contrast to the Ridge, this site is subject to some human disturbance as it is a popular fishing access point to Hebgen Lake and is surrounded and crossed by unimproved roads.

Site 3 (Forest) is approximately 40 m from the Valley site, and lies on the same soil type, but it is located under a closed canopy of lodgepole pine (*Pinus contorta*).

Climate Data

Precipitation data were obtained from the Western Regional Climate Center for the weather station West Yellowstone 9 NNW (station # 248859) located 9 miles north northwest of the town of West Yellowstone. Data included monthly mean totals for years 2001 through 2005 as well as the 80-year average (1924 through 2004) for monthly precipitation. Data were regressed against calculated population invasiveness values to assess the effects of precipitation on population growth. Regression analyses were performed using S-Plus 2000 (Mathsoft Inc.). To assess the effects of precipitation on invasiveness, the water year was taken as July through June because invasiveness calculations were based on June counts of *L. vulgaris* stems (e.g., precipitation from July 2001 to June 2002 was used to evaluate invasiveness from 2001 to 2002). Henceforth, years will be referred to as years 1, 2, 3, 4 or 5 (i.e., 1 = July 2001 – June 2002, 2 = July 2002 – June 2003, 3 = July 2003 – June 2004, 4 = July 2004 – June 2005 and 5 =July 2005 – June 2006).

Total annual solar radiation values were generated through a script in ArcView GIS (version 3.2) using slope and aspect values obtained from a 10 m resolution digital elevation model of the area (McCune and Keon 2002). These annual solar radiation values were mapped to each population monitored as located using a Global Positioning System (GPS) with an accuracy of approximately 1 m.

Plot Establishment and Monitoring

Within sites, *L. vulgaris* patches for monitoring were chosen based on availability, resulting in three patches, two patches and one patch at the Ridge, Valley and Forest sites, respectively. Each patch was a discrete population, separated by at least 10 m from any other populations. A permanent grid with 1-m^2 sub-sections, divided into 1/16-m^2 cells, was established over the entirety of each patch by marking the corners with rebar posts. The grids were positioned such that perimeter sub-sections straddled the edge of the *L. vulgaris* patch. A complete census of the whole patch was performed in the first year, which facilitated the determination of spatial autocorrelation within the patch using semivariance calculated in VESPER (Minasny et al. 2005).

During sampling in subsequent years, 1-m^2 monitoring quadrats, divided into 1/16-m^2 cells, were randomly assigned to the grid sub-sections within each patch, stratified by edge and interior positions. All plots were permanently marked for future sampling, and the same quadrat cells were sampled each subsequent year. Table 1 shows the number of quadrats monitored within each population. Unequal sampling effort was necessitated by the different size populations. This highlights the fact that the method is developed for NIS that are rare in the region of interest but still of concern to managers.

The permanent 1-m^2 quadrats were monitored each June at the Ridge from 2001 to 2006 and at the Valley and Forest from 2002 to 2006. Monitoring consisted of counting the number of *L. vulgaris* vegetative stems and seedlings within each 1/16-m^2 cell.

Table 3.1. Number of interior, edge and total 1-m^2 quadrats monitored in each *Linaria vulgaris* population.

	Population[1]					
	1	2	3	4	5	6
Interior	7	6	4	3	3	3
Edge	6	6	4	3	3	3
Total	13	12	8	6	6	6

[1]Populations 1, 2 and 3 are at the Ridge; populations 4 and 5 are at the Valley; population 6 is at the Forest.

Soil Characteristics

For each population, seven soil sub-samples, from 10 to 15 cm deep, were collected and composited into one sample. Each sample was submitted to Agvise Laboratories and analyzed for soil fertility and basic soil physical properties. Analyses included texture, bulk density, cation exchange capacity, percent moisture at 1/3 and 15 bar, percent organic matter, pH, nitrate-N, Olsen P, zinc, iron, manganese, boron, soluble salts, and base saturation.

Calculation of Population Growth Rates

Population growth rate (e.g., annual growth rate for 2002 – 2003) and mean growth rate (mean of all annual growth rates) were calculated for each population studied. Population growth rates were taken as the mean of all of the individual growth rates from each of the 1-m^2 quadrats. The individual growth rates were calculated as N_{t+1}/N_t where N_t is the number of stems within the quadrat at a given time *t* and N_{t+1} is the number of stems in that same quadrat at the subsequent time step. The data were transformed by adding 1 to each stem count value so as to avoid the problem of dividing by zero in cases where there were no stems at time *t*. These calculations were made with

the knowledge that the system is open, and that individuals present at time $t+1$ were not necessarily the progeny of individuals present at time t. However, the assumption was made that immigration into the system equaled emigration, and therefore, growth rate was a suitable measure of population growth.

Calculation of Invasiveness

For the purpose of this work, invasiveness was defined as a population increasing in density and / or spatial extent. Invasiveness (I) was calculated as a function of the change in stem density in 1/16-m^2 cells and change in occupancy of these cells, as follows:

$$I = (\alpha - \beta) + \gamma,$$

where: α = proportion of cells with a growth rate > 1
β = proportion of cells with a growth rate < 1
γ = change in proportion of cell occupancy

The scale of 1/16-m^2 was chosen to examine population demographics at the scale of individual ramets. The use of this smaller scale is especially important when monitoring occupancy, because it would be rare for an entire densely populated 1-m^2 quadrat on the population edge or interior to change from being occupied to not occupied over the course of a year, whereas quadrats immediately outside of the population that were originally empty may become occupied by a few ramets. In such a case, the overall population may be decreasing, but the invasiveness calculation would be skewed toward a positive result. Using data from each 1/16-m^2 cell avoids this issue, and provides a more accurate representation of a population's change in area occupied.

Determination of population growth rate trajectories (i.e., increasing or decreasing population size) in individual cells was made by simply determining if growth rate was greater than or less than 1. Then for a given pair of years, the numbers of cells with increasing and decreasing populations, respectively, were summed. These values were divided by the total number of cells monitored to calculate the proportion of cells exhibiting increasing and decreasing populations to give α and β, respectively. Change in cell occupancy between a pair of years was calculated by summing the total number of cells occupied in the individual years and then subtracting the number at t_1 from the number at t_2. This value was changed to a proportion by dividing by the total number of cells to give γ. Changes in growth rate and area occupied were assumed to be equally important in determining a population's invasiveness, and therefore the growth rate term ($\alpha - \beta$) and the cell occupancy term (γ) were summed. Invasiveness values were calculated separately for cells in edge and interior quadrats. This allows for the reporting of different edge and interior invasiveness values, which could be useful for larger populations where population dynamics may differ between edge and interior positions. For the small populations evaluated in this study, there were no differences in edge and interior, and the values were summed to get a total invasiveness value ranging between -4 and +4 (i.e., because the density and area terms are proportions, they have maximum and minimum values of +1 or -1, respectively, for both edge and interior patch positions, leading to maximum and minimum possible values of +4 and -4, respectively).

Bootstrap Analysis

Calculating invasiveness from an original data set provides only one possible outcome for that population from a relatively small sample size. To make reliable comparisons with other populations or between years, the statistical power of the data set was increased through a bootstrap analysis (Gotelli and Ellison 2004). Stem counts for a pair of years were randomly resampled with replacement within years to create a new data set. Invasiveness was recalculated from the new data set as described above. This procedure was repeated 1000 times for each population to obtain the best estimate of the distributions and means of invasiveness. ANOVA was performed and Tukey HSD confidence intervals determined to evaluate differences in invasiveness between years and populations. Bootstrapping was conducted in R and statistical analysis was performed with S-Plus 2000.

Evaluation of the Method

We were interested in how well invasiveness values calculated from raw field data compared to invasiveness values calculated from bootstrapped data. A simple percent difference calculation for the two results is insufficient to evaluate the difference because of the importance of scale. For example, the invasiveness results from the two methods could be 0.2 (raw data) and 0.1 (bootstrapped data). Using the equation:

$$\%\ difference = (I_{Raw\ Data} - I_{Bootstrapped\ Data}) / I_{Raw\ Data} \times 100,$$

there is a 50% difference between methods. Likewise, the results could be 4 (raw data) and 2 (bootstrapped data), which would still be a 50% difference. However, invasiveness values of 0.1 and 0.2 indicate that a population is not (or only very slightly) invasive,

whereas the values of 2 and 4 indicate populations that are moderately and very strongly invasive, respectively. Thus, deviation between results for the first pair of values is unimportant, but it is very important for the second pair of values. To compensate for this scale effect, differences are evaluated in terms of the total possible range of invasiveness, which is 8. The equation for adjusted percent difference is then:

$$\%\ Difference = ((8\text{-}I_{RawDataValue}) - (8\text{-}I_{Bootstrapped\ Value})) / (8\text{-}I_{RawDataValue})$$

Also of interest is the correlation between invasiveness values and λ values, determined by calculating Pearson's correlation coefficient for the bootstrapped invasiveness values and the corresponding λ values.

Results

Climatic Conditions

Mean annual precipitation for years 1, 2 and 3 was approximately 15 cm (27 %) below the 80 year average, which is indicative of the drought conditions existing in southwest Montana since 1999 (NCDC 2004; Figure 3.1). In year 4, as drought conditions lessened, precipitation was approximately equal to the 80-year average and in year 5 precipitation exceeded this average by nearly 2 cm (Figure 3.1).

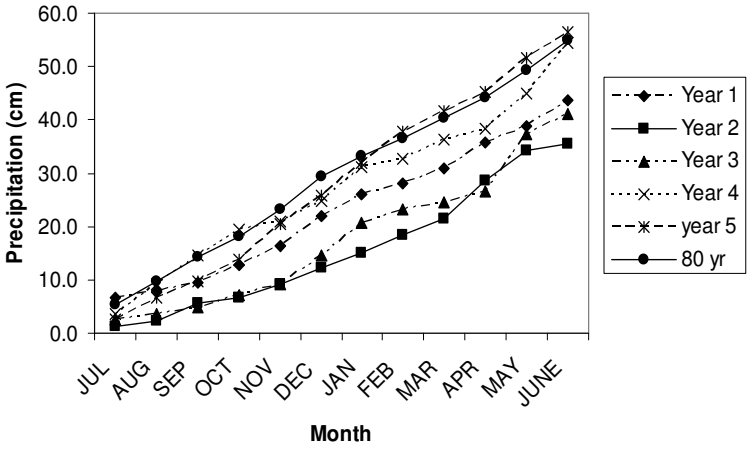

Figure 3.1. Cumulative annual (July to June) precipitation from Western Regional Climate Center weather station located 9 miles NNW of West Yellowstone, Montana. Year 1 = 2001 – 2002, Year 2 = 2002 – 2003, Year 3 = 2003 – 2004, Year 4 = 2004 – 2005, Year 6 = 2005 – 2006.

There was a significant difference in precipitation between years ($P<0.001$). Annual precipitation for years one through 5 were 43.8 cm, 35.4 cm, 41.2 cm, 54.4 cm and 56.5 cm, respectively. However, there was not a significant relationship between total annual precipitation and invasiveness ($P=0.332$) (Figure 3.2a).

Annual solar radiation was significantly different between sites ($P<0.001$). Mean values for the Ridge, Valley and Forest sites are 0.946 MJ cm^{-2} yr^{-1}, 0.707 MJ cm^{-2} yr^{-1} and 0.699 MJ cm^{-2} yr^{-1}, respectively. Annual solar radiation was not a significant predictor of invasiveness ($P=0.249$) (Figure 3.2b). It should also be noted that the value of annual solar radiation is calculated without reference to vegetation cover, and actual solar radiation reaching the ground, particularly under a tree canopy, would be less than the value calculated from the GIS data.

Site Differences in Soil Characteristics

The texture of soil at the Ridge (based on % sand for comparison purposes) was significantly different (P=0.003) than that at the Valley and Forest, which did not differ from one another. Soil from all populations at the Ridge was classified as loam while the soil from populations at the Valley and Forest was sandy loam. Invasiveness was not significantly (P=0.203) correlated with % sand (Figure 3.2c). Ridge soil had higher values of cation exchange capacity, water holding capacity, nitrate, pH, soluble salts and boron than the other two sites. Soil at the Valley and Forest had greater concentrations of phosphorus, zinc, iron and manganese and had greater bulk density. The complete soil sample results are presented in Table 3.2.

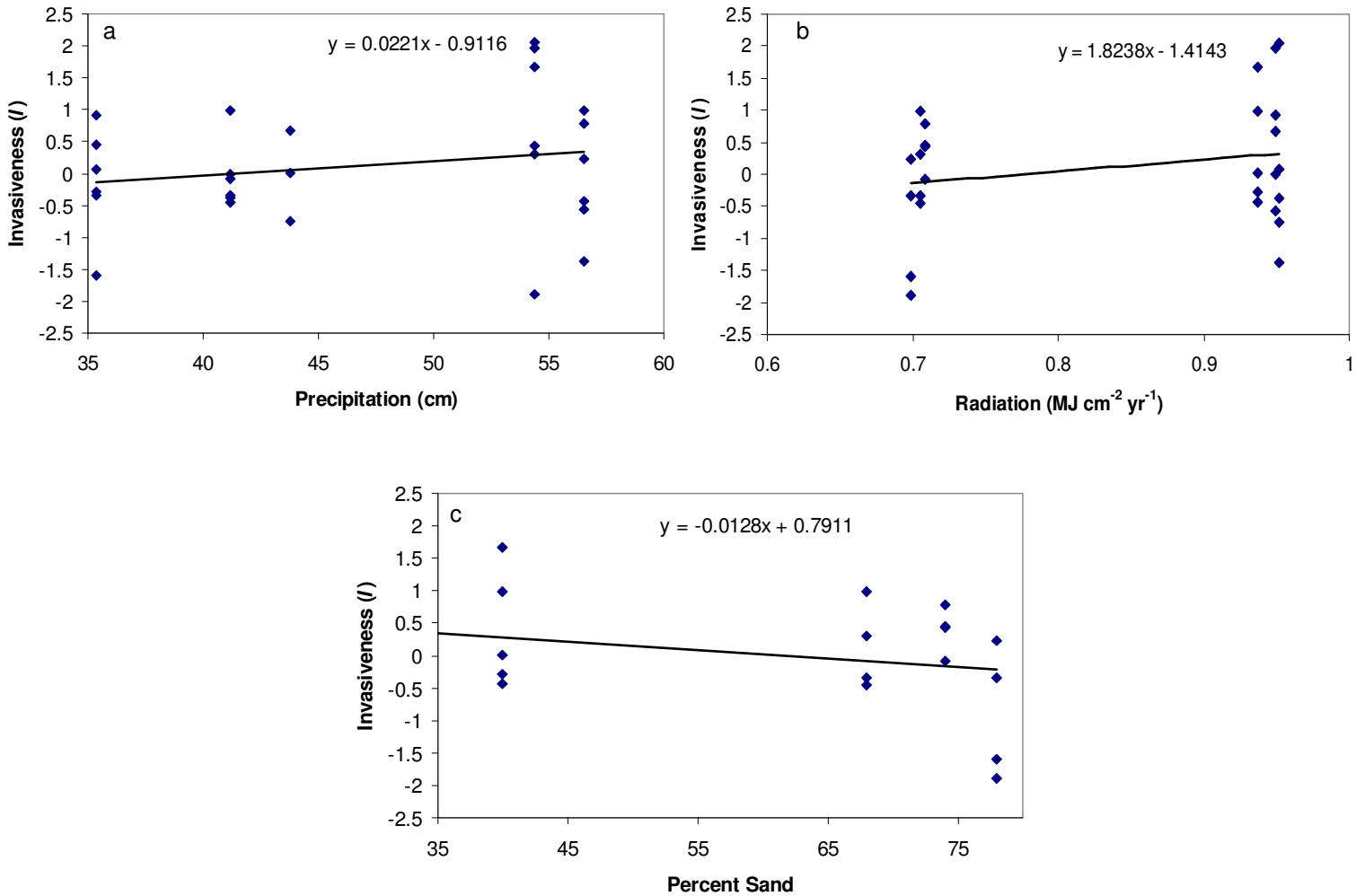

Figure 3.2. Regression of (a) annual precipitation against mean invasiveness (all sites), (b) annual solar radiation at each site against mean invasiveness (*I*) (all years) and (c) texture (represented by % sand) against mean invasiveness (all years).

Population Growth Rates

Mean population growth rates varied between and among populations, however, temporal variation was strong enough to mask any significant differences between sites (P = 0.710). The mean growth rates for the Ridge, Valley and Forest sites were 4.03 (SD = 20.00), 3.72 (SD = 9.54) and 0.91 (SD = 1.07) (Figure 3.3a). The highest mean annual growth rate of any population was 46.9 for population 3 at the Ridge between 2004 and 2005, while the lowest mean annual growth rate was 0.3 for the Forest population during these same years. Population 3 also had the highest overall growth rate (mean of all years) while population 6 had the lowest and was generally less than 1.0. Other populations generally had positive, but low growth rates.

Table 3.2. Results of analysis of soil samples collected at each *Linaria vulgaris* population.

Parameter	Population[1]					
	1	2	3	4	5	6
% Sand	40	34	34	74	68	78
% Silt	40	46	48	6	12	12
% Clay	20	20	18	20	20	10
Texture	loam	loam	loam	sandy loam	sandy loam	sandy loam
Bulk Density (g/cc)	1	0.97	1.01	1.11	1.07	1.13
CEC (meq/100 g)	34.9	35.1	31.1	13.1	13.9	7.8
% Moisture at 1/3 bar	30.9	32.5	29.1	17.8	21.7	12.1
% Moisture at 15 bar	14	15.5	13.1	8	8.5	5.6
% Organic Matter	7	7.2	5.5	5.7	6.2	3.7
pH	8.3	8.2	8.2	6.6	6.2	5.9
Nitrate-N (ppm)	4	7	3.5	1.5	3.5	1
Olsen P (ppm)	5	6	5	11	12	12
Soluble Salts (mmhos/cm)	0.21	0.26	0.2	0.08	0.07	0.02
Zinc (ppm)	2.03	2.07	1.95	6.99	6.71	3.53
Iron (ppm)	13.8	21.4	15.2	40.3	60.3	76.2
Manganese (ppm)	4.6	4.3	3	8	13.3	14.7
Boron (ppm)	1.21	1.49	1.43	0.23	0.17	0.11

Parameter	Population[1]					
	1	2	3	4	5	6
Base Saturation						
Potassium (ppm)	234	421	387	228	213	110
Calcium (ppm)	5937	5876	5086	1597	1420	643
Magnesium (ppm)	377	335	349	201	200	118
Sodium (ppm)	15	13	12	14	16	15
Hydrogen (ppm)	14	18	18	28	46	33

[1]Populations 1, 2 and 3 are at the Ridge; populations 4 and 5 are at the Valley; population 6 is at the Forest.

Population Invasiveness Index (Raw Field Data)

Semivariance calculations indicated that spatial autocorrelation was nonexistent at population edges and was nonexistent or minimal within population interiors. This spatial independence indicated that the method of calculating *I* based on data collected from 1/16-m^2 quadrat cells was not biased through correlation with adjacent cells, and the method of calculating invasiveness was appropriate.

Mean invasiveness from all years was not significantly different between sites (P = 0.072). However, in some years there were significant site differences (Figure 3.3b). In year 4, sites varied (P = 0.001) from highly invasive at the Ridge (*I* = 1.90, SD = 0.20) to near neutral at the Valley (*I* = 0.4, SD = 0.09) to declining at the Forest (*I* = -1.90, no SD because there is only one population). In year 5, which was anomalous in terms of invasiveness and total precipitation (i.e., drought conditions subsided and the annual precipitation was 13 cm greater than the annual mean of the previous 4 years), invasiveness at sites varied (P = 0.05) from *I* = -0.79 (SD = 0.51) at the Ridge to *I* = 0.23 (no SD) at the Forest to *I* = 0.89 (SD = 0.13) at the Valley. In all other years, invasiveness was highest at the Ridge, followed by the Valley and then the Forest. If the

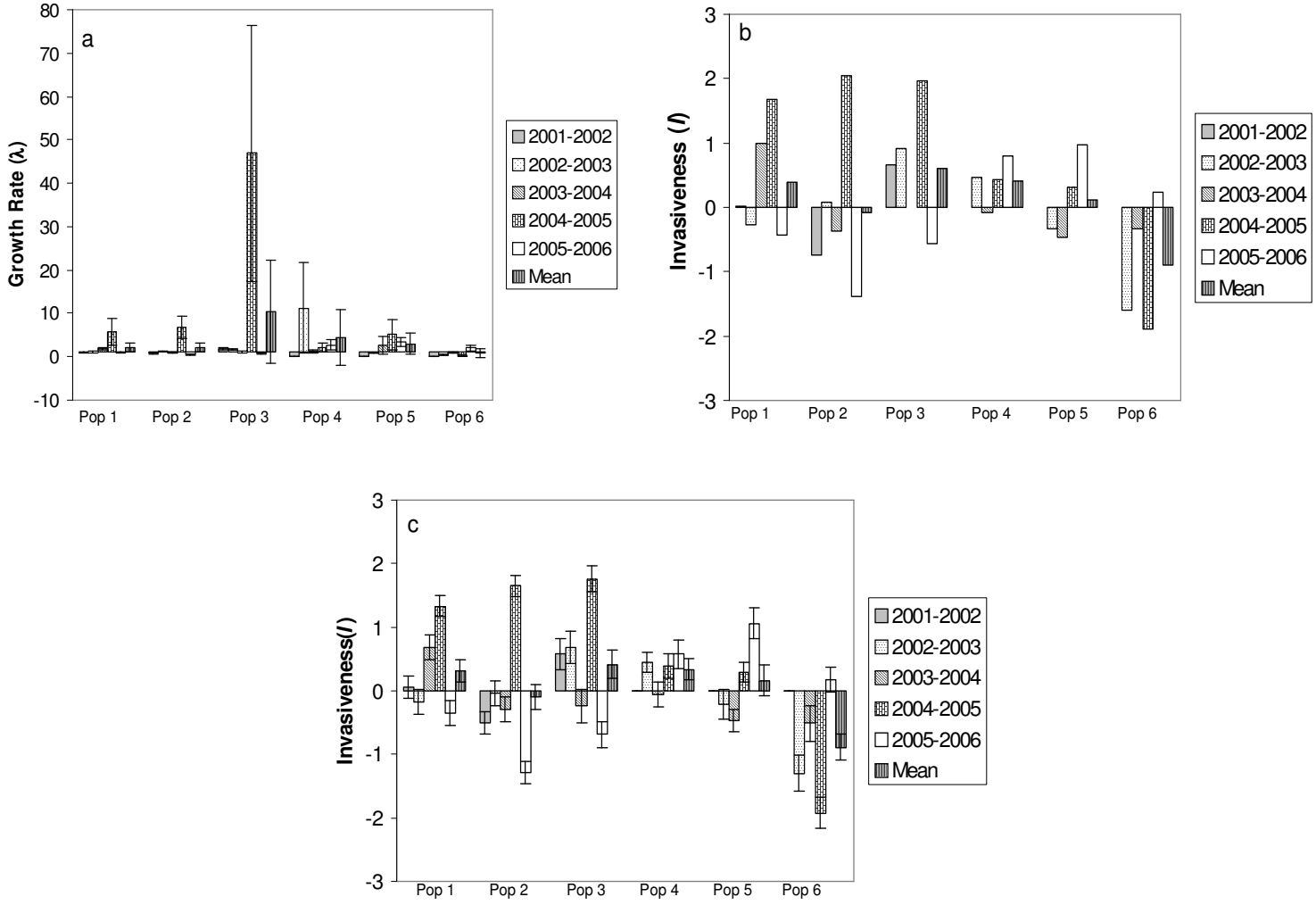

Figure 3.3. (a) *Linaria vulgaris* population growth rates (λ) for all populations and years. (b) Population invasiveness (*I*) values for all populations and years calculated from raw data. (c) Population invasiveness values for all populations and years calculated from bootstrapped data. Error bars represent +/- one standard deviation.

anomalous year 5 data were removed from the analysis, then the mean invasiveness for all years for the Ridge site (I = 0.58) was significantly more invasive than the Forest site (I = -1.28) (P = 0.0086). Removal of this data prior to analysis could be justified, as land managers are often interested in long-term population invasiveness trends and may be less concerned with yearly changes resulting from temporal weather patterns, although they would consider this information useful.

Populations 3 (Ridge) and 6 (Forest) were the most and least invasive, respectively, with mean population I values of 0.60 (SD = 0.96) and -0.90 (SD = 1.01) (Figure 3.3b). Populations 1 and 2 (Ridge) had mean I values of 0.40 (SD = 0.90) and -0.07 (SD = 1.30), respectively, while mean I values for populations 4 and 5 (Valley) were 0.40 (SD = 0.36) and 0.13 (SD = 0.66), respectively. The highest I for any year was 2.05 for population 2 (Ridge, 2004-2005) while the lowest was -1.90 for population 6 (Forest, 2004-2005).

Population Invasiveness Index (Bootstrapped Data)

The mean values of invasiveness calculated from the bootstrap method are presented in Figure 3.3c. These values closely mirrored raw data invasiveness values and like the raw data they varied considerably by population and year.

Methods Comparison

The two methods (using raw data and bootstrapped data) of calculating invasiveness generally provided similar results (Figure 3.3). The adjusted percent differences ranged from the smallest of 0.09% to the greatest of –6.76%, with a mean of

–0.79% (Table 3.3)and standard deviation of 0.02. The traditional method of looking at population invasiveness in terms of λ provided similar results to the bootstrapped calculations of invasiveness. These values were also well correlated, with a Pearson's correlation coefficient of 0.82 (Figure 3.4).

Table 3.3. Adjusted % differences for *Linaria vulgaris* invasiveness calculations by different methods[1]

	Population[2]					
Year	1	2	3	4	5	6
2001-2002	0.53	2.63	-1.25	ND[3]	ND	ND
2002-2003	1.17	-1.42	-3.42	-0.11	1.36	3.17
2003-2004	-4.44	1.01	-3.00	0.29	-.14	-2.12
2004-2005	-5.51	-6.76	-3.46	-0.63	-0.29	-0.24
2005-2006	0.95	1.00	-1.50	-2.97	1.13	-0.73
Mean	-1.16	-0.27	-2.46	-0.81	0.50	0.13

[1]A positive value indicates that invasiveness calculated from raw data is less than invasiveness calculated from bootstrapped data. A negative value indicates vice versa.
[2]Populations 1, 2 and 3 are at the Ridge; populations 4 and 5 are at the Valley; population 6 is at the Forest.
[3]ND = No data. These populations were not sampled in first year of study.

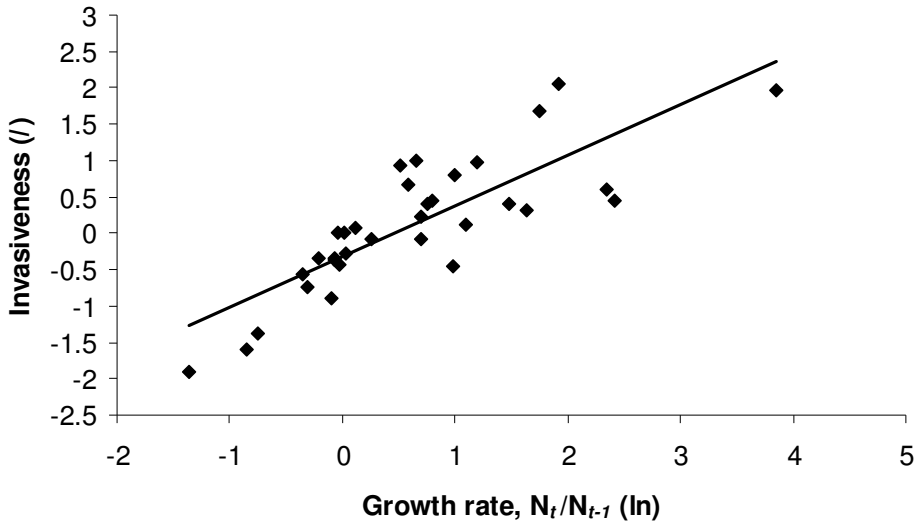

Figure 3.4. Correlation of *Linaria vulgaris* invasiveness with growth rate (λ).

Discussion

The degree of *L. vulgaris* population invasiveness was variable between sites and within different populations and years. Using the *I* values, population 3 at the Ridge had the highest mean invasiveness of 0.60 followed by Population 4 at the Valley with an invasiveness of 0.40. Population 6 at the Forest had the lowest calculated invasiveness of –0.9. On the site level, the mean invasiveness of the Valley (0.26) as slightly more than that of the Ridge (0.21), and both the Ridge and Valley had invasiveness values much greater than that of the Forest (-0.9).

Variability in Population Invasiveness

Populations at the Ridge generally had higher invasiveness values than populations at the Valley and Forest sites for the first four years. This trend reversed in the fifth year (2005-2006), and the difference was strong enough that the overall mean invasiveness of the Ridge was less than that of the Valley. Invasiveness of all Ridge populations differed somewhat from each other and also varied by year, with invasiveness being negative in some years. Overall, the mean invasiveness of populations 1 and 3 was positive and higher than the Valley and Forest populations. The mean invasiveness of population 2 was slightly negative, with only population 6 exhibiting a lower invasiveness value.

The greater invasiveness at the Ridge in 4 of 5 years could be an indication of more suitable habitat conditions at this site. Lajeunesse (1999) observed *L. vulgaris* to be highly competitive on south facing slopes such as the slope at the Ridge site. Also, the

populations at the Ridge are on a soil that is potentially more suitable for growth of *L. vulgaris*, and plant growth in general. As shown in Table 3.2, this soil has greater cation exchange capacity (2.5 and 4.3 times more than Valley and Forest sites, respectively), nitrate-N (1.9 and 4.8 times more than Valley and Forest sites, respectively) and water holding capacity (% moisture at 1/3 bar; 1.6 and 2.5 times more than Valley and Forest sites, respectively). The Ridge also receives greater annual solar radiation than the other sites, which was positively correlated with this invasiveness. Finally, the typical trend of increasing precipitation with elevation suggests that populations at the Ridge could receive more precipitation than those at the other sites, although we did not collect rain gauge data to confirm precipitation received at each site.

Populations 4 and 5 at the Valley had invasiveness values generally less than those at the Ridge (except in the last year), but much greater than the population at the Forest. Population 4 was invasive in four of five years and the mean invasiveness was positive, while population 5 was only invasive in two of four years and the mean was lower, but still positive. The differences in invasiveness of these two populations are likely the result of a slight change in slope, aspect and shading. They are within 50 m of each other and share a common soil type, but population 4 is on a flat open bench while population 5 slopes gently to the northwest and is partially shaded in the afternoons by mature lodgepole pine trees located approximately 10 m to the west.

Population 6 at the Forest, located near populations 4 and 5 but entirely under a canopy of lodgepole pine, showed negative invasiveness (declining population) in all years but the last, and the mean invasiveness was strongly negative. Other populations in

the same area have been noted to decline as a result of canopy closure (Pauchard et al. 2003). We have observed an increase in canopy cover over the study period and this may explain the overall decline of population 6.

Temporal variation in invasiveness of *L. vulgaris* populations appeared to be related to annual precipitation. Population invasiveness at the Ridge responded weakly to additional rainfall, with populations 1 and 2 having a positive response and population 3 no response. This site is located on a limestone-derived clay soil, which has a relatively high water holding capacity (Table 3.2). Populations here may be able to utilize the additional soil water to increase their growth rate. However, the additional water was also available to the native plant community, and competition with native plants could possibly account for the lack of a relationship of population 3 and the weakly positive relationships of the invasiveness of populations 1 and 2 with precipitation. Populations at the Valley exhibited stronger responses to annual precipitation. These sites are located on a well-drained soil, so less water was generally available to plants through the growing season than at the Ridge. However, *L. vulgaris*, with its taproot and extensive lateral root system may be better equipped than many of the native species to extract water from the well-drained soil (Saner et al. 1995). Therefore, the ability of *L. vulgaris* to out-compete the native plant species for water in this environment could explain its increased invasiveness with precipitation. Population 6 at the Forest responded weakly, but positively to additional precipitation. This weak response may be an indication that *L. vulgaris* was already taxed in this poor quality habitat.

Accuracy, Value and Applicability of Method

Examining how closely the invasiveness values correlated with the traditional calculations of population growth rates (λ) was a test of the precision of the method for calculating invasiveness. The calculated invasiveness index and λ are highly correlated (Pearson's $r = 0.82$). With such high correlation, it could be argued that λ was a suitable metric for determining invasiveness. However, our method of calculating invasiveness provides a unique estimation of NIS patch dynamics because it incorporates spatial information (i.e., change in patch area in terms of change in cell occupancy). Incorporation of spatial data was useful because it allowed for detection of new colonization on the population perimeter or local extinction within the population. One could imagine a scenario where the mean λ for a population was slightly less than 1, indicating a declining population, but the patch was expanding around the edges. Such a population could be invasive, and our methodology for calculating invasiveness would detect and quantify this invasiveness, whereas simply making a determination based on λ would indicate a non-invasive population. Another advantage of our method is that it quantifies invasiveness in a finite range (-4 to +4) whereas λ can theoretically range from 0 to infinity. The standardization of the index between –4 and +4 facilitates the comparison of invasiveness between different populations, over time and between species. Furthermore, while calculating invasiveness from raw field data and bootstrapping this data provided similar results, the bootstrap method was a statistically more appropriate way of estimating invasiveness considering the small sample size typically necessitated by logistical constraints (size of populations being monitored and

time requirements for monitoring). The purpose of this work though, was to develop a quick and simple method of determining population invasiveness. Therefore, using the raw field data without bootstrap analysis to calculate invasiveness appears to be a suitable method, though populations require monitoring over time because there is considerable temporal as well as site variation in invasiveness.

Invasiveness of NIS populations may be significantly different depending on the environments in which they grow. The fact that invasiveness varies by site will allow land managers to tailor management to individual populations (or groups of proximate populations). Furthermore, field surveys of NIS, in conjunction with spatial analysis and mapping of the environment in a geographic information system (GIS), allows for the generation of probability of occurrence maps for NIS (Rew et al. 2005). These predictive maps incorporate fine-scale (10 m or 30 m) terrain data such as slope, elevation, aspect or other environmental features (e.g., roads, wildfire areas, and logging), and can be used to delineate very similar environments into smaller units for management. This combination of tools facilitates fine-scale management in situations such as at the Valley where populations in close proximity have different invasiveness values resulting from differences in slope and aspect.

This method has only been evaluated for *L. vulgaris*, which due to its low seed viability, short seed dispersal distance, and predominantly clonal growth habit, has discrete patch boundaries. The method should, and is, being tested on non-clonal annual and perennial species that reproduce sexually and have very short seed dispersal distances (e.g., not wind, water or animal dispersed). This method may not be appropriate for

species with long seed dispersal distances, because it relies on being able to track the survival and subsequent reproduction of the majority of new ramets and genets generated by the populations. Thus, any individual that established outside of the existing marked boundary of the population being monitored would not be identified. However, no method will ever be able to track all propagules; there will always be a possibility of some being moved long distances. It should be noted though, that seed dispersal distances are often overestimated (Sheldon and Burrows 1973). For example, *Cirsium arvense*, of the Asteraceae family, produces achenes with large feathery pappi that have good aerodynamic efficiency (Sheldon and Burrows 1973). However, (Bakker 1960) showed that only 10 percent of trapped airborne plumes at 10 meters from the parent plant contained achenes and the number quickly declined with longer distances. Given that few seeds may move long distances, but that these events could be important, we could use the information from our invasiveness index, determining which populations are invasive in which environments, and combine these data with the predictive modeling mentioned above (Rew et al. 2005) to search other suitable environments for establishment of any new populations. Finally, our methodology could easily be modified to work for populations that do not have discrete boundaries, by changing the monitoring quadrat layout (i.e., edge and interior quadrats) to a random placement of quadrats within the population, perhaps with a larger spatial separation, to account for longer-range seed dispersal.

This method has only been tested, and is most applicable, at population/fine spatial scales. Patterns and processes of plant invasions vary at different spatial scales,

essentially necessitating the need for monitoring at multiple scales (Pauchard et al. 2003; Pysek and Hulme 2005; Pauchard and Shea 2006). For example, species that have longer dispersal distances highlight the need to also monitor metapopulations and invasiveness at broader spatial scales (Pysek and Hulme 2005) to determine longer distance dispersal and more general patterns.

The method may not be appropriate for use on new infestations of NIS that are known to be problematic in the area. In such a case, an early detection / early response strategy may be warranted (Mack et al. 2000). One such method for early detection is an adaptive sampling approach in which continuous sampling is conducted in concentric circles a set distance around the initial population identified. As new populations are encountered, sampling continues in concentric circles from these populations (Prather 2006). However, isolated populations are the exception rather than the rule. More often managers are dealing with numerous populations of a NIS scattered over a large area. We envision our methodology as being applied in this type of situation. A small number of populations within a relatively homogeneous area (in terms of soil, precipitation, vegetation, slope, etc.) would be monitored and the invasiveness values calculated used to represent other populations within the area.

It is recommended that populations of NIS be monitored for at least two seasons before beginning any control actions, if warranted by results of monitoring. However, if the NIS has a history of being invasive in a given area and there are strong concerns that it will spread, management actions should commence upon discovery of the populations. In this case, it is recommended that a part of the population or metapopulation be left

untreated and monitored to assess the effectiveness of the management practices and the natural variation of the population.

There are three possible management outcomes from monitoring and calculating invasiveness of a population. First, if the calculated invasiveness is strongly negative, then certainly control is not warranted, and a manager's budget would be better spent on other populations. Second, if the invasiveness is near zero, then the population is not spreading, and again does not currently warrant management. Finally, in cases where the calculated invasiveness is strongly positive, some form of control is likely appropriate. In all cases, even when populations are managed, it is recommended that monitoring continue. Only after several years of monitoring, can temporal trends in population invasiveness be determined or the effectiveness of management actions evaluated.

Conclusions

Not all populations of *L. vulgaris* are equally invasive, and we have developed a spatially sensitive index for determining relative invasiveness of *L. vulgaris* populations in the area of West Yellowstone, MT. The methodology developed for evaluating *L. vulgaris* invasiveness is generic and can be applied to other perennial NIS populations and in other locations. Evaluating invasiveness of NIS populations by site will allow land managers to prioritize populations in terms of which ones deserve immediate attention because of their aggressive expansion, which should simply be monitored because they are currently not expanding, and which can be monitored less regularly since monitoring indicates that the populations are going locally extinct. Such a

prioritization will promote the management of NIS on a population specific basis rather than a species basis. This will allow the management focus to be directed at populations that are truly invasive, help stretch the budgets of land managers and alleviate off-target effects often associated with broad scale management.

CHAPTER 4

EFFECTS OF DISTURBANCE AND ENVIRONMENT ON *LINARIA VULGARIS* COLONIZATION AND PATCH EXPANSION

Introduction

Linaria vulgaris (yellow toadflax) is a non-indigenous plant species (NIS) from Eurasia that has invaded the western and northeastern United States and western Canada, and is generally found in drier open rangelands and along roadsides or other disturbed areas (Lajeunesse et al. 2000). Locally it has invaded disturbed areas of the Gallatin National Forest near West Yellowstone, Montana (Pauchard et al. 2003). It has also been found near West Yellowstone in locations undisturbed by human activities (Pauchard et al. 2003) and *L. vulgaris* could invade from the Gallatin National Forest into the adjacent Yellowstone National Park (Olliff et al. 2001; Whipple 2001). It is a perennial species that reproduces both vegetatively and by seed (Saner et al. 1995), and was chosen for this study because of its purported invasiveness (Saner et al. 1995; Pauchard et al. 2003). In addition, *L. vulgaris* is well suited for population studies because, through its clonal growth form and short dispersal rate, it tends to form discrete patches (Nadeau and King 1991; Saner et al. 1995).

A large body of literature (Hobbs 1989; Hobbs and Huenneke 1992; Burke and Grime 1996; Lozon and MacIsaac 1997; D'Antonio et al. 1999; Lonsdale 1999) supports the idea that plant invasions are facilitated by disturbance. The study area for this research has been subject to various types of disturbance, including logging, road construction, grazing and wildfire since the late 1800's (Pauchard et al. 2003). A major

objective of this research was to assess the response of *L. vulgaris* to disturbances both in terms of change in patch density and patch expansion. The experimental disturbances used for this research included burning, clipping (to simulate grazing), soil disturbance via digging (to simulate disturbance by pocket gophers (*Thomomys* spp.)) and herbicide application. The first three types of disturbance were chosen because they are common in the study area and have been suggested to increase the spread of NIS. Studies have shown increases in Dalmatian toadflax (*Linaria dalmatica*) (a close relative of *L. vulgaris*) following prescribed fire (Phillips 2000; Jacobs and Sheley 2003), but data specific to *L. vulgaris* is not available. Grazing also increases the abundance of NIS (DiTomaso 2000; Mack et al. 2000; Keeley et al. 2003). Finally, pocket gopher activity increases the dominance of NIS in plant communities (Hobbs et al. 1988; Hobbs and Mooney 1991). Herbicide application, using Picloram (Tordon*K^{TM}), was implemented to assess how *L. vulgaris* responded to the treatment most often applied by the Gallatin National Forest Hebgen Lake Ranger District weed control workers. Picloram, from the pyridine family of herbicides, is a growth regulator that is very effective on most broadleaf species, including *L. vulgaris* (DowAgroSciences 1998).

A second objective of the research was to assess how *L. vulgaris* invasiveness varied in different environments or habitats. Invasiveness of a species would logically vary along a habitat suitability gradient. This is based on classical niche assembly theory and competition theory, which in essence states that a niche will be occupied by the species which is best suited for it (Grinnell 1928; Gause 1934; Hutchinson 1957; Hutchinson 1959; Tilman 1982). Thus, one would expect that a given NIS would be best

suited for a particular habitat or environment and would not be equally invasive in all. Study plots were established in four distinct environments – Clearcut, Meadow, Riparian and Wildfire burn.

A third objective was to evaluate the effect of patch position differences on *L. vulgaris* ramet density dynamics. Of specific interest was how population growth differed between just outside the original patch boundary, on the edge of the patch, and in the patch interior. Such information could elucidate the overall patch dynamics of *L. vulgaris* (e.g., positional density dependence or patch expansion/decline).

The final objective was to assess implementation of a new method of quantifying population invasiveness (see Chapter 3). This objective also stems from the idea that not all NIS populations in all environments are equally invasive. Therefore, a method that quantifies invasiveness would provide a tool for land managers to prioritize NIS populations for management.

Materials and Methods

Site Descriptions

Four sites, representing different environments and management conditions within the Gallatin National Forest near West Yellowstone, MT, were selected for this research (Table 4.1). The sites included an area that was logged in the mid 1980s (Clearcut Site), formerly forested land that burned in a wildfire in 1988 (Wildfire Site), a low-lying area adjacent to a riparian system (Riparian Site) and a sagebrush

(*Artemesia tridentata)* / grassland meadow (Meadow Site). Complete site descriptions including soil and climate are presented in Chapter 2.

Plot Establishment and Initial Monitoring

Patches of *L. vulgaris* were located and plots were established at each site in May 2004. A discrete patch was defined as a group of plants all within 2 m of each other. Any plant that was 2 m (approximately 1.5 times the maximum distance measured between ramets on rhizomes in a sandy area near the sites) or more from the group was considered to be outside of the patch. At each of the Clearcut, Meadow and Wildfire Sites, three separate patches were identified as suitable patches for plot establishment. At the Riparian Site, only one large patch located parallel to the road, was suitable for this experiment.

After *L. vulgaris* patches were located, paired monitoring plots were randomly placed around the edge of the patches. For each pair, one plot was placed on the edge of the patch such that *L. vulgaris* plants were located within the entire plot area. A plot was then located immediately adjacent to the first plot and just outside of the area with dense *L. vulgaris* growth such that there were a minimal number of *L. vulgaris* stems within the plot. The *L. vulgaris* patches had distinct edges, so establishing edge and outside plots in this manner was easily accomplished. Monitoring plots were also established within the interior of patches. Dimensions of the plots were 75 cm x 75 cm. The number of plot pairs varied by site depending on the number of treatments to be implemented, which was dependent upon the size of the patch. At the Clearcut and Wildfire Sites, each of the 3 patches received 8 plot pairs (8 edge and 8 outside plots x 3 patches = 48 plots) and a

total of 5 interior plots were located within the 3 patches. At the Meadow Site, 10 plot pairs were established for each patch (10 edge and 10 outside plots x 3 patches = 60 plots) and each patch had 2 interior plots (6 total). At the Riparian Site, with only one large patch, a total of 16 plots pairs (16 edge and 16 outside plots = 32 plots) and 3 interior plots were established (Table 4.1).

Subsequent to plot establishment, and prior to implementing any treatments, initial data from plots were recorded. These data included the stem density and percent cover of *L. vulgaris*, stem density and percent cover of each native species, percent cover of litter and percent cover of bare ground. For bunch grasses or plants that form ground cover (such as mosses, *Eriogonum umbellatum*, *Phlox* spp., etc.), stem density is not a meaningful measure, so only percent cover was recorded. A 75 cm x 75 cm (Figure 4.1) sampling frame was used to facilitate the measurements. The frame was divided by string into four 25 cm x 25 cm (i.e., 1/16-m^2) sections (cell), with a 12.5 cm buffer around all sides. To avoid edge effects, only the plants within the four internal squares were counted. Percent cover was recorded to the nearest 1 percent. Stem counts and percent cover of species were recorded separately for each cell within the frame.

Experimental Treatments

Treatments included burning, vegetation clipping, soil disturbance (digging), herbicide application and control (no treatment). Treatments were randomly assigned to plots and implemented in June 2004.

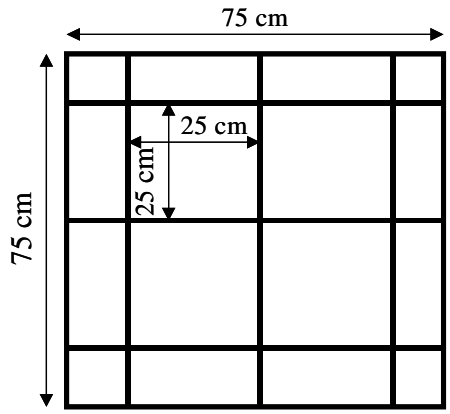

Figure 4.1. Schematic of sampling frame used for plot monitoring. Only the four internal cells, 25 cm x 25 cm or 1/16th m^2 each, were used for monitoring. The additional area around the perimeter of the quadrat provided a buffer and was not monitored.

Control. For comparison purposes, control plots where no treatment was implemented were established at each site. In the Clearcut, Meadow and Wildfire Sites, two pairs of control plots per patch were established. In the Riparian Site, a total of five control plots were established.

Herbicide. The herbicide treatment was intended to kill *L. vulgaris* plants as well as other broadleaf plants. Plots at all sites received herbicide treatment, with 2 plot pairs per patch sprayed at the Clearcut, Meadow and Wildfire Sites, and a total of five plot pairs sprayed at the Riparian Site. The herbicide used was Picloram (Tordon*K^{TM}), which was applied a single time to plots at a rate of 1 quart per acre (0.5 lb a.e.) as per the guidelines of the Hebgen Lake Ranger District of the Gallatin National Forest (Lamont, pers. comm. 2004).

Soil Disturbance. The soil disturbance treatment represents small gap disturbances created by burrowing animals such as *Thomomys* spp. This treatment was

performed at all four sites. Two pairs of plots per patch were disturbed at the Clearcut, Meadow and Wildfire Sites. At the Riparian Site, with only one large patch, a total of five plot pairs were disturbed.

Vegetation was removed from plots with a pulaski and soil was then removed to a depth of 7 cm, which was determined to be the average depth of disturbance by *Thomomys* spp. at the Meadow Site. Soil that was removed was passed through a 1.6-cm sieve to remove large rhizomes, roots or other plant fragments. Soil retained on the sieve was discarded and soil passing through was spread evenly back into the disturbed area.

Burning. Burning was intended to represent a fast moving, high intensity wildfire. Plots at the Clearcut, Meadow and Wildfire Sites were selected for burning. Two pairs (edge and outside) of plots per patch were randomly assigned for burning. Plots at the Riparian Site were not burned because this low-lying wet area is unlikely to burn in a wildfire. Also, with the single *L. vulgaris* patch at the Riparian Site, plots were limited and were reserved for other treatments.

Prior to burning, plot pairs to receive the treatment were framed with a 33-cm high rectangular piece of sheet metal to prevent fire from escaping the plots. A U.S. Forest Service crew then created the burns using a propane torch. Flame from the torch was applied to each plot for approximately 30 seconds until all vegetation had been consumed. The fire was allowed to burn out naturally, but any smoldering wood or adjacent vegetation was extinguished with water before moving on to the next plot.

Clipping. Clipping was intended to represent a single grazing episode. Two plot pairs per patch at the Meadow Site only, received the clipping treatment. In these plots, all vegetation was cut to ground level with garden shears. Table 4.1 provides a summary of all of the plots that were established at each site.

Table 4.1. Summary of plots established at each site[1]

Treatment	Number of Plots Per Site				Total Plots
	Clearcut	Meadow	Riparian	Wildfire	
Control	12	12	12	12	48
Herbicide	12	12	10	12	46
Dig	12	12	10	12	46
Burn	12	12	0	12	36
Clip	0	12	0	0	12
Total Plots	48	60	32	48	188

[1]Number of plots includes both edge and outside plots, but not interior. All interior plots were controls (no treatment) and the number per site was as follows: Clearcut = 5, Wildfire = 5, Riparian = 3, Meadow = 6.

Plot Monitoring

Plots were initially monitored before any treatments were implemented in May 2004. Subsequent to application of treatments in June 2004, plots were monitored for initial re-growth of *L. vulgaris* and other vegetation in July 2004. Plots were also monitored at the end of the growing season in late September 2004. Plots were monitored in late May and in late August of 2005 and early June and mid September of 2006. Data recorded for each monitoring event included density and percent cover for each species as well as percent cover of litter and bare soil within each 1/16-m^2 cell of the monitoring frame. The purpose of spring counts of *L. vulgaris* was to track the stem

density of seedlings and small vegetative shoots across years, while the aim of the fall counts was to track the stem density of mature plants.

Soil Samples

Soil samples were collected from each site on May 19 and 20, 2005 for the purpose of determining background soil characteristics. All samples were obtained from within patches of *L. vulgaris*, but not within areas that had previously received any type of experimental treatment. A 5 cm-diameter hand auger was used to obtain samples from the upper 15 cm of soil. Five samples, composited from seven subsamples that were thoroughly mixed in a stainless steel bowl, were collected at each site. Samples were immediately placed in a cooler with ice until they were transported to a cold storage room at the Montana State University Plant Growth Center. One half of each sample was submitted to the Montana State University Soil Testing Laboratory (Soil Laboratory) on May 24, 2005. The remainder of each sample was retained for additional tests.

Laboratory Analysis. Samples that were submitted to the Soil Laboratory were analyzed for ammonium (NH_4^+), potassium (K^+), Olsen phosphorus (P), organic matter, electrical conductivity (EC) and pH according to standard laboratory procedures.

Texture. Soil particle size was determined using a modified Bouyoucos method (Bouyoucos 1936; Day 1965; Gee and Bauder 1979). This method is based on Stokes law which states that larger, denser particles will settle faster in a water column than will smaller less dense particles. By measuring the specific gravity of a soil-water solution at specific times, the proportions of sand, silt and clay in the soil can be determined.

To begin the procedure, 50 grams of oven dried soil were mixed with 25 ml of a sodium hexametaphosphate solution and water to disperse clay particles. This solution was then placed in a 1,000 ml graduated cylinder and filled with water. The solution was vigorously mixed with a plunger, and a hydrometer reading was taken after allowing soil particles to settle for 40 seconds. Because the larger sand particles settle out quickly, this reading gives the grams of silt and clay in suspension. Another reading was taken after two hours when the silt had settled, giving the grams of clay in solution. After correcting for water temperature and the weight of sodium hexametaphosphate in solution, the texture, in terms of percent sand, silt and clay was calculated. From this, the textural class of each soil was determined.

Coarse Fragments. Coarse fragments are any particles such as pebbles or cobbles that are greater than 2 mm in diameter. The coarse fragment content for each sample was determined by sieving 50 g of soil through a 2 mm sieve and calculating the amount retained on the sieve.

Moisture Content. Each sample was weighed in its field moist condition, dried in an oven at 40 C, and then re-weighed. The moisture content was determined as the weight of the water divided by the weight of dry soil.

Potentially Mineralizable Nitrogen. Potentially mineralizable nitrogen (PMN) is the amount of organic nitrogen in soil that can be biologically mineralized to a form available to plants (NO_3^- or NH_4^+). PMN for the soil samples was calculated following the method of Bundy and Meisinger (1994). First, a split of each soil sample in field-

moist condition was submitted to the Soil Laboratory for analysis of NH_4^+. Then, for a second split, the following procedure was used:

1. Five grams of field-moist soil was mixed with 12.5 ml of deionized water in a 50 ml centrifuge tube and incubated in a 40 C water bath for 7 days.
2. At the termination of incubation, 12.5 ml of 2M KCl was added to the slurry so that the final solution was 1 M KCl.
3. The resulting slurry was shaken for 30 minutes, centrifuged, and the extract analyzed for NH_4^+-N by the Soil Laboratory.
4. PMN was calculated as the NH_4^+-N from this incubation/extraction minus the NH_4^+-N from the non-incubated soil split.

Data Analysis

Population Growth Rates. *L. vulgaris* population growth rates were calculated both as lambda (λ) and continuously as the change in number of stems over time ($\delta N/\delta t$) based on stem counts in each 1/16 m^2 cell of the sampling frame. When calculating λ, all stem count values were transformed by adding 1 to the original number of stems counted in each cell to avoid the problem of dividing by 0 when no stems were present in a cell for a given year. Values of λ were then calculated N_{t+1}/N_t where N_t is the number of stems within the quadrat at a given time t and N_{t+1} is the number of stems in that same quadrat at the subsequent time step. Values of $\delta N/\delta t$ were calculated simply by subtracting N_{t-1} from N_t. The periods for which growth rates were calculated were spring 2004 – spring 2005, fall 2004 – fall 2005, spring 2005 – spring 2006 and fall 2005 – fall

2006. The spring 2004 count of stems was conducted just prior to the implementation of treatments, and thus the values of λ and $\delta N/\delta t$ from spring 2004 to spring 2005 represent the population growth rate as affected by the treatments in the first full year.

Invasiveness Index. Invasiveness was defined as a population increasing in density and / or spatial extent. Therefore, invasiveness was calculated as a function of the change in stem density in 1/16-m^2 cells and change in occupancy of these cells, as follows:

$$I = (\alpha - \beta) + \gamma,$$

Where: α = proportion of cells with a positive growth rate

β = proportion of cells with a negative growth rate

γ = change in proportion of cell occupancy

Determination of growth rate ($\delta N/\delta t$) trajectories (positive or negative) in individual cells was made by simply subtracting the stem density at t_1 from the density at t_2 (e.g., spring 2003 density – spring 2002 density). Then for a given pair of years, the numbers of cells with positive and negative growth rates were summed. These values were divided by the total number of cells monitored to calculate proportion of cells with positive and negative growth rates to give α and β, respectively.

Change in cell occupancy between a pair of years was calculated by summing the total number of cells occupied in the individual years and then subtracting the number at t_1 from the number at t_2. This value was changed to a proportion by dividing by the total number of cells to give γ. The possible range of invasiveness was between -4 and +4.

Calculation of invasiveness was performed using a script written in the software package R (version 2.3.1) (Appendix A).

Correlation Between Invasiveness Index and Population Growth Rates. As with population growth rate (λ), the invasiveness index was calculated for the time periods of spring 2004 – spring 2005, fall 2004 – fall 2005, spring 2005 – spring 2006 and fall 2005 – fall 2006. We were interested in how closely the calculated values of invasiveness were related to the traditional measure of population growth rate (i.e., λ). This relationship was determined by calculating Pearson's correlation coefficient (Microsoft Excel 2000) for each invasiveness value and the corresponding value of λ.

Statistical Analyses. Growth rate was calculated as both the asymmetrically distributed variable λ and the continuous variable $\delta N/\delta t$. The value of λ, calculated as N_{t+1}/N_t, is always a positive number, and is therefore truncated at zero. In many cases of calculating population growth rate, this assures that the variable is not normally distributed (i.e., it is positively skewed), meaning that it often violates the assumption of normality which is necessary for performing analysis of variance (ANOVA). In contrast, the continuous variable $\delta N/\delta t$ can range on either side of zero and may have a normal distribution, making it more appropriate for evaluation through ANOVA. Because of this, λ values were used only for comparison with calculated invasiveness values, and statistical analyses of *L. vulgaris* growth rate were only performed on $\delta N/\delta t$ data. For these analyses, one way ANOVA and Tukey-Kramer multiple comparisons (P-value = 0.05) (S-PLUS 2000) were used to examine site and treatment differences. Annual

differences were not evaluated statistically as insufficient data exist to examine long-term trends.

For soil data, differences in site characteristics were examined through one-way ANOVA Tukey-Kramer multiple comparisons. In these analyses, the specific soil parameter (e.g., pH, organic matter, potassium, etc.) was the dependent variable and the site was the independent variable. To assess possible soil effects on population growth rates, mean values of soil parameters at each site were regressed against mean $\delta N/\delta t$ values for all four time periods.

Results

Population Growth Rates

Growth rate values of λ and $\delta N/\delta t$ were calculated for the four time periods previously listed: spring 2004 – spring 2005, fall 2004 – fall 2005, spring 2005 – spring 2006, and fall 2005 – fall 2006. For each time period, the growth rates were calculated for each treatment at all sites. Mean λ and $\delta N/\delta t$ values are presented in Figures 4.2 and 4.3, respectively. Mean values with standard deviations are presented in tables in Appendix B. Values of λ and $\delta N/\delta t$, being calculated from the same data, expectedly exhibit the same trends, but because of the superior statistical properties of $\delta N/\delta t$, as discussed above, only these values will subsequently be discussed with respect to site, treatment and annual differences.

Annual Differences in $\delta N/\delta t$. Variability in $\delta N/\delta t$ over time can be an important factor in determining the overall invasiveness of a population of NIS, however this variability is the result of temporal differences in growing condition (e.g., precipitation, nutrient availability) and is of little use for predicting future invasiveness. This study found differences in *L. vulgaris* growth rates between years for all sites and treatments, there does not appear to be a consistent pattern relating year to site or treatment, and temporal variation is not discussed further in this text.

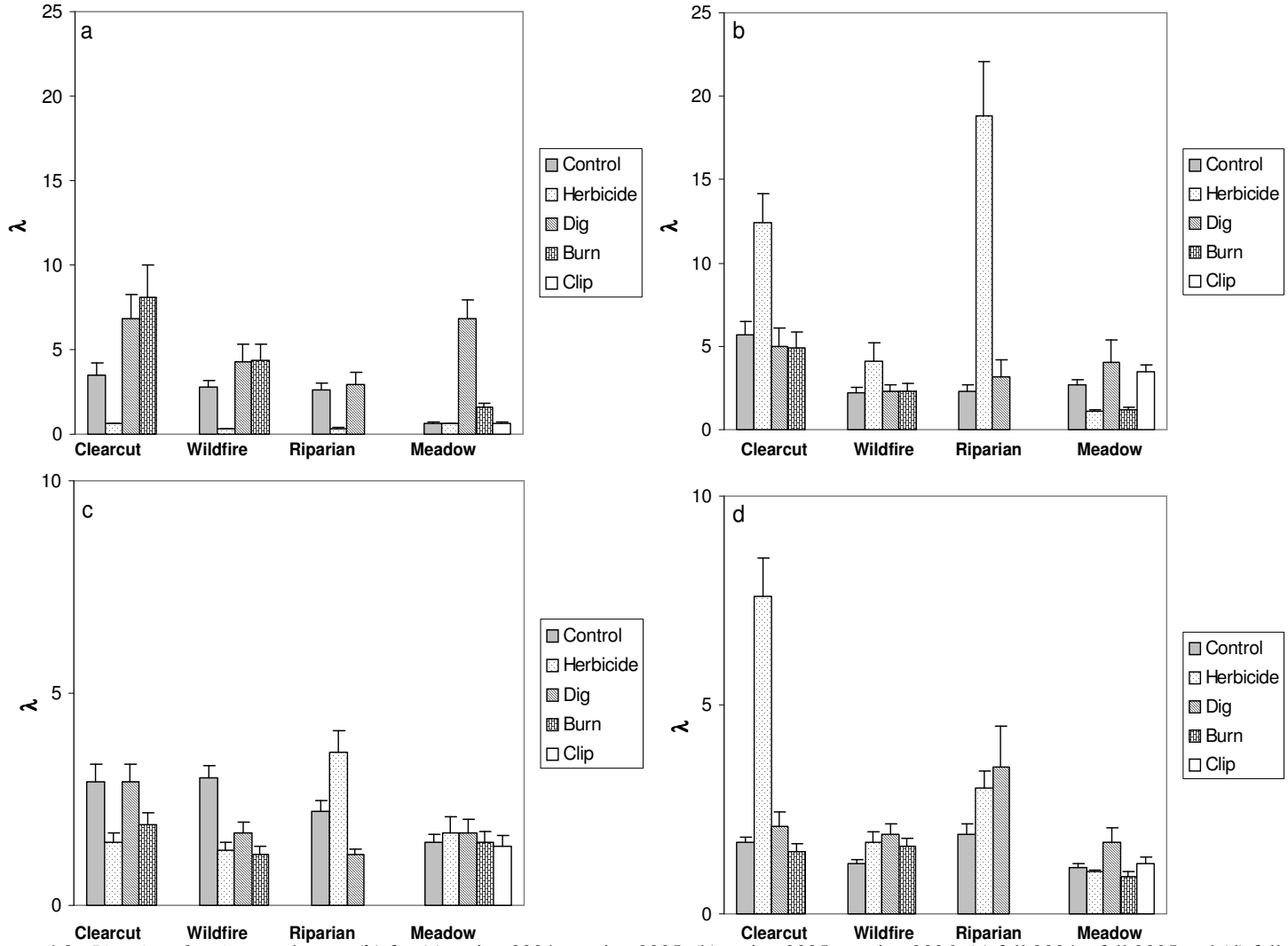

Figure 4.2. *Linaria vulgaris* growth rates (λ) for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments and sites. Error bars show standard error. For Clearcut and Wildfire control plots, N = 68. For Riparian control plots, N = 60. For Meadow control plots, N = 72. For other treatments at Riparian Site, N = 40. For all other treatments, N=48.

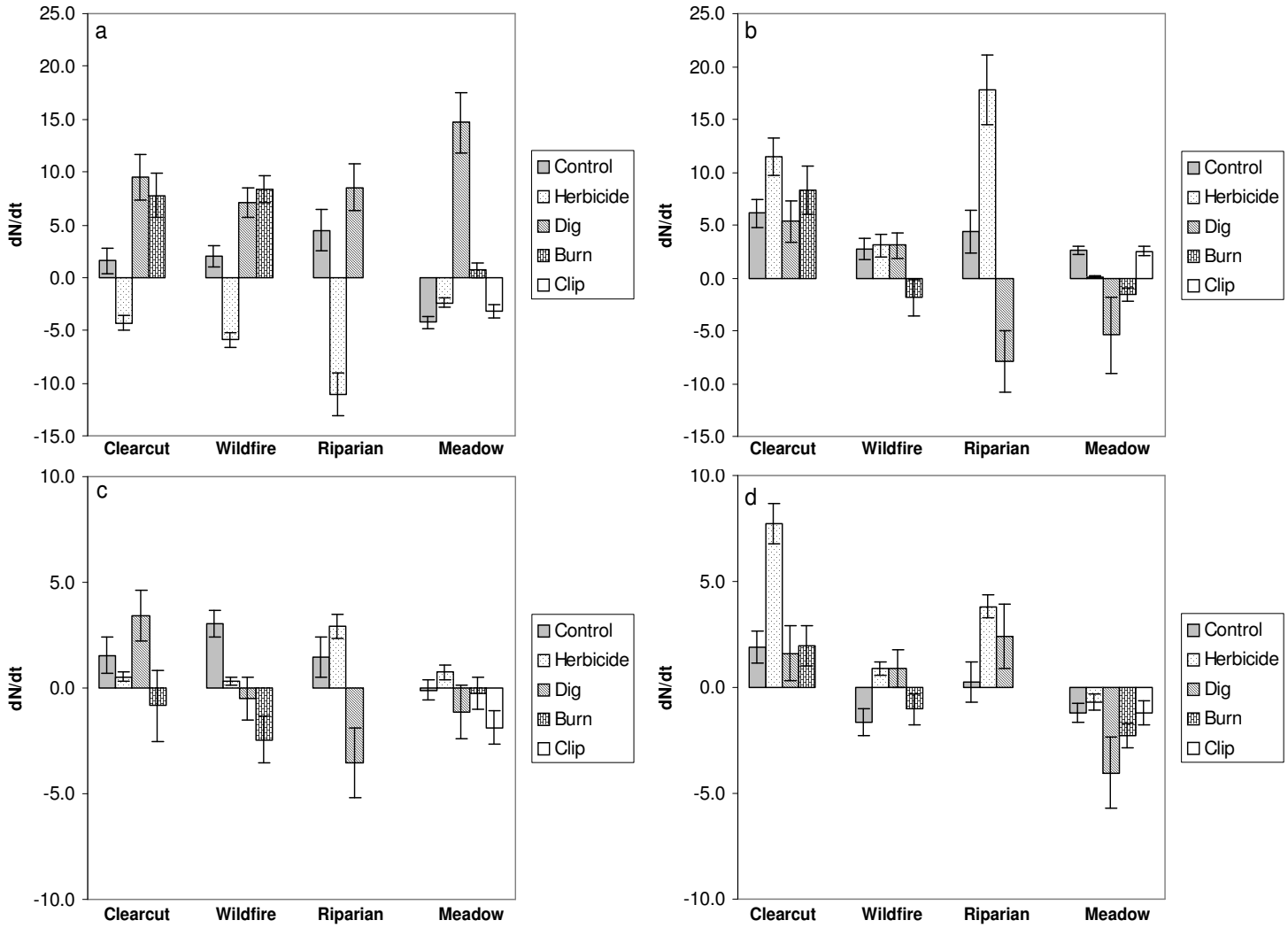

Figure 4.3. *Linaria vulgaris* growth rates (δN/δt) for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments and sites. Error bars show standard error. For Clearcut and Wildfire control plots, N = 68. For Riparian control plots, N = 60. For Meadow control plots, N = 72. For other treatments at Riparian Site, N = 40. For all other treatments, N=48.

Site Differences in δN/δt. Just as certain years may produce higher δN/δt values for a species, different sites (because of varying habitat suitability) may also lead to different δN/δt values. In this study, growth rates of *L. vulgaris* varied by site for a given treatment, although no consistent patterns were identified. For the control treatment, δN/δt was generally lowest in the grass-dominated Meadow, but differences were not always statistically significant (Figure 4.4). For the herbicide treatment, δN/δt values for spring 2004 – 2005 were all less than one (i.e., *L. vulgaris* stem density declined to near zero after treatment), resulting in the expected treatment response. In subsequent sampling periods, δN/δt values were highest in the Clearcut or Riparian Sites following herbicide treatment (Figure 4.5). Growth rate was similar for the digging treatment at all sites for spring 2004 – 2005, after which *L. vulgaris* at the Meadow consistently had the lowest δN/δt (though not always significantly), while the Clearcut and Riparian Sites typically exhibited the highest δN/δt (Figure 4.6). For the burn treatment, δN/δt values were generally highest in the Clearcut and lowest in the Meadow with Wildfire δN/δt generally similar to the Meadow (Figure 4.7).

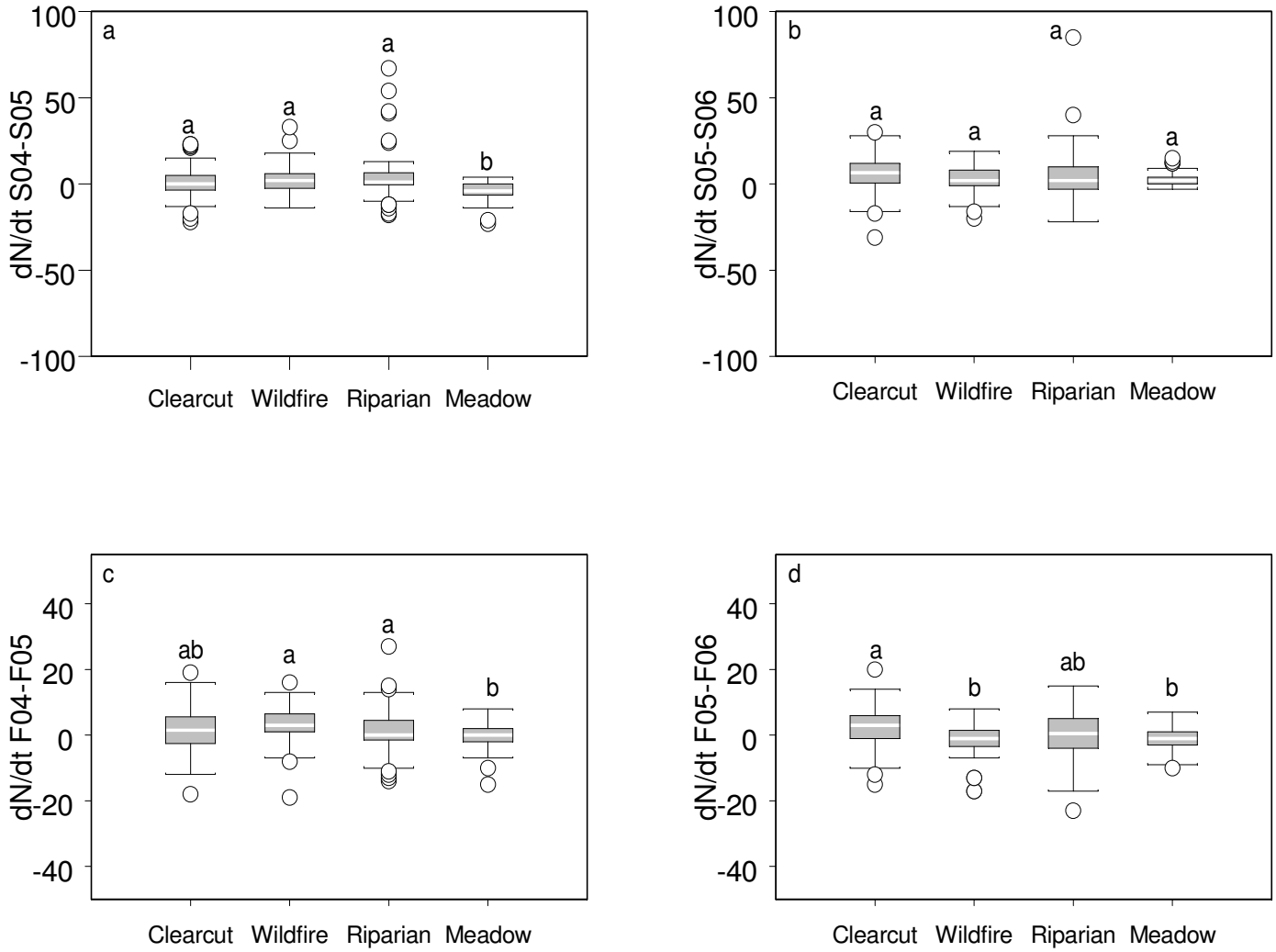

Figure 4.4. *Linaria vulgaris* growth rates (δN/δt) for Control treatment for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all sites. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

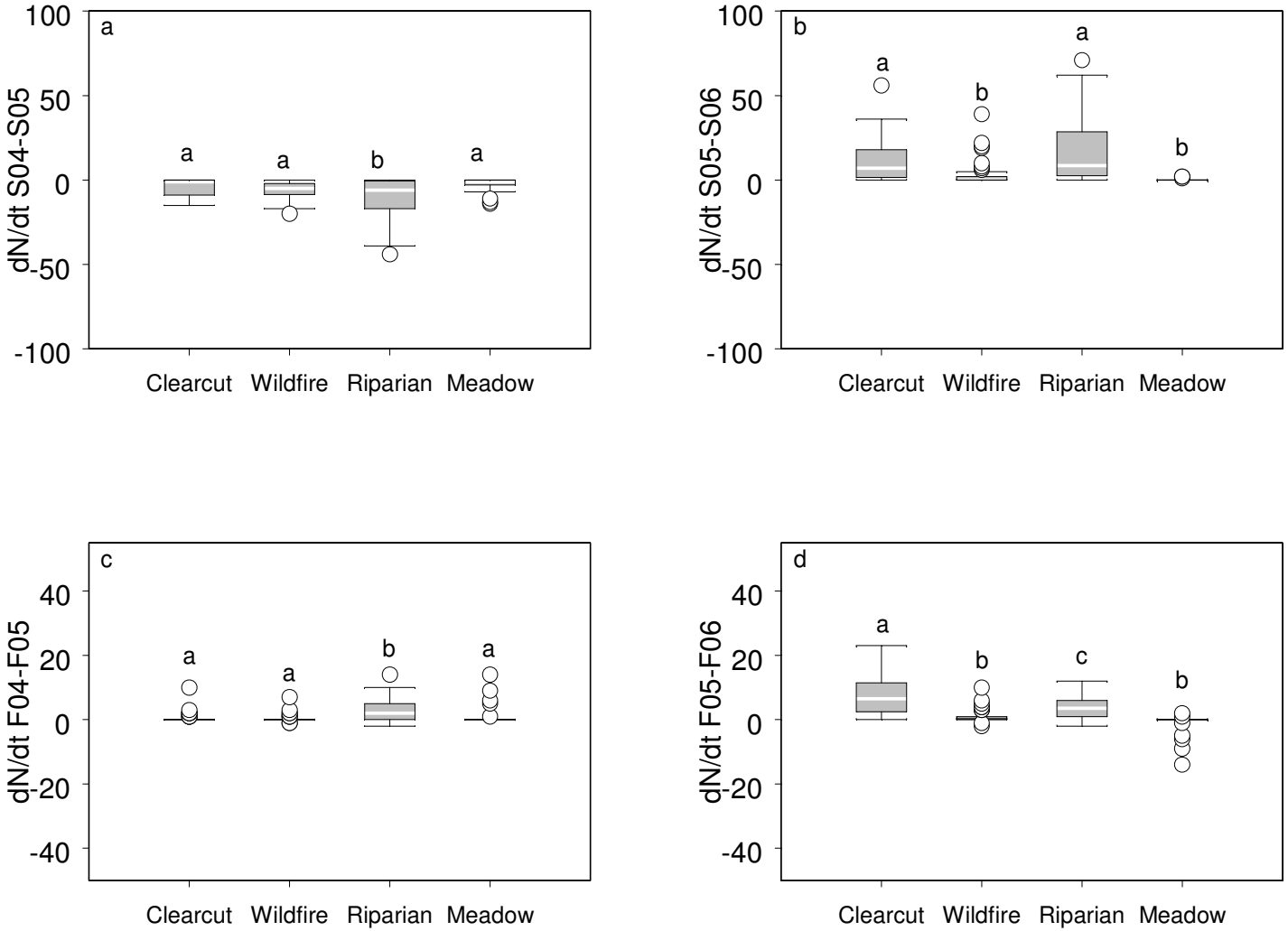

Figure 4.5. *Linaria vulgaris* growth rates (δN/δt) for Herbicide treatment for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all sites. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

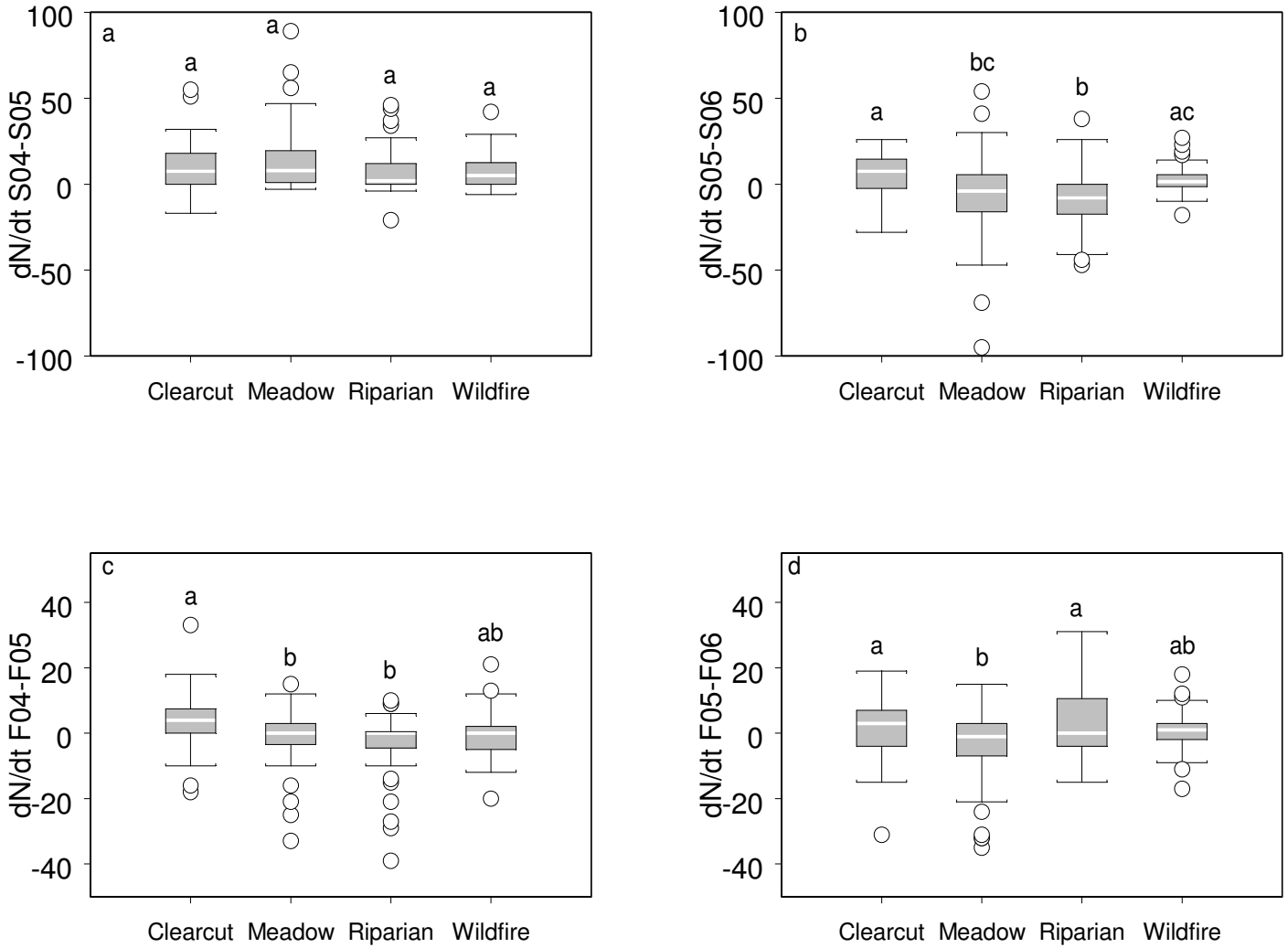

Figure 4.6. *Linaria vulgaris* growth rates (δN/δt) for Dig treatment for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all time periods and sites. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

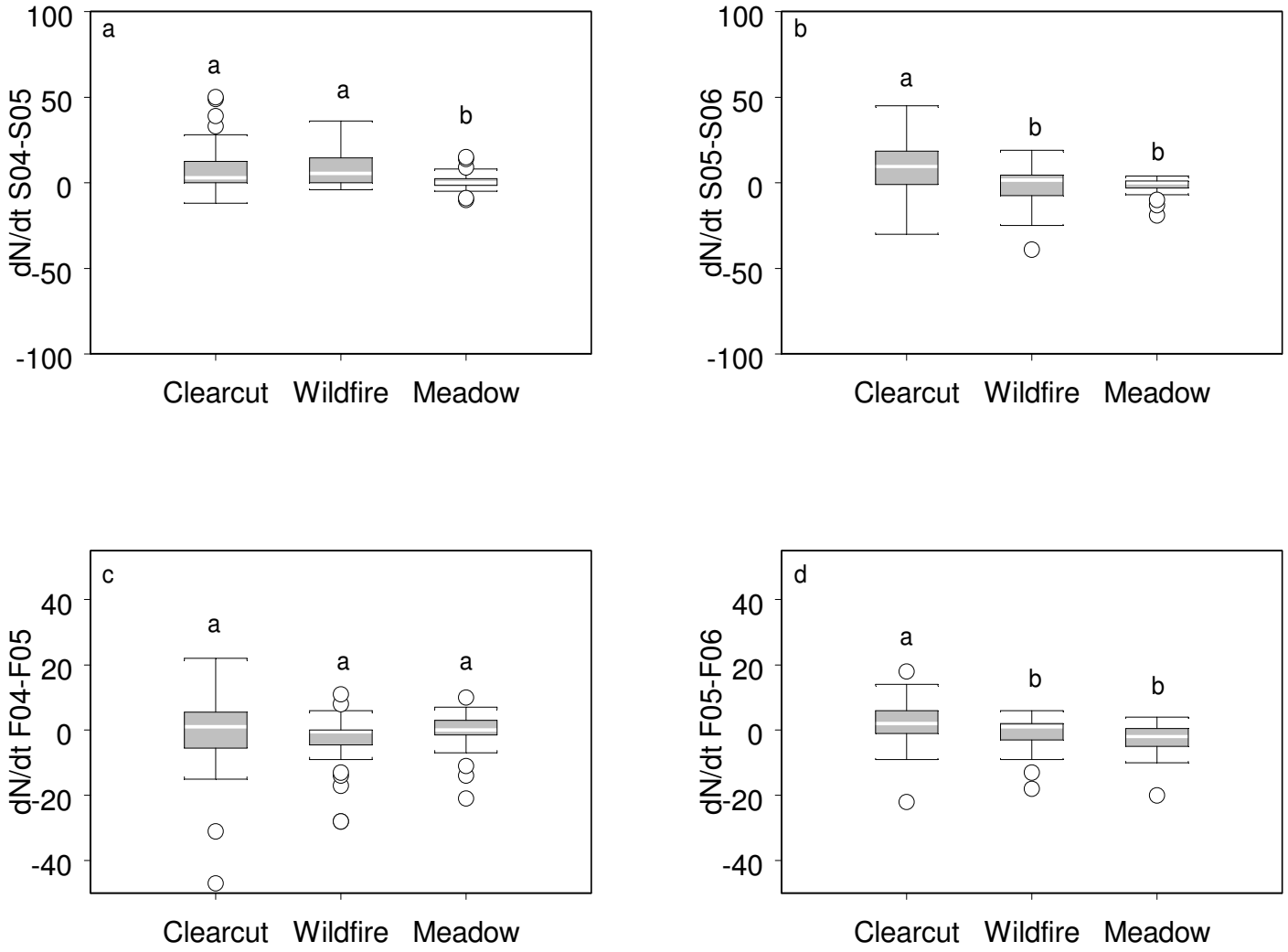

Figure 4.7. *Linaria vulgaris* growth rates (δN/δt) for Burn treatment for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all sites. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

Plot Position Differences in δN/δt. Differences in δN/δt values for different patch positions (i.e., interior, edge or outside) can help identify the overall invasiveness of a population as well as elucidate its possible mechanisms of invasion (e.g., advancing front with declining patch interior or non-advancing population acting as a potential propagule source for other patches). For control plots on all sites, *L. vulgaris* δN/δt values in outside plot positions were generally greater than or equal to values in edge and interior positions indicating that populations were expanding spatially. There were usually no significant differences between edge and interior positions, although there were some exceptions, notably the Wildfire Site where edge and interior δN/δt values differed, but did not follow a consistent pattern (Figures 4.8 – 4.11).

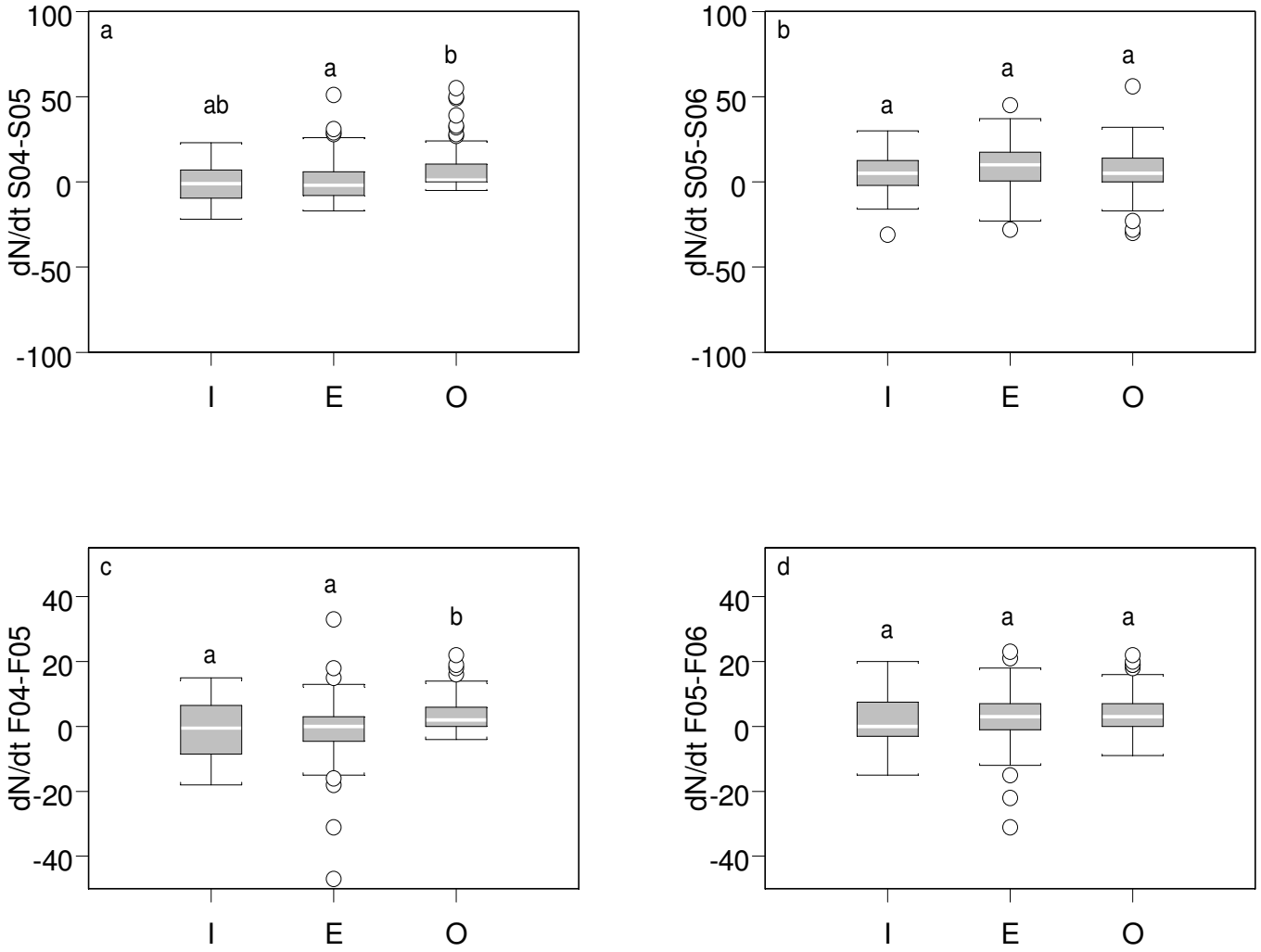

Figure 4.8. *Linaria vulgaris* growth rates (δN/δt) for Clearcut Site for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for different plot positions. I=Interior, E=Edge, O=Outside. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

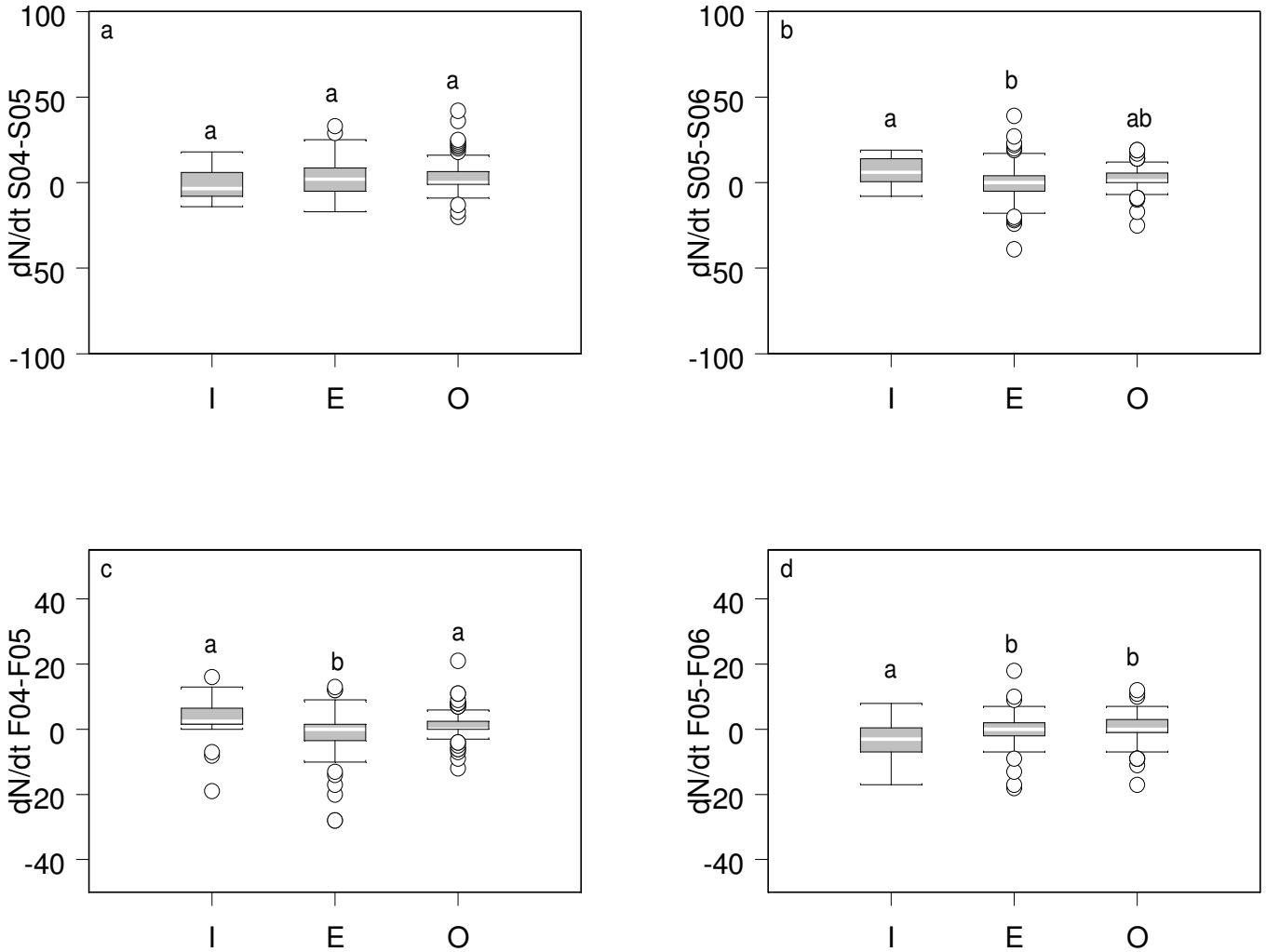

Figure 4.9. *Linaria vulgaris* growth rates (δN/δt) for Wildfire Site for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for different plot positions. I=Interior, E=Edge, O=Outside. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

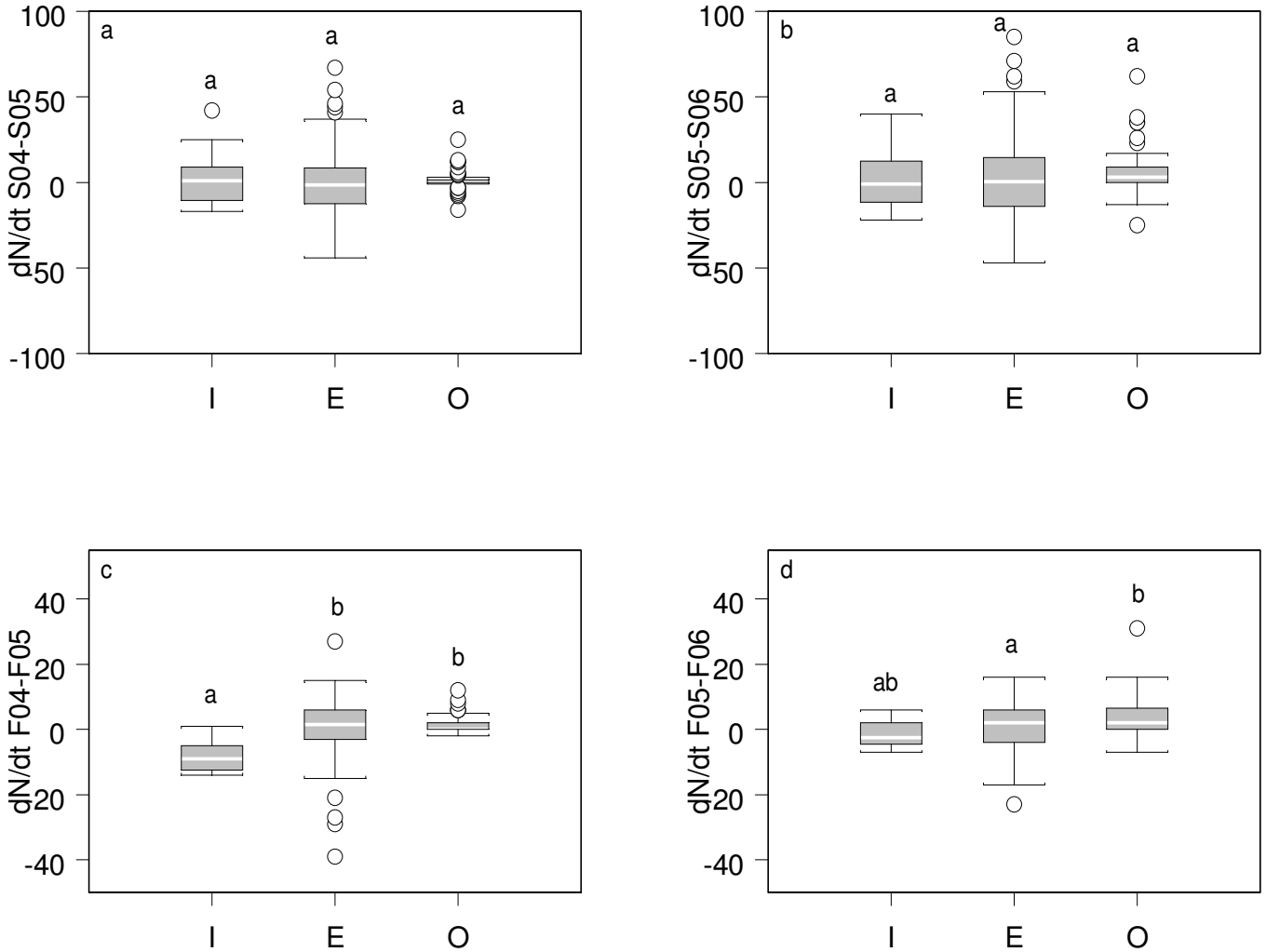

Figure 4.10. *Linaria vulgaris* growth rates (δN/δt) for Riparian Site for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for different plot positions. I=Interior, E=Edge, O=Outside. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

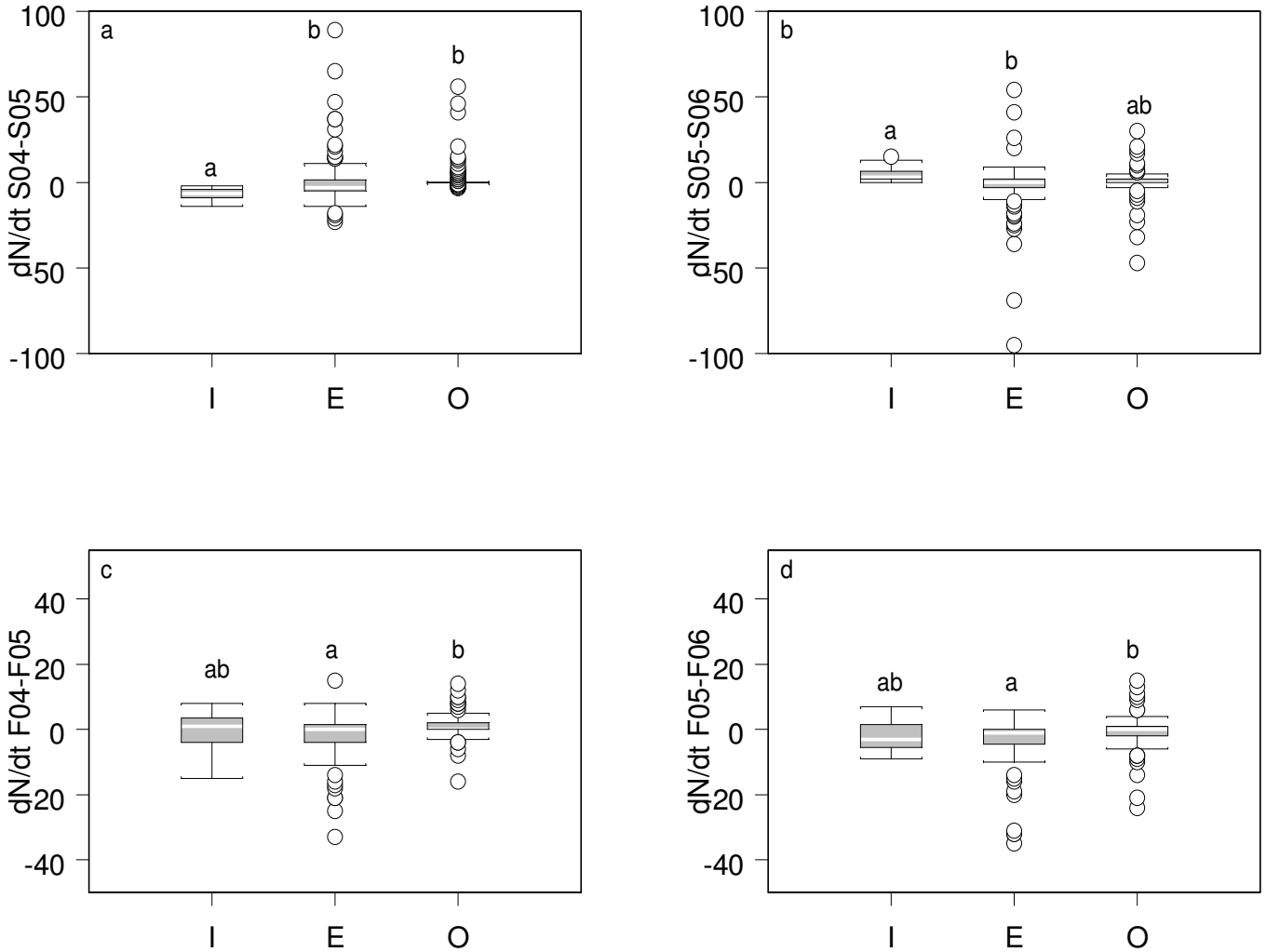

Figure 4.11. *Linaria vulgaris* growth rates (δN/δt) for Meadow Site for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for different plot positions. I=Interior, E=Edge, O=Outside. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

Treatment Differences in δN/δt. One of the main objectives of this research was to examine disturbance effects on the growth rate and colonization potential of *L. vulgaris*. Both plots on the edge and just outside of existing *L. vulgaris* patches (i.e., edge and outside plots) were used to evaluate effects of disturbance on growth rate and colonization, while just outside plots were used to assess disturbance effects on colonization. For each site, treatment effects were analyzed separately for edge and outside plot positions because δN/δt differed for edge and outside plots.

To illustrate treatment differences in δN/δt, and to show the change in *L. vulgaris* density over time, two sets of plots are presented. The first set (Figures 4.12 – 4.19) consists of box plots of δN/δt for each treatment, and there are separate plots for edge and outside plots as well as for spring and fall counts. The second set (Figures 4.20 – 4.23) consists of time series plots of *L. vulgaris* stems counted per 1/16-m^2 cell for each treatment. These plots provide a quantification of the actual number of *L. vulgaris* stems within cells rather than the change in number of stems. This is useful when evaluating the overall impact of treatments rather than just their relative differences. Results for each site are discussed below.

For the Clearcut, there were generally no differences in δN/δt values between treatments after the initial treatment response from spring 2004 – spring 2005 (Figures 4.12 and 4.13). A major exception is for the herbicide treatment for the time period of spring 2005 – spring 2006. During this period, the herbicide treatment resulted in a significantly higher value of δN/δt when compared with the other treatments.

At the Clearcut, the burn and dig treatments generally increased stem counts within plots (Figure 4.20). The only exceptions were the burn treatment from fall 2004 – fall 2005 and the dig treatment from fall 2005 – fall 2006. The stem density in plots with no treatment (control) also increased, but not as greatly as with the burn or dig treatments. Clearcut plots treated with herbicide showed decreased stem density from spring 2004 – spring 2005, but density increased after that point to levels higher than the densities prior to treatment (Figure 4.20).

At the Wildfire Site, after the first year response which showed Control, Dig and Burn treatments resulted in higher $\delta N/\delta t$ values than the Herbicide treatment, there were few statistical differences in $\delta N/\delta t$ values (Figures 4.14 and 4.15). Where there were differences after the first year, the Control, Herbicide and Dig treatments generally produced $\delta N/\delta t$ values greater than the Burn treatment.

With the exception of the Herbicide treatment, stem densities at the Wildfire Site generally increased in the first year after treatments (Figure 4.21). Dig and Burn treatments were an exception in edge plots from fall 2004 – fall 2005 with stem densities decreasing. After the first year, all treatments, with the exception of Burn (spring 2005 – 2006 edge plots) and Burn and Control (fall 2005 – fall 2006 edge plots) resulted in increased stem density. This included the Herbicide treatment which resulted in decreased stem densities in the year following treatment, but increased densities in subsequent years (Figure 4.21).

At the Riparian Site, the Herbicide treatment resulted in lower $\delta N/\delta t$ values than the Control and Dig treatments from spring 2004 – spring 2005 in both edge and outside

plots (figures 4.16 and 4.17). These results did not persist through the other time periods. After the initial period following treatment, herbicide treatment resulted in $\delta N/\delta t$ values generally significantly greater than for the Control or Dig treatments in edge plots. In the outside plots, there were no treatment differences in $\delta N/\delta t$ after the first year.

Trends in stem density varied at the Riparian Site (Figure 4.22). Stem counts typically increased in undisturbed control plots. For edge plots that were disturbed by digging, after an initial increase in density, the density decreased. In the outside plots, however, digging resulted in a steady density increase. Application of herbicide resulted in decreased stem densities in both edge and outside plots in the first year, but stem counts subsequently increased to well above their original densities (Figure 4.22).

At the Meadow Site there were few differences in $\delta N/\delta t$ resulting from the different treatments (Figures 4.18 and 4.19). Plots treated by digging showed an increased numbers of stems, while stem counts in plots receiving other treatments generally declined or remained constant. Stem counts in plots treated by digging declined after the initial period of spring 2004 – spring 2005 in which they rose (Figure 4.23).

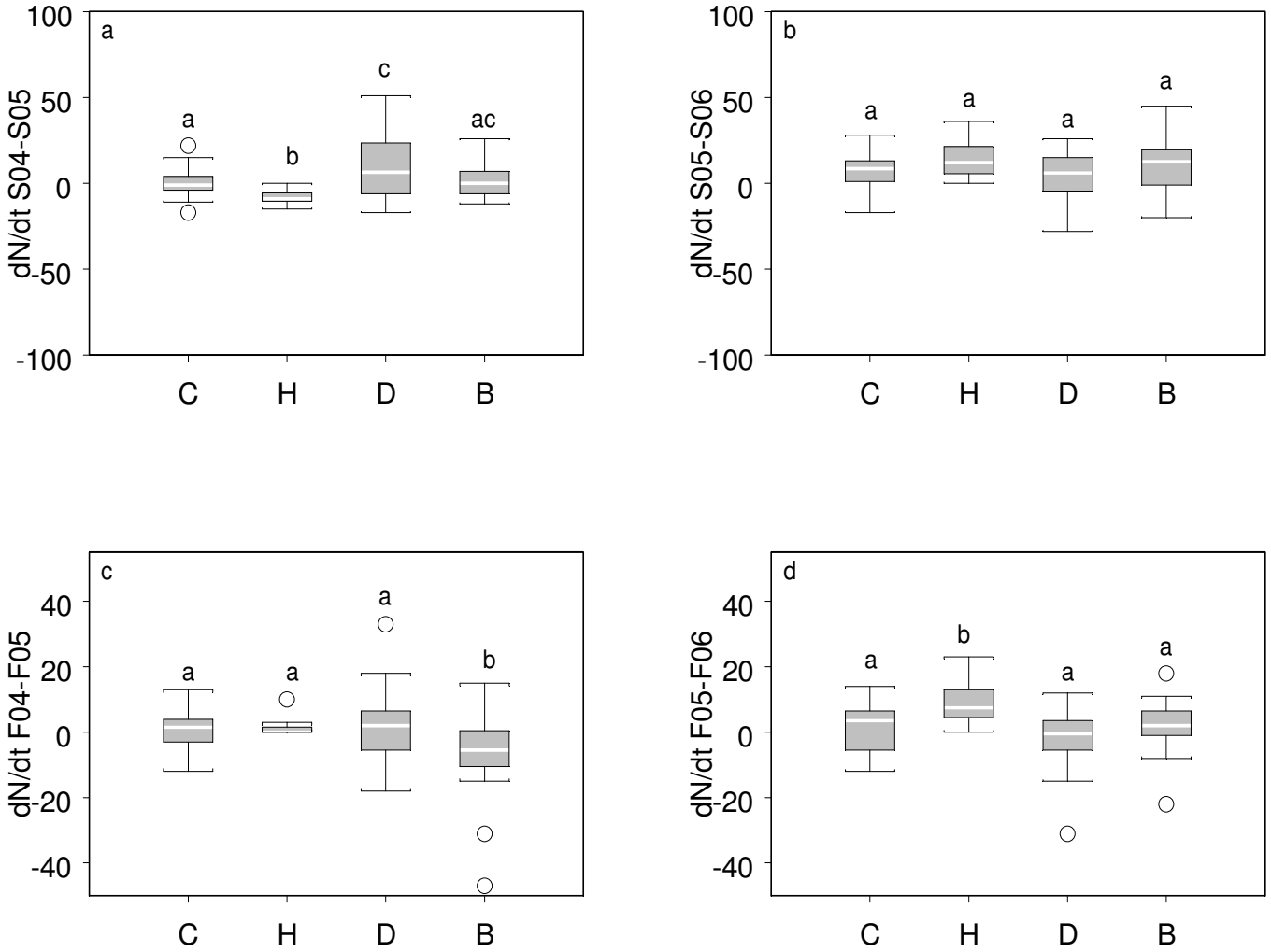

Figure 4.12. *Linaria vulgaris* growth rates (δN/δt) for Clearcut Site Edge plots for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments. C=Control, H=Herbicide, D=Dig, B=Burn. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

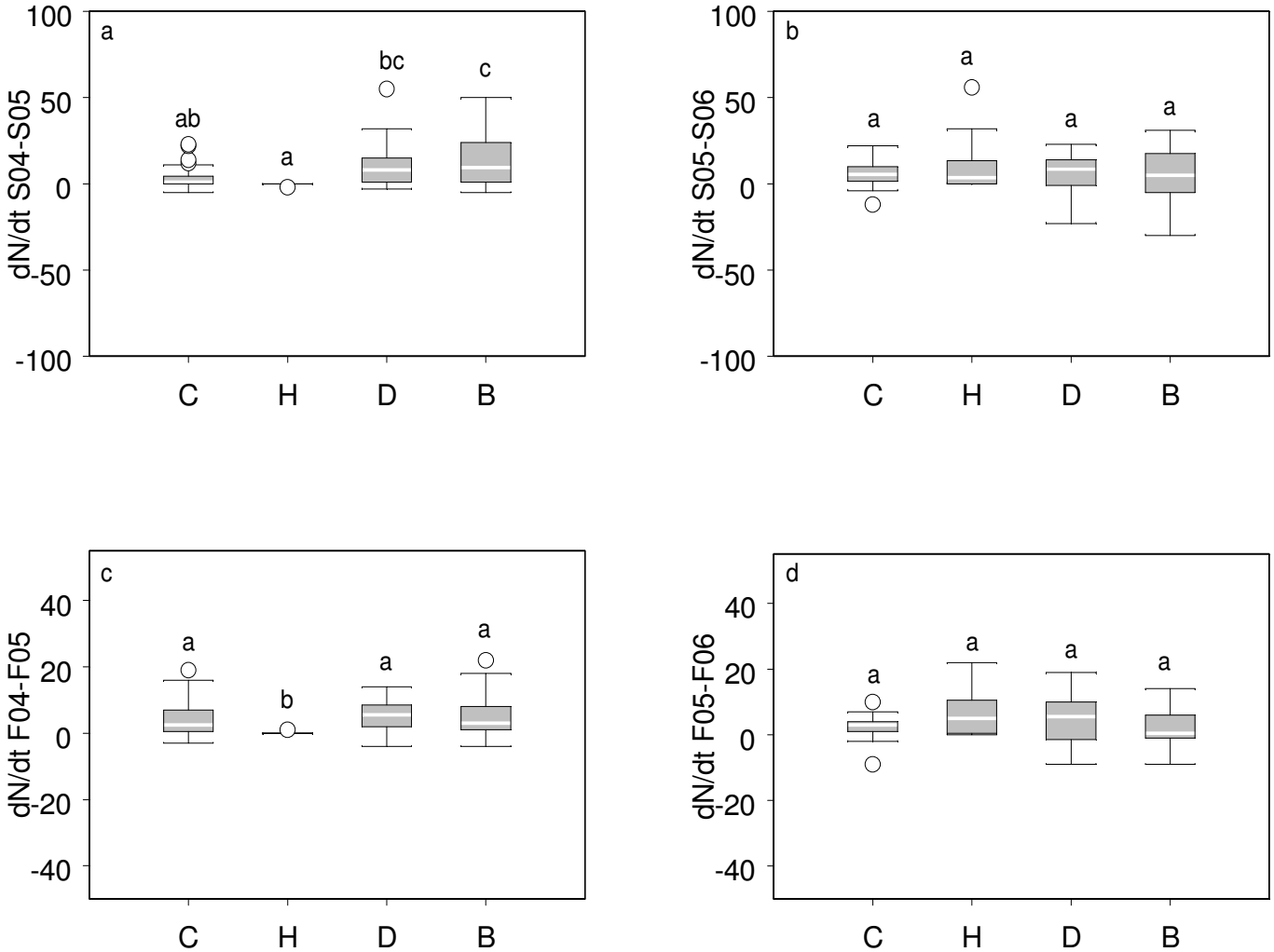

Figure 4.13. *Linaria vulgaris* growth rates (δN/δt) for Clearcut Site Outside plots for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments. C=Control, H=Herbicide, D=Dig, B=Burn. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

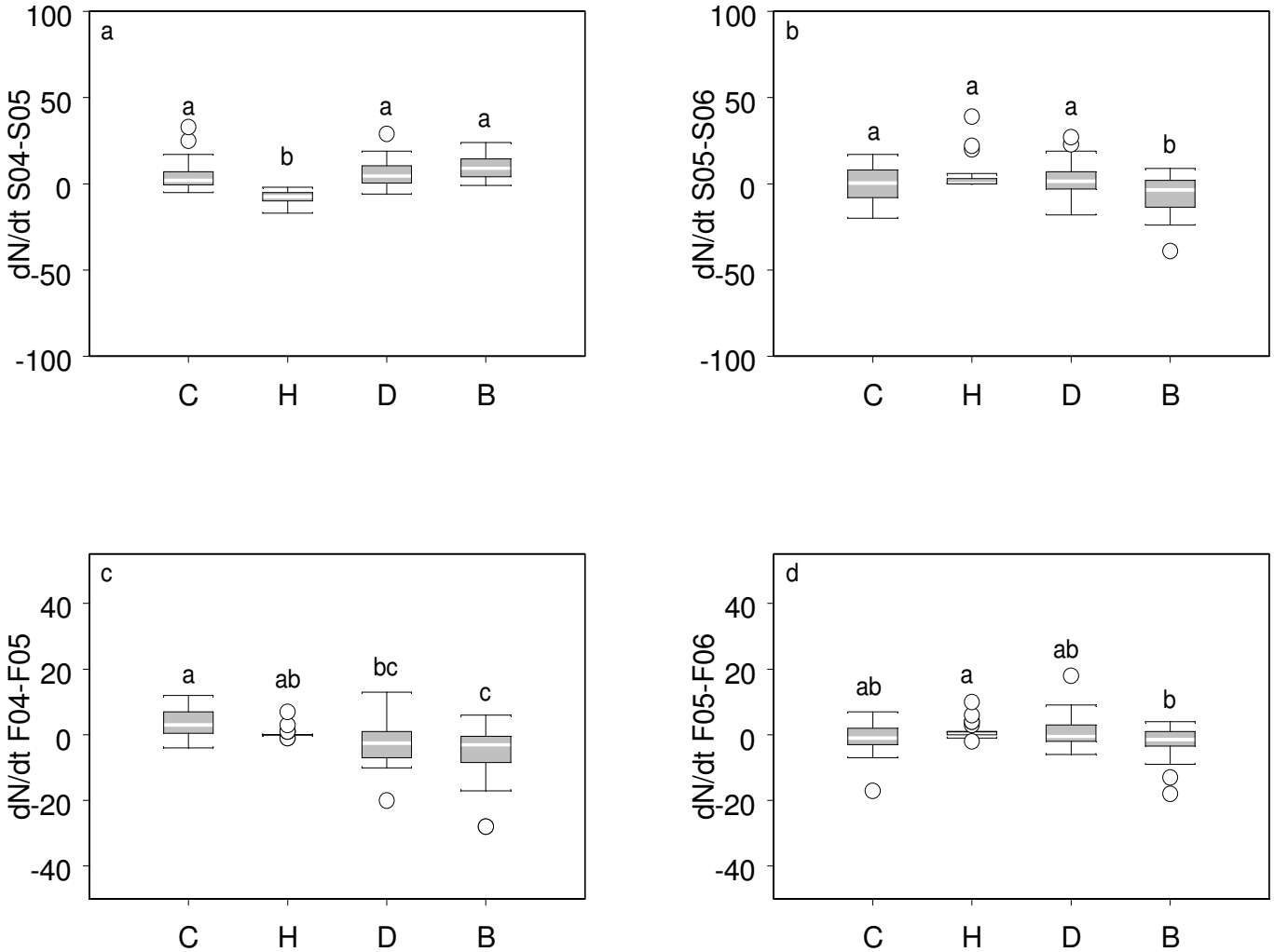

Figure 4.14. *Linaria vulgaris* growth rates (δN/δt) for Wildfire Site Edge plots for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments. C=Control, H=Herbicide, D=Dig, B=Burn. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

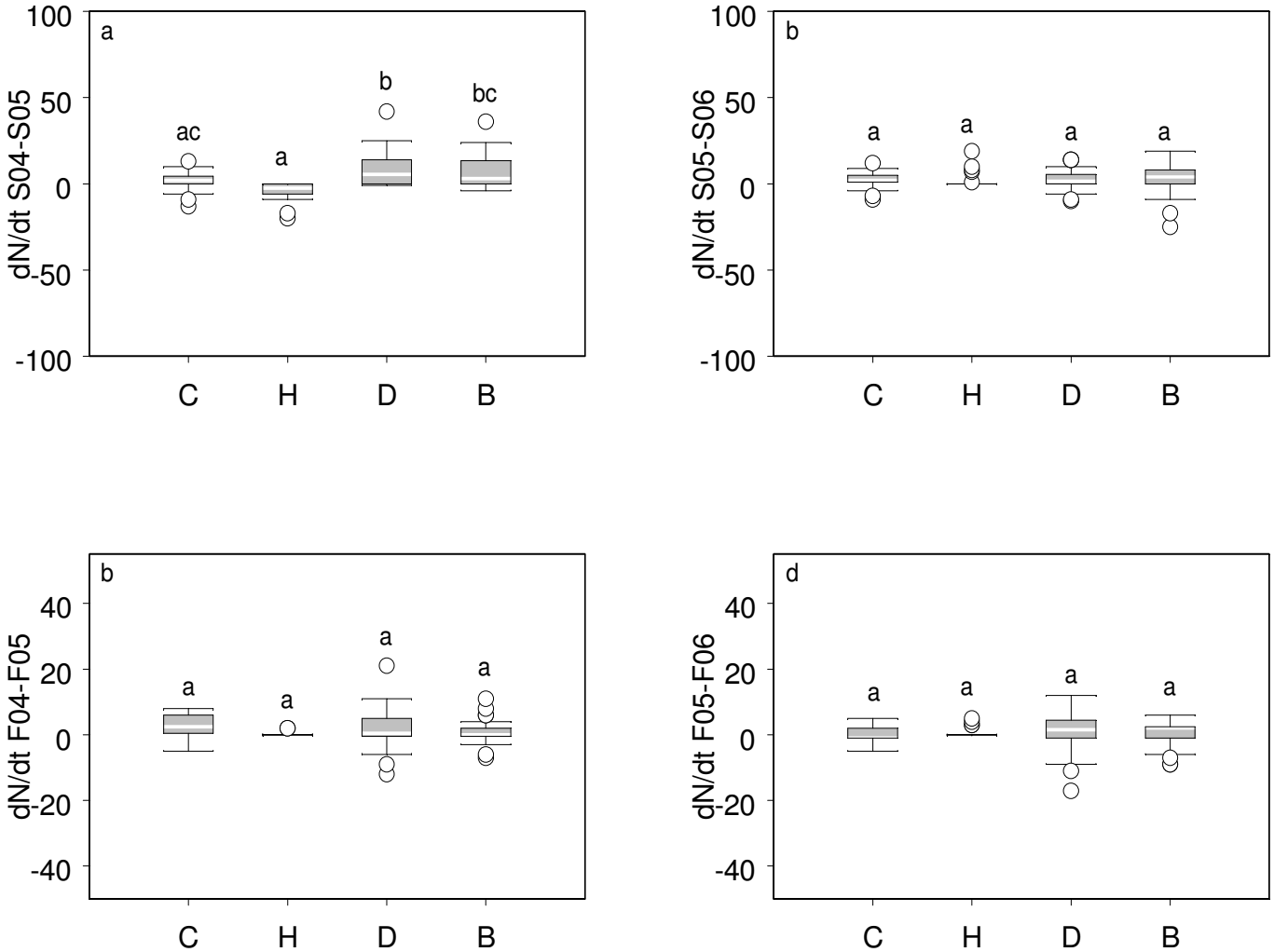

Figure 4.15. *Linaria vulgaris* growth rates (δN/δt) for Wildfire Site Outside plots for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments. C=Control, H=Herbicide, D=Dig, B=Burn. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

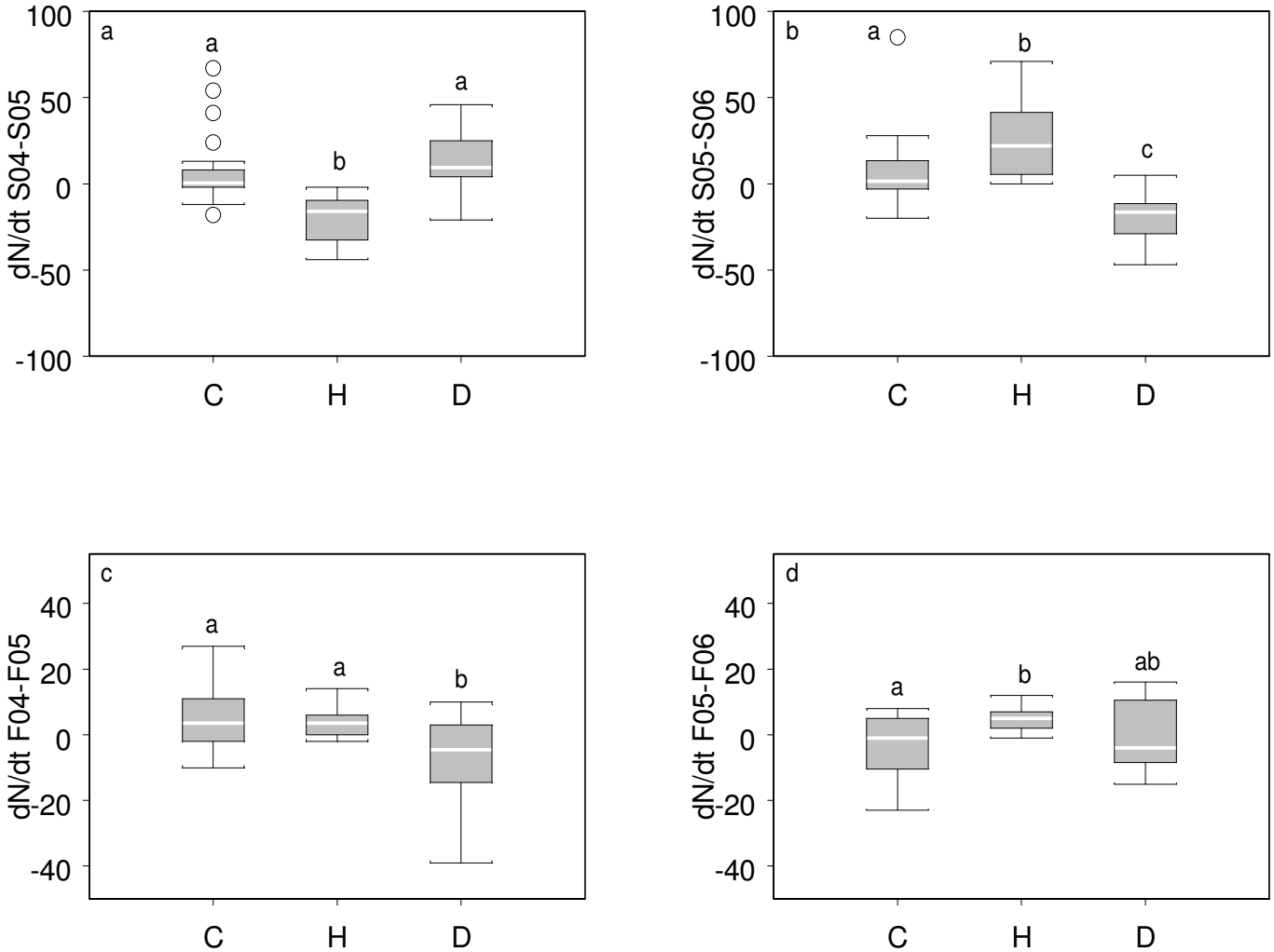

Figure 4.16. *Linaria vulgaris* growth rates (δN/δt) for Riparian Site Edge plots for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments. C=Control, H=Herbicide, D=Dig, B=Burn. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

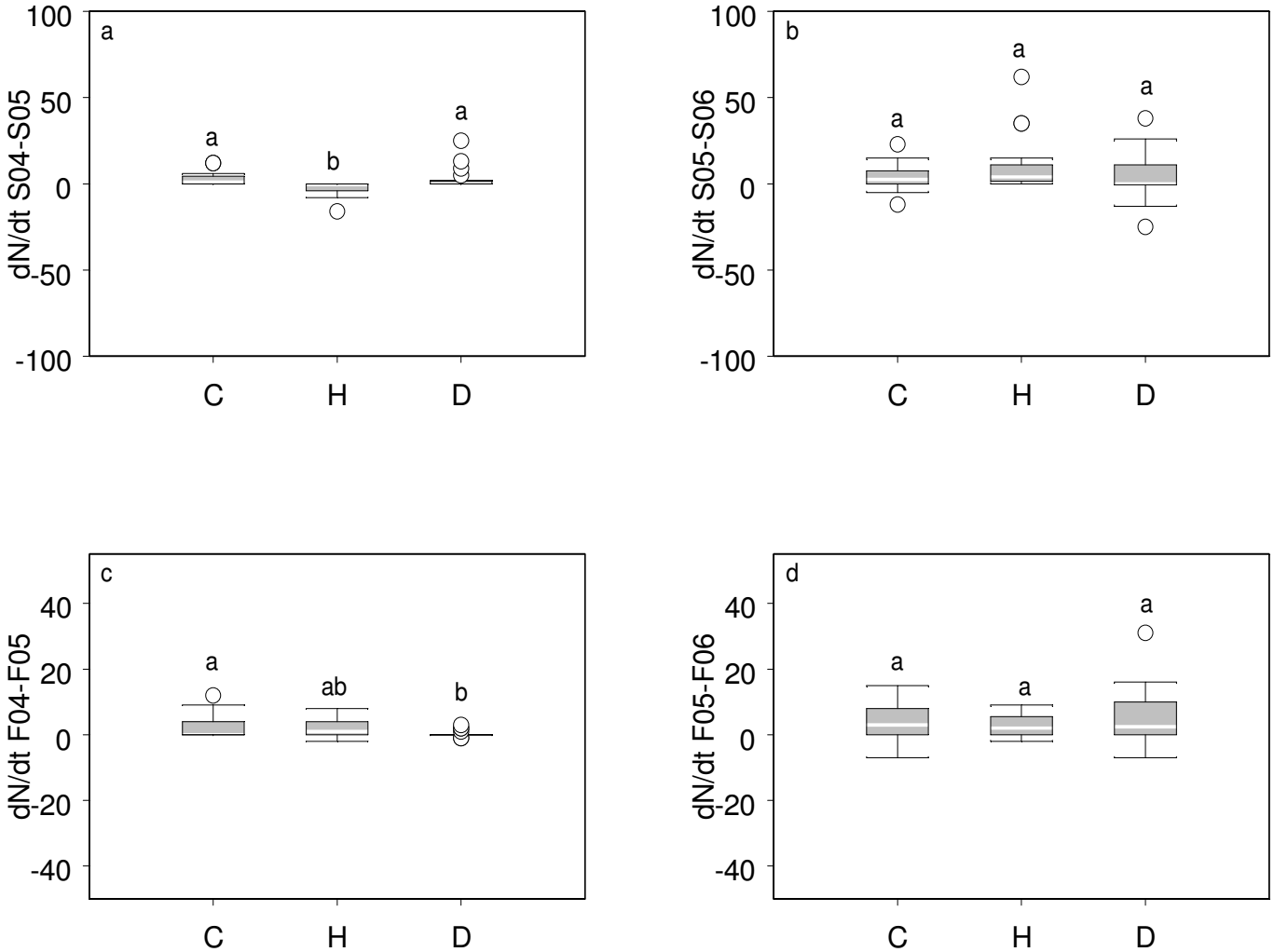

Figure 4.17. *Linaria vulgaris* growth rates (δN/δt) for Riparian Site Outside plots for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments. C=Control, H=Herbicide, D=Dig, B=Burn. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

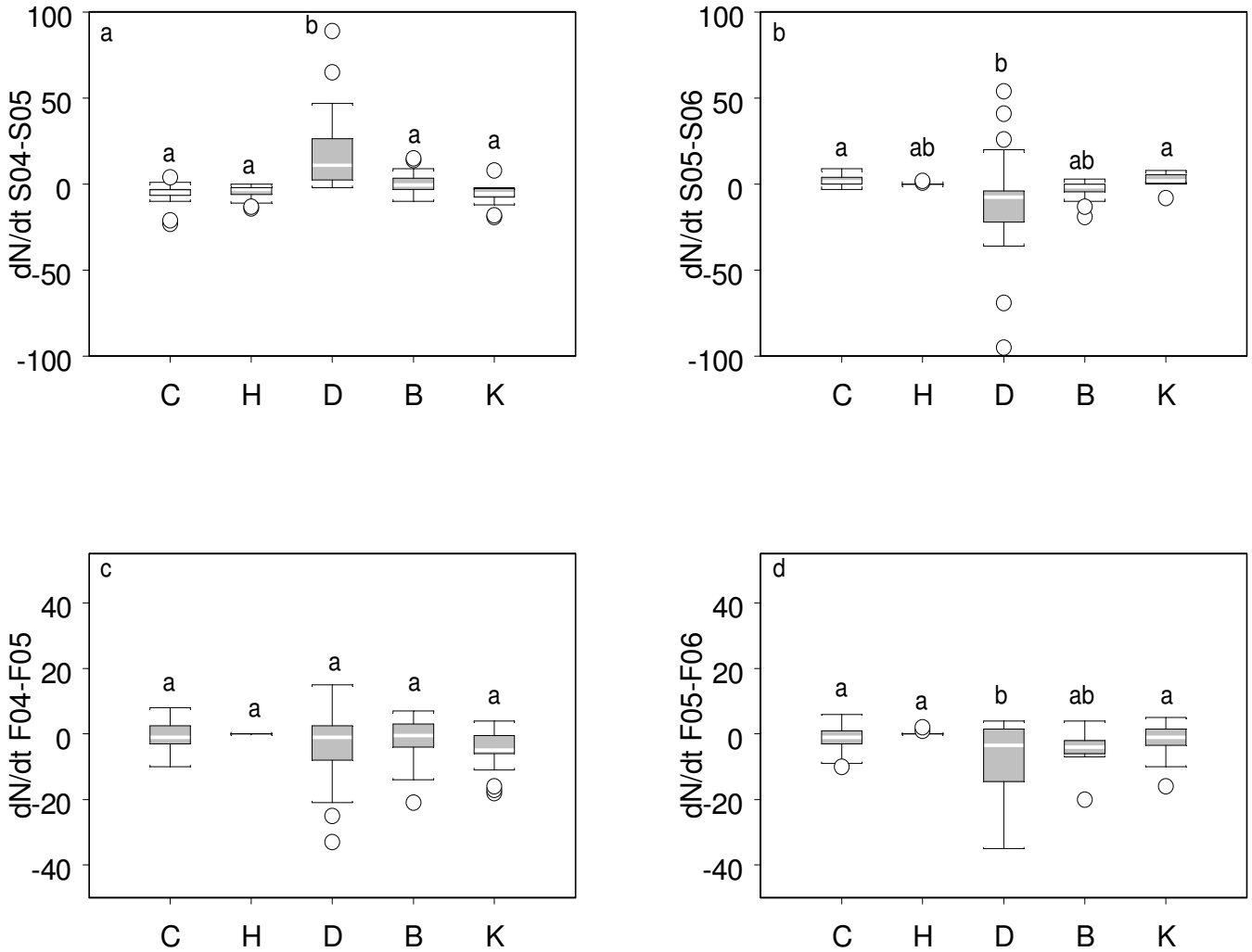

Figure 4.18. *Linaria vulgaris* growth rates (δN/δt) for Meadow Site Edge plots for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments. C=Control, H=Herbicide, D=Dig, B=Burn. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

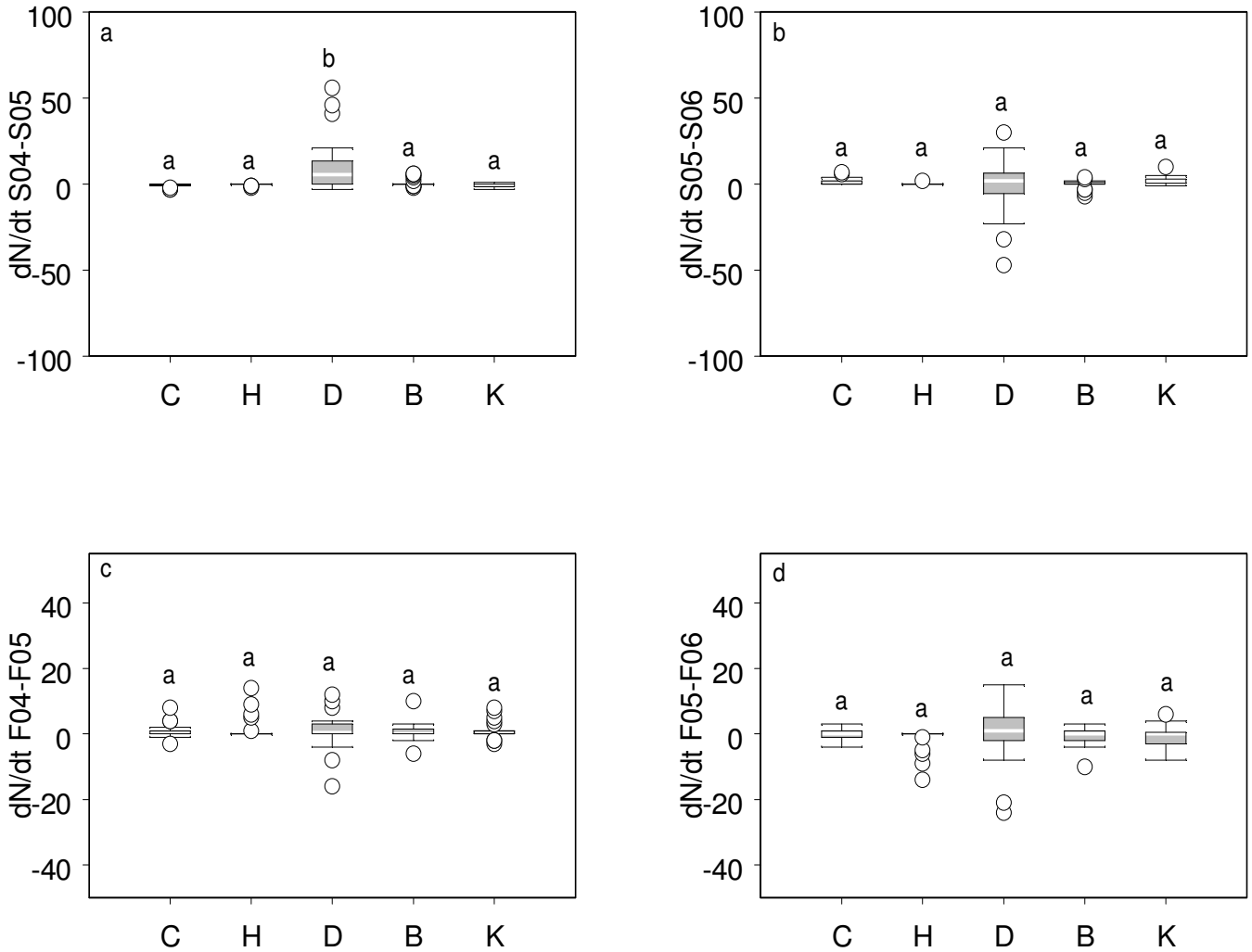

Figure 4.19. *Linaria vulgaris* growth rates (δN/δt) for Meadow Site Outside plots for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006 for all treatments. C=Control, H=Herbicide, D=Dig, B=Burn. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons.

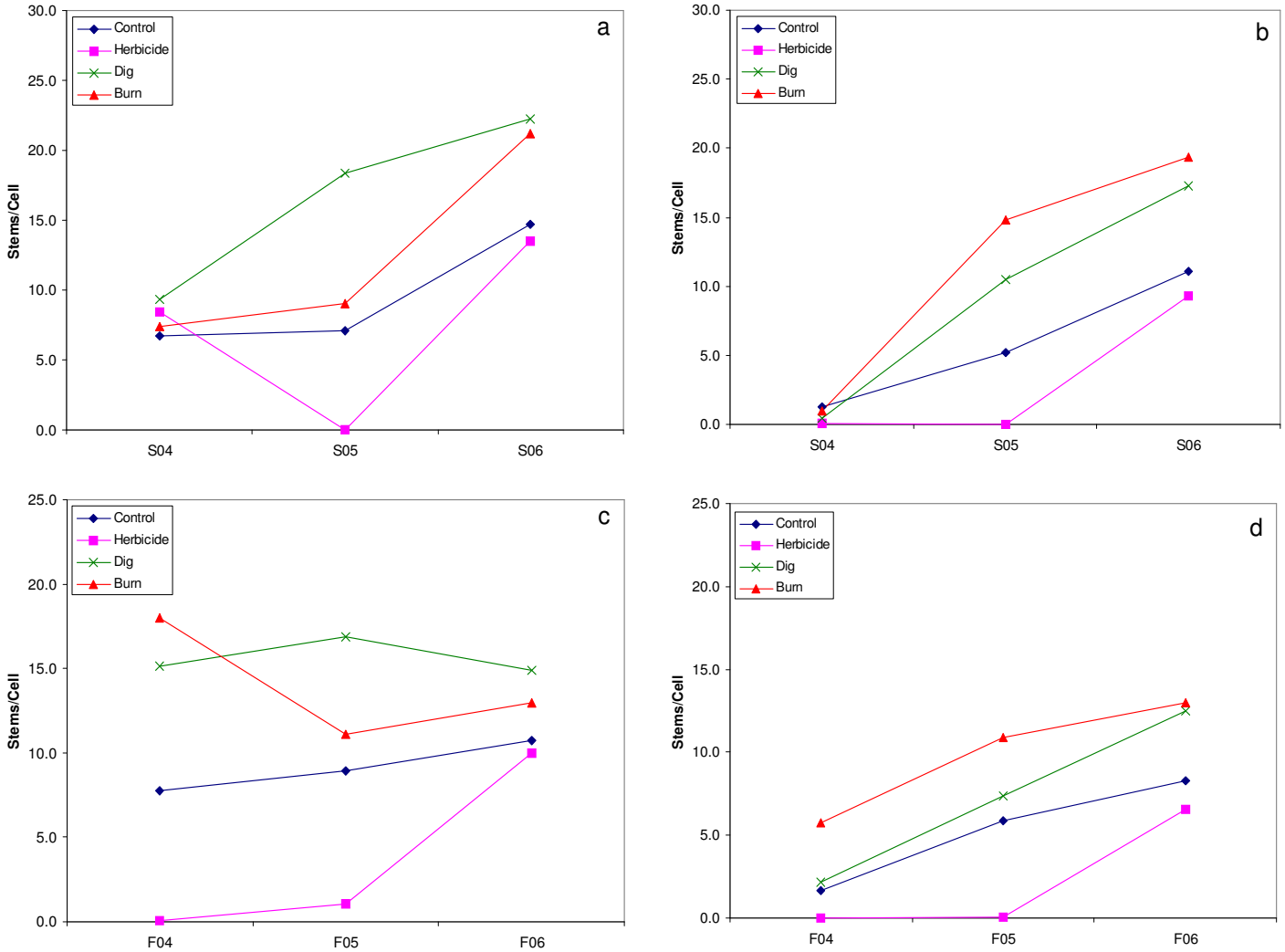

Figure 4.20. *Linaria vulgaris* stem counts over time for Clearcut Site (a) spring Edge plots, (b) spring Outside plots, (c) fall Edge plots and (d) fall Outside plots. S04=Spring 2004, S05=Spring 2005, S06-Spring 2006, F04=Fall 2004, F05=Fall 2005, F06-Fall 2006.

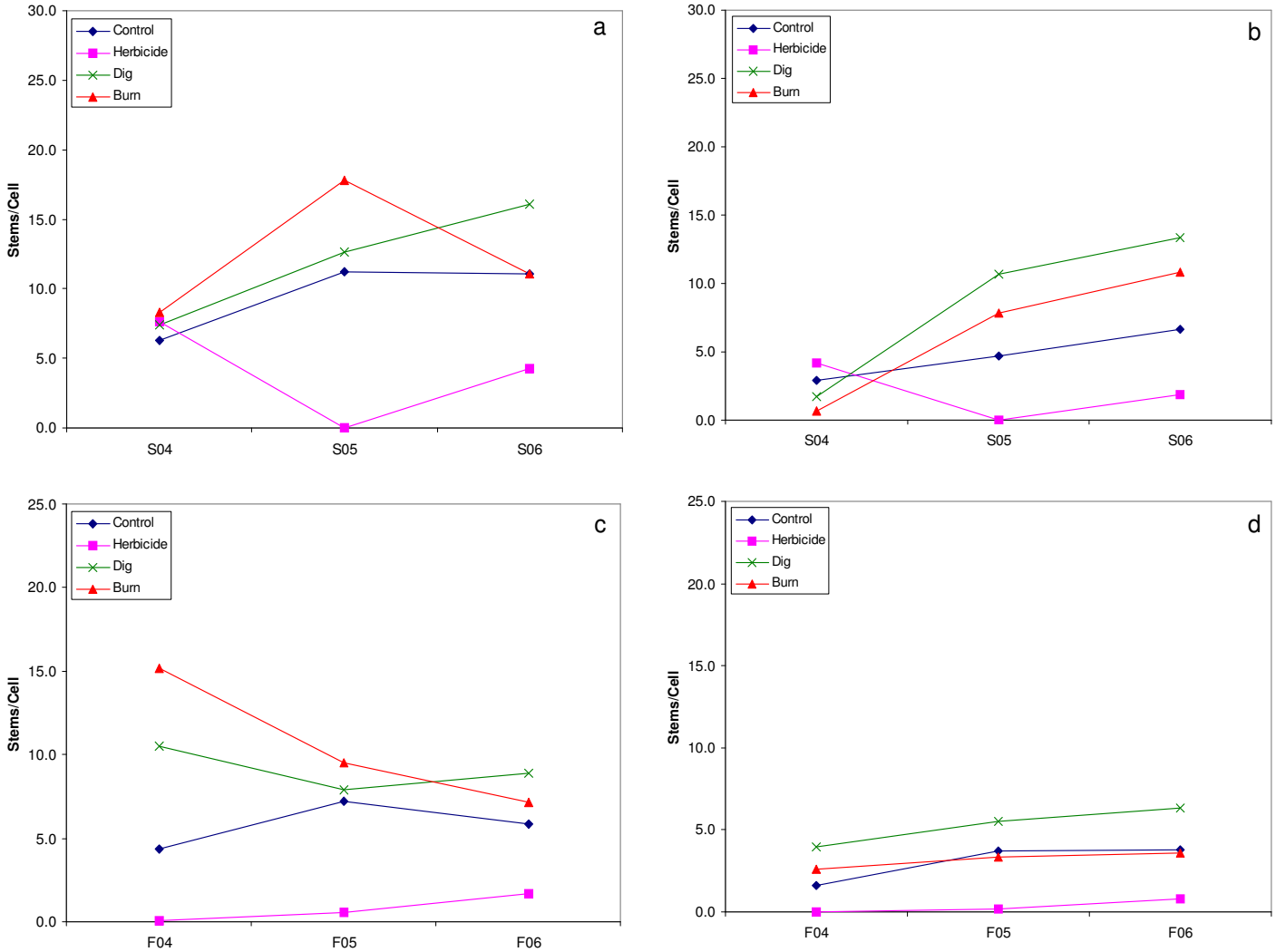

Figure 4.21. *Linaria vulgaris* stem counts over time for Wildfire Site (a) spring Edge plots, (b) spring Outside plots, (c) fall Edge plots and (d) fall Outside plots. S04=Spring 2004, S05=Spring 2005, S06-Spring 2006, F04=Fall 2004, F05=Fall 2005, F06-Fall 2006.

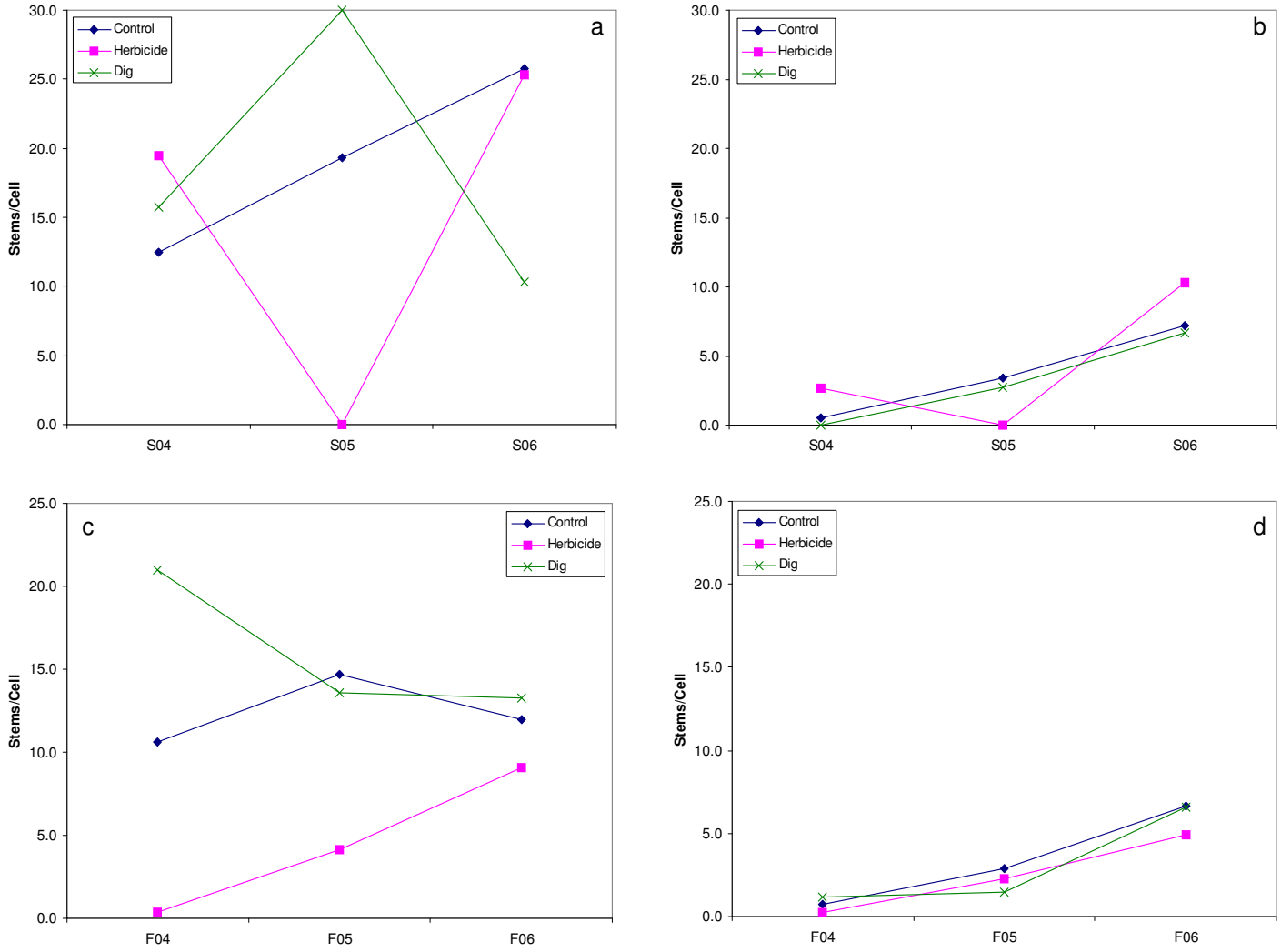

Figure 4.22. *Linaria vulgaris* stem counts over time for Riparian Site (a) spring Edge plots, (b) spring Outside plots, (c) fall Edge plots and (d) fall Outside plots. S04=Spring 2004, S05=Spring 2005, S06-Spring 2006, F04=Fall 2004, F05=Fall 2005, F06-Fall 2006.

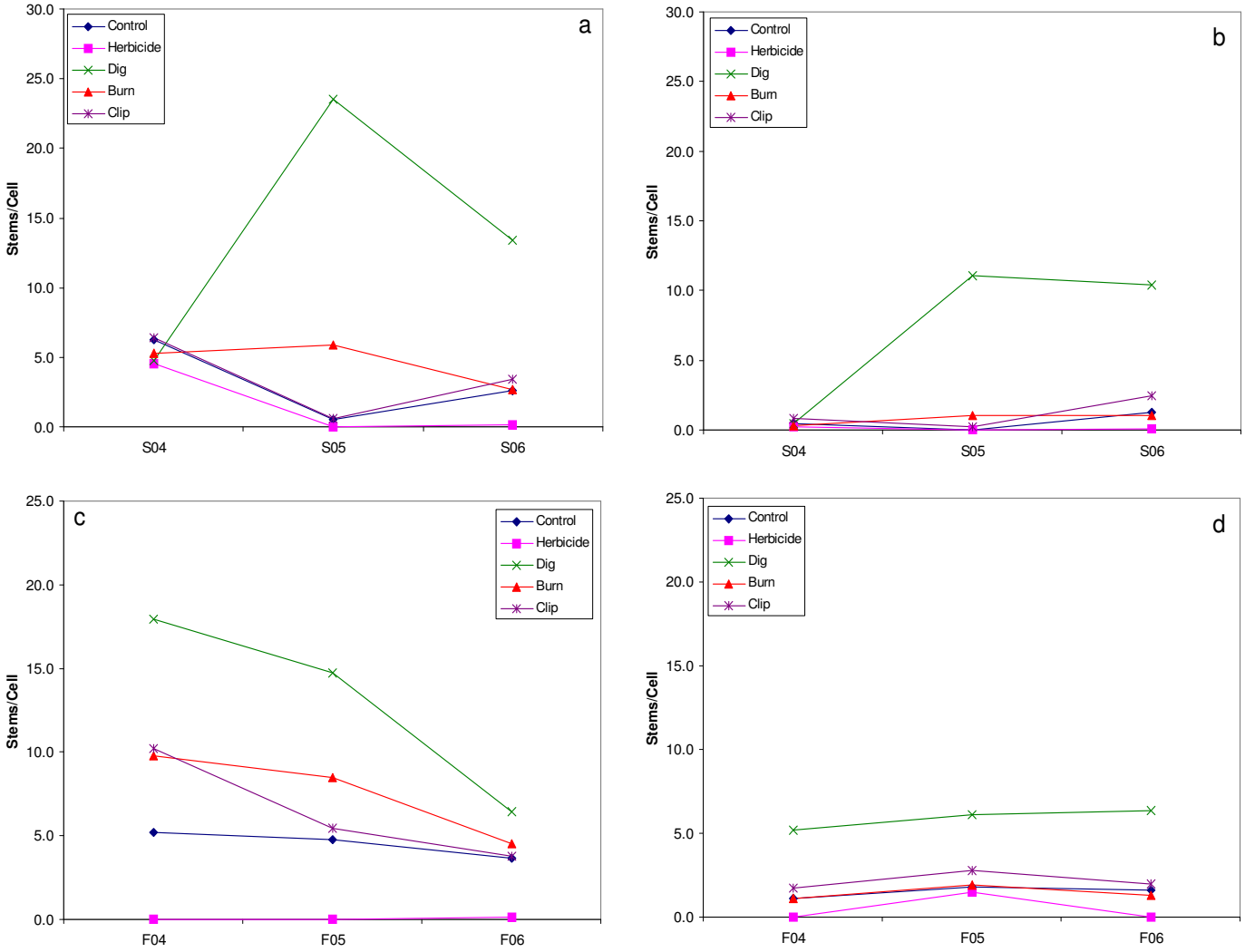

Figure 4.23. *Linaria vulgaris* stem counts over time for Meadow Site (a) spring Edge plots, (b) spring Outside plots, (c) fall Edge plots and (d) fall Outside plots. S04=Spring 2004, S05=Spring 2005, S06-Spring 2006, F04=Fall 2004, F05=Fall 2005, F06-Fall 2006.

Invasiveness Index

Population invasiveness was calculated from changes in stem density and changes in cell occupancy within plots over a period of one year. The possible range of the Invasiveness Index was from -4 to +4. Values of zero (or very near to zero) indicate a population in equilibrium, while positive or negative values indicate invasive or declining populations, respectively. Invasiveness values are presented in Figure 4.24 which shows population invasiveness for each treatment and site over each of the four time periods. Note that error bars are not included on the graphs because the method for calculating invasiveness uses all density and occupancy values for a given time period to obtain a single value of invasiveness. Tabulated invasiveness data are included in Appendix B.

For the time period of spring 2004 – spring 2005 (initial response to treatment), Undisturbed control populations at the Clearcut, Riparian and Wildfire Sites were slightly invasive, with an invasiveness of around 1, while the Meadow Site populations were in decline with an invasiveness of -2. Populations treated by digging and burning exhibited invasive values slightly higher than the Control populations, with the exception of burning at the Meadow Site, which resulted in an invasiveness of near zero. The Herbicide treatment resulted in populations that were declining at all Sites (Figure 4.24).

During the period of fall 2004 – fall 2005 (year following treatment), most populations were slightly invasive. Exceptions to this generalization are the Control and Clip treatments at the Meadow which resulted in invasiveness values near zero, the Dig treatment at the Riparian Site also resulting in an invasiveness value near zero, and the Burn treatment at the Wildfire Site that resulted in a slightly negative invasiveness value.

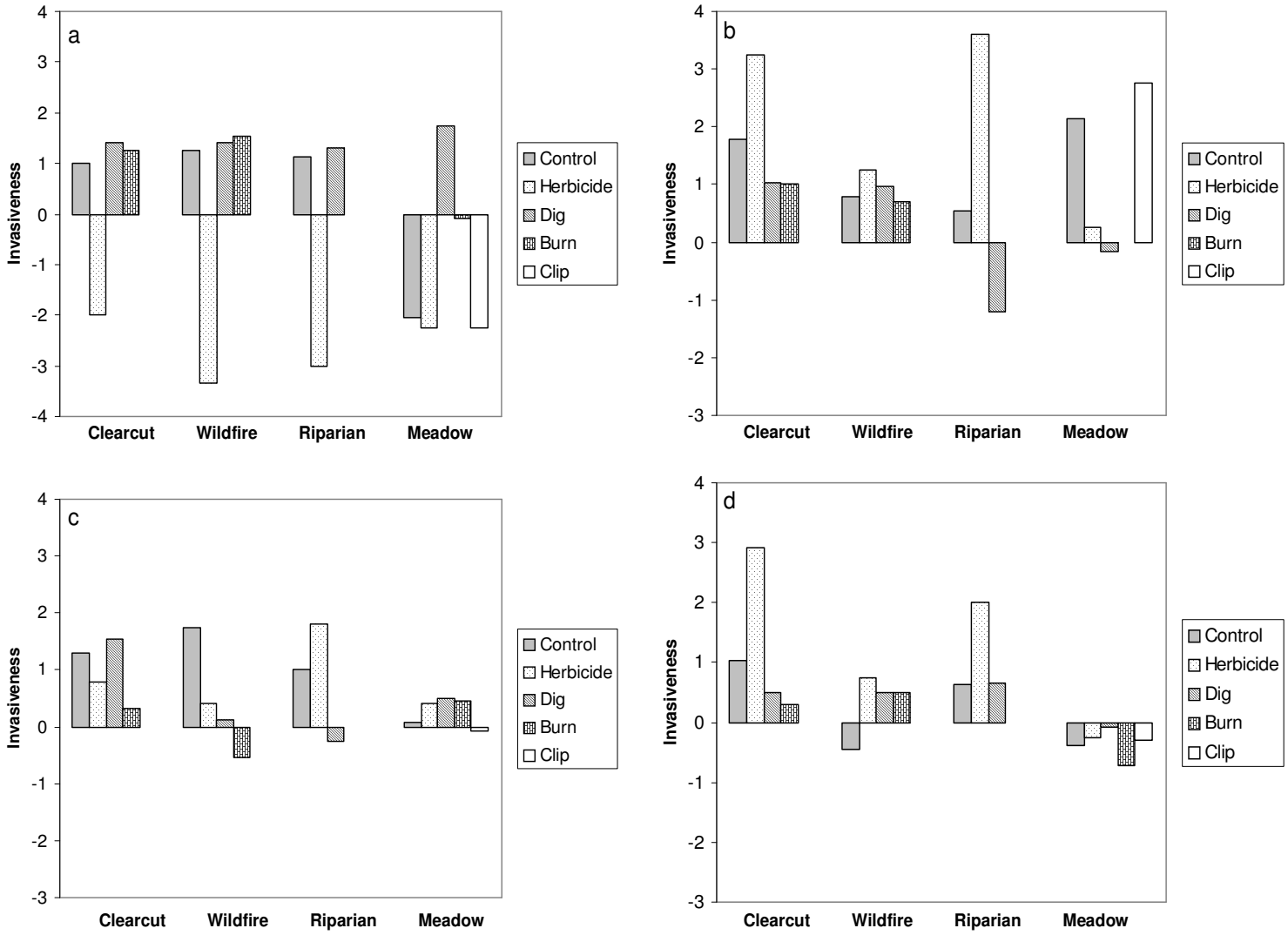

Figure 4.24. Invasiveness Index for *Linaria vulgaris* for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006. Values greater than zero indicate increasing populations and values less than zero indicate declining populations.

Invasiveness values calculated from stem counts from spring 2005 – spring 2006 (full year following treatment) were generally positive and higher than previous time periods. Populations in the Clearcut and Meadow Sites that received herbicide applications were particularly invasive with values greater than three. The Control and Clip treatments in the Meadow Site also resulted in moderately high invasiveness values. All other treatments resulted in slightly invasive populations, except for the Burn, Dig and Herbicide treatments in the Meadow which showed populations near equilibrium, and the Dig treatment at the Riparian Site which produced populations slightly in decline.

A similar trend was observed with the data from fall 2005 to fall 2006, with the exception that all treatments in the Meadow resulted in population in equilibrium or slightly in decline. At the other sites, the Herbicide treatments produced the highest value of invasiveness, particularly at the Clearcut and Riparian Sites where invasiveness values were approximately 3 and 2, respectively. Other treatments resulted in populations that were slightly invasive, or near equilibrium, with the exception of the Control treatment at the Wildfire Site, which resulted in a population slightly in decline.

Correlation Between Invasiveness Index and λ

An objective of this part of the study was to determine whether quantifying invasiveness through the simple method of calculating an index that incorporates both change in population area and density provided similar results to the traditional calculation of population growth rate (λ). This was done by comparing the Invasiveness Index and λ for each time period using Pearson's correlation coefficient. The Pearson's

correlation coefficients for spring 2004 – spring 2005, fall 2004 – fall 2005, spring 2005 – spring 2006 and fall 2005 – fall 2006 were 0.81, 0.92, 0.72 and 0.86, respectively. Plots of λ versus Invasiveness Index are included in Figure 4.25.

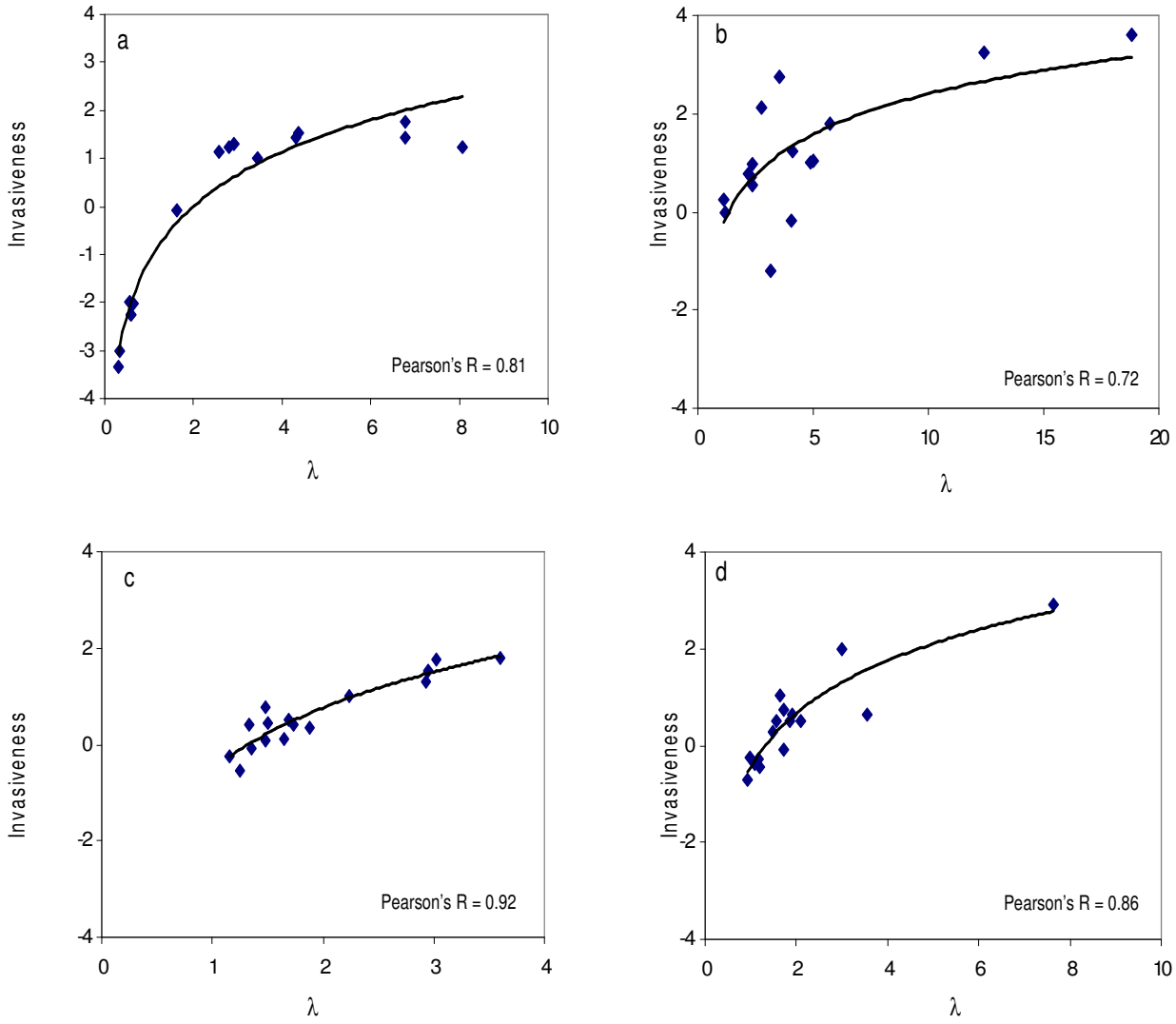

Figure 4.25. Correlation between *Linaria vulgaris* invasiveness and growth rate (λ) for (a) spring 2004 – spring 2005, (b) spring 2005 – spring 2006, (c) fall 2004 – fall 2005 and (d) fall 2005 – fall 2006. Pearson's correlation values are based on all treatments.

Soil Properties and Invasiveness

Soil sample analysis indicated differences in physical properties of soils from the four sites. Soil textures at the Clearcut, Meadow, Riparian and Wildfire Sites were found to be sandy loam, silty loam, sandy loam / loamy sand, and sandy loam, respectively. Texture and textural class results for the soil samples are presented in Table 4.2 and Figure 4.26. The Meadow soil had the highest moisture content (34 %) while the Wildfire soil had the lowest moisture content (13 %). Soil moisture contents at the Clearcut and Riparian Sites were between those of the Meadow and Wildfire soil, and not significantly different from each other based on Tukey-Kramer multiple comparisons (Figure 4.27a). The Meadow soil had significantly less coarse fragments (9 %) than the other 3 sites which were not significantly different from each other (Table 4.3 and Figure 4.27b).

Laboratory analysis also showed differences in chemical properties of the soils (Table 4.4). The Meadow soil had a significantly higher level of potassium (482 mg/kg) than the Clearcut (141 mg/kg) and Wildfire (147 mg/kg) which were not significantly from each other. The Riparian soil (246 mg/kg) was significantly different from the others (Figure 4.27c). Electrical conductivity values followed a somewhat similar trend, except the Meadow (0.06 mmhos/cm) had the highest, the Wildfire (0.02 mmhos/cm) had the lowest, and the Clearcut (0.04) and the Riparian (0.04) were not different from each other (Figure 4.27d). The Clearcut (7.7 mg/kg) and Meadow (6.7 mg/kg) had the highest levels of organic matter followed by the Riparian (4.7 mg/kg) and Wildfire (2.2 mg/kg) soils which were not significantly different from each other (Figure 4.28a). The Clearcut

(18.4 mg/kg) and Wildfire (12.4 mg/kg) had the highest concentrations of phosphorus with the Riparian (10.6 mg/kg) and Meadow (5.6 mg/kg) being lower and not different from each other (Figure 4.28b). The Clearcut soil had the lowest pH (5.2) and the Wildfire (6.3) soil had the highest with the Meadow (6.0) and Riparian (5.8) falling between (Figure 4.28c). The Meadow (71 mg/kg) had the highest level of PMN, followed by the Clearcut (20 mg/kg) and the Riparian (32 mg/kg) which were not significantly different from each other, and then the Wildfire (6 mg/kg) (Figure 4.28d).

Table 4.2. Mean sand, silt and clay percentages and textural class values for soils from each site (n=5 per site). Standard deviations are in parentheses.

Site	Sand (%)	Silt (%)	Clay (%)	Textural Class[1]
Clearcut	72 (0.6)	22 (1.2)	6 (0.9)	SL
Meadow	21 (2.2)	62 (3.7)	17 (1.8)	SiL
Riparian	75 (4.4)	17 (3.9)	8 (1.7)	SL/LS
Wildfire	71 (0.9)	18 (2.6)	11 (1.8)	SL

[1]SL = sandy loam, SiL = silty loam, LS = loamy sand

Table 4.3. Mean moisture content and coarse fragment content of soil for each site (n=5 per site). Standard deviations are in parentheses.

Site	Moisture Content (%)	Coarse Fragments (%)
Clearcut	21.9 (4.8)	28.4 (8.4)
Meadow	34.0 (3.8)	9.1 (9.9)
Riparian	19.4 (4.4)	37.8 (11.3)
Wildfire	13.3 (0.6)	31.2 (12.1)

Table 4.4. Mean soil data for each site (n=5 per site) from Montana State University soil laboratory. Standard deviations are in parentheses.

Site	K (mg/kg)	EC (mmhos/cm)	OM (mg/kg)	P (mg/kg)	pH	PMN (mg/kg)
Clearcut	140.8 (19.9)	0.04 (0.01)	7.7 (2.7)	18.4 (5.6)	5.2 (0.4)	19.8 (7.8)
Meadow	482.4 (18.7)	0.06 (0.01)	6.7 (0.8)	5.6 (1.2)	6.0 (0.1)	71.1 (11.3)
Riparian	245.6 (65.1)	0.04 (0.01)	4.7 (0.5)	10.6 (2.0)	5.8 (0.2)	32.1 (11.9)
Wildfire	146.8 (31.8)	0.02 (0.00)	2.2 (0.3)	12.4 (4.4)	6.3 (0.1)	5.8 (2.3)

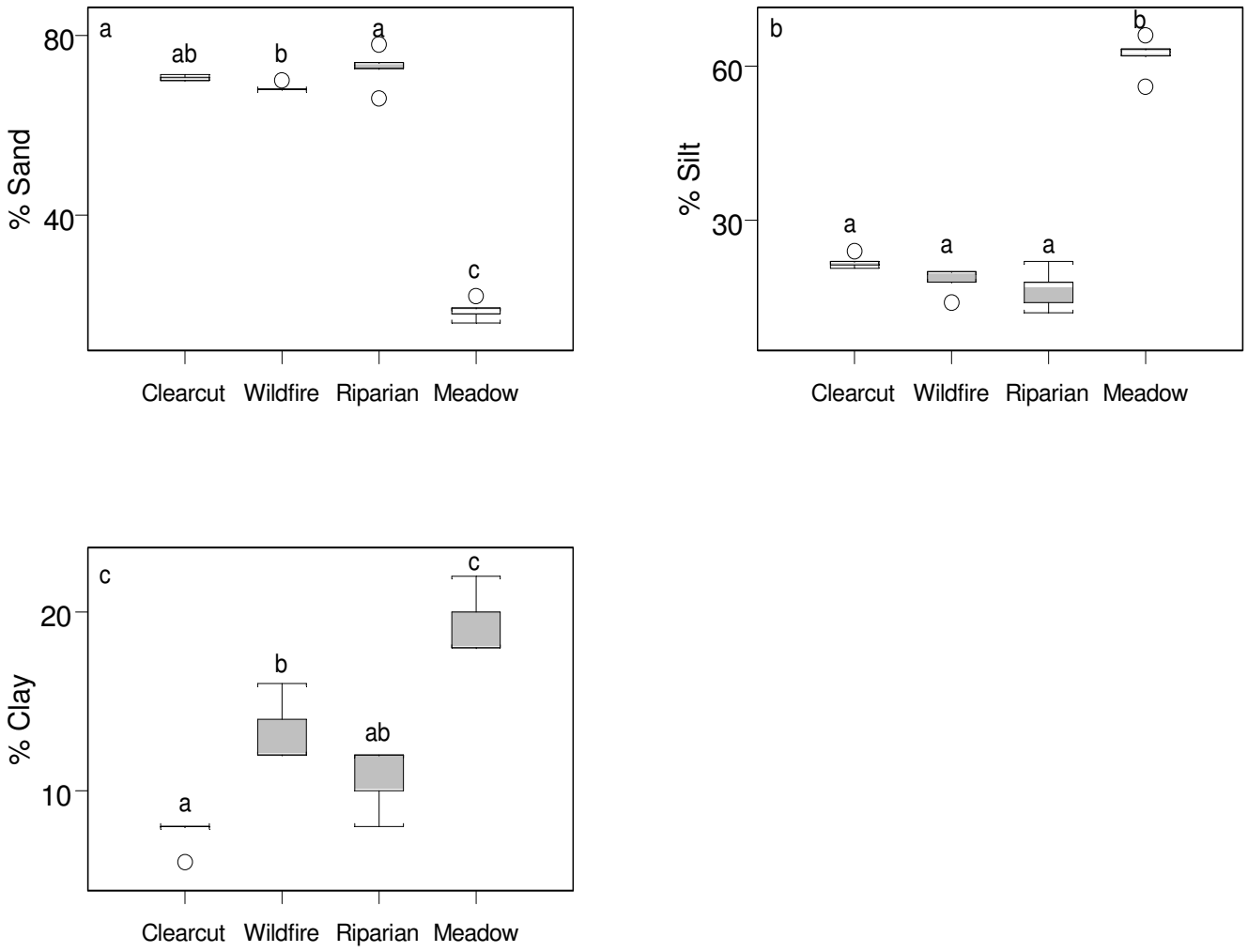

Figure 4.26. Soil texture differences in (a) % sand, (b) % silt and (c) % clay at each site. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons. N = 5 per site.

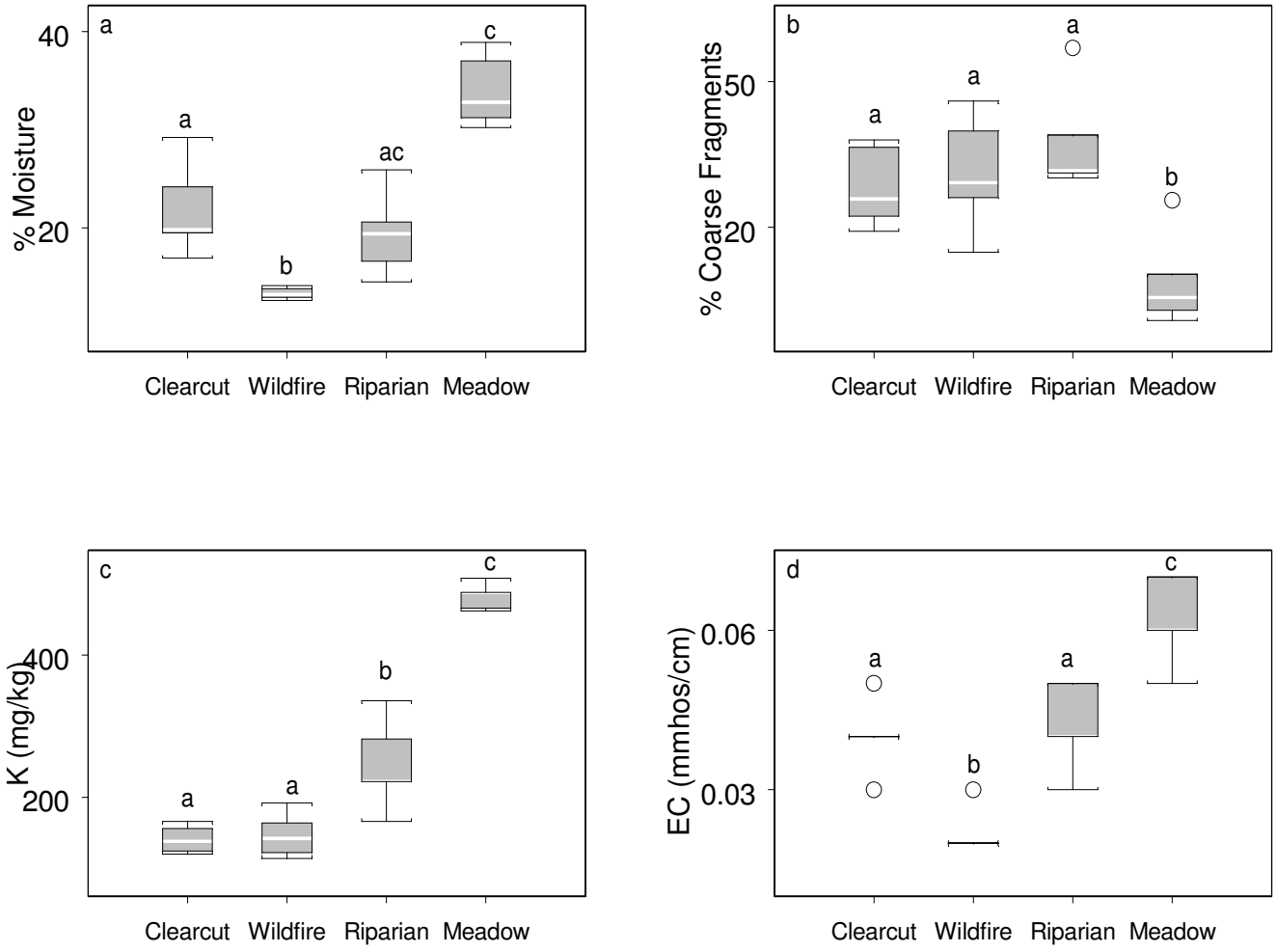

Figure 4.27. Differences in (a) % moisture, (b) % coarse fragments, (c) potassium (K) and (d) electrical conductivity (EC) at each site. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons. N = 5 per site.

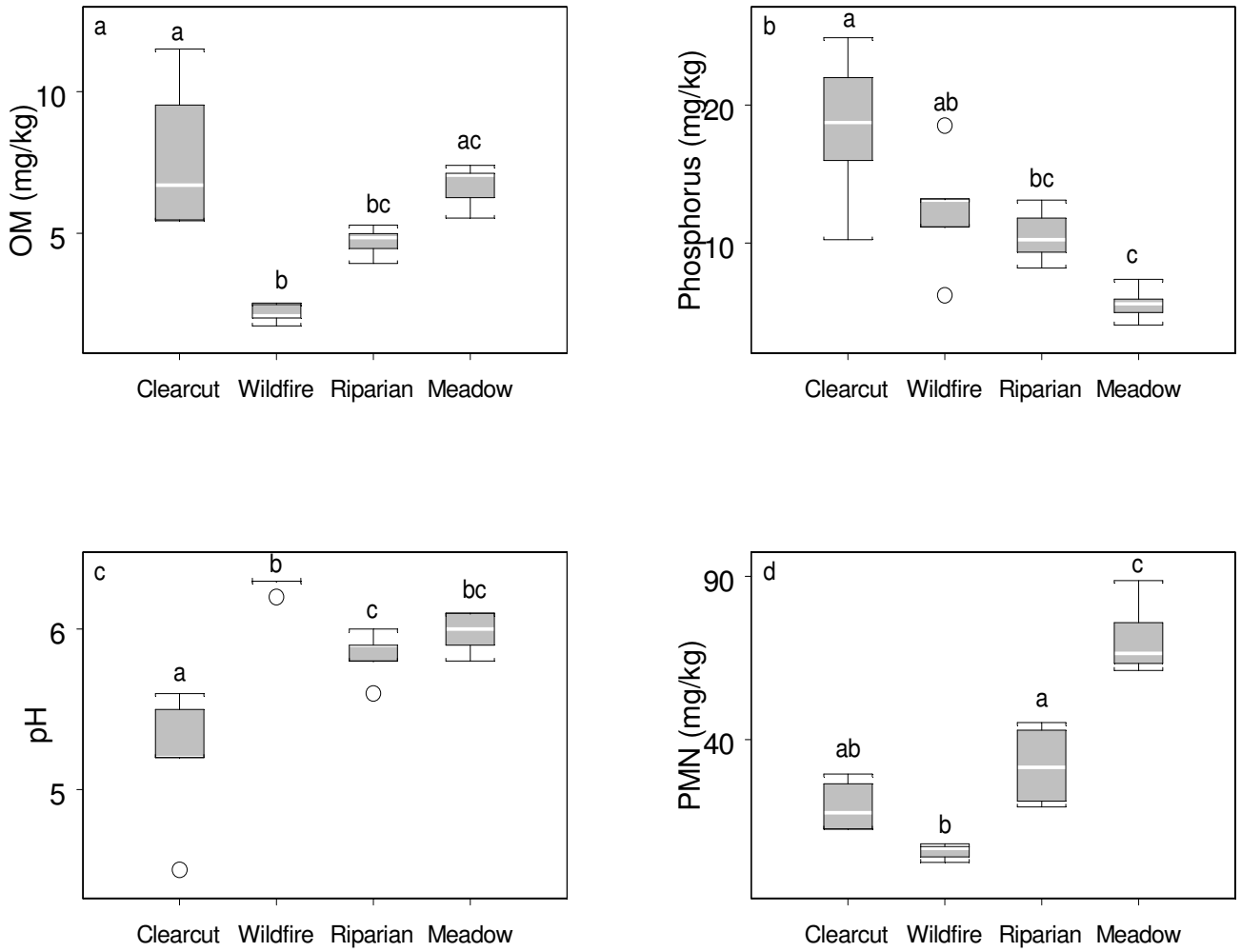

Figure 4.28. Differences in (a) organic matter (OM), (b) Phosphorus (P), (c) pH and (d) potentially mineralizable nitrogen (PMN) at each site. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons. N = 5 per site.

Discussion

L. vulgaris Population Response to Disturbance

Plot Position Differences. An objective of this research was to determine how *L. vulgaris* populations responded to disturbance, both in terms of population expansion and change in population density. The disturbances tested were burning, soil disturbance via digging, clipping of vegetation and application of herbicide.

All treatments, including the untreated Control, generally resulted in expanding populations ($\lambda > 1$ and Invasiveness > 0). That is, outside plots that initially had few *L. vulgaris* plants within them, had higher growth rates and became more populated during the course of the study. Growth rates within edge plots were significantly lower than in outside plots, though generally still positive. Exceptions to this include the Dig treatment at the Wildfire and Riparian Sites, and the Control and Burn treatments and the Meadow Site, which produced negative growth rates during some time periods. Growth rates within interior plots, which were all Control plots, varied from strongly positive to strongly negative, with overall growth rates at each site being approximately in equilibrium or slightly positive.

Lower growth rates within interior, and to some extent, edge plots may be explained by density dependence (Hutchings 1997). *L. vulgaris* often grows in dense stands, as was true for the populations studied, and such dense growth could be responsible for growth rates near equilibrium. In contrast, higher growth rates in the edge plots may have resulted from the lack of intraspecific competition in these plots. This effect was somewhat tempered at the nonnative grass dominated Meadow because of the

much greater interspecific competition at that site (see Chapter 5 for more details on species richness, diversity and percent cover across sites).

L. vulgaris Growth Across Environments. An additional objective was to evaluate how *L. vulgaris* population response to treatments differed across environments. At the Meadow Site, treatments resulted in lower growth rates than the other sites and the lowest invasiveness values. Populations at the Clearcut Site responded most vigorously to treatments, resulting in high growth rates and elevated invasiveness values. Riparian and Wildfire Site population response to treatments was generally between that of the Meadow and Clearcut Sites, although populations were still invasive. The different population performance at the four sites, here measured by the Invasiveness Index, may be explained by the idea of a habitat suitability gradient across which a species has varying levels of vigor (Grinnell 1928; Gause 1934; Hutchinson 1957; Hutchinson 1959). Based on this notion, one would expect that if sites are different from one another in terms of precipitation, temperature, slope, aspect and soil properties, then plant populations may have different growth rates, and different responses to disturbance. The Clearcut, Riparian and Wildfire Sites all had similar slope, aspect and elevation, while the Meadow Site was slightly higher in elevation and had a more northerly aspect. Soil properties for the first three sites are similar, except the Clearcut Site had higher levels of organic matter and P. The Meadow Site had higher levels of K, PMN, moisture and EC, and lower levels of P than the other sites. Soil textures were also significantly different. The Meadow soil was finer textured than the other sites with more silt and clay and less sand. Regression analysis showed EC, PMN and percent silt to be negatively related to

$\delta N/\delta t$ in some years while percent sand was positively related. The negative response of $\delta N/\delta t$ to low sand and high silt content in the soil was consistent with the literature (Saner et al. 1995), which states that *L. vulgaris* performs better in coarse, well-drained soils. Overall, however, results did not show any trends that could consistently explain site differences in invasiveness. There could, however be other soil properties or interactions that help to explain differences in invasiveness. These possibilities were not explored further, though, because they have limited usefulness in terms of *L. vulgaris* management (with further research, however, soil analysis data may be useful for understanding variability in *L. vulgaris* population growth).

Effects of Specific Treatments. Another objective of this research was to determine how *L. vulgaris* populations responded to specific types of disturbance. A somewhat surprising result was that the Dig, Burn and Clip treatments generally did not produce λ and $\delta N/\delta t$ values that were significantly different from the control treatment (Figures 4.12 – 4.19). An even more interesting result is that the application of herbicide often led to higher λ and $\delta N/\delta t$ values and more invasive populations the second year following treatment. The fact that herbicide application increased λ can somewhat be explained simply by the formula used to calculate λ (i.e., $\lambda = N_{t+1}/N_t$). In the year after application of the herbicide, the populations declined. As *L. vulgaris* began to re-grow, it was doing so in plots with very few individuals. Thus, any re-growth would result in a large value of λ. The same is true for the calculation of the Invasiveness Index, which is based on change in density and cell occupancy within plots. The higher $\delta N/\delta t$ values and

the higher stem counts within plots cannot be so easily explained, however. In the Clearcut and Riparian Sites (Figures 4.20 and 4.22) the stem counts have risen to well above their pre-herbicide application numbers and in some cases to levels greater than in the Control and Dig plots. At the Wildfire Site, *L. vulgaris* stem density in plots treated with herbicide did not surpass the density in plots that received other treatments, but was rising at a faster rate as indicated by the slopes of the lines (Figure 4.21). At these sites, the application of herbicide effectively eliminated all native forbs, possibly allowing for the vegetative re-growth of *L. vulgaris* in a competition free environment. Only at the Meadow Site was herbicide application effective at reducing *L. vulgaris* density and keeping it low (Figure 4.23). The success of herbicide in the Meadow can likely be attributed to the dense populations of grass (primarily the non-native species *Poa pratensis*) that formed a near monoculture after the application of herbicide. The grass in these plots may effectively out-compete *L. vulgaris* and prevent re-infestation as has been show with spotted knapweed (*Centaurea maculosa*) and leafy spurge (*Euphorbia esula*) after herbicide treatment (Sheley et al. 2000; Rinella and Sheley 2005).

Management Considerations

While the literature on *L. vulgaris* response to disturbance is sparse, it does generally indicate that the species responds favorably to burning (Saner et al. 1995; Lajeunesse 1999), soil disturbance (Nadeau et al. 1992) and grazing (Lajeunesse 1999). Initial results of *L. vulgaris* re-growth after experimental disturbances in this study seem to generally agree with the literature. However, in the years following treatment, there were no significant differences in growth rates between the treated plots and controls.

Thus, it seems that any decision to manage *L. vulgaris* populations following disturbance cannot be justified on the premise that the disturbance will result in more invasive populations. These results were, however, limited to the area of the study, which may be approaching the temperature limits for vigorous *L. vulgaris* growth (pers. obs.). More importantly than dictating when one should or should not manage *L. vulgaris* in this study area, the results suggest variability in population growth and invasive potential, and thus illustrate the necessity of monitoring to determine a population's invasiveness before management decisions are made.

Another important treatment effect identified in the research is the fact that herbicide application resulted in increased *L. vulgaris* population growth rates and invasiveness in the second year after treatment. This result may be dismissed by land managers, because it is already known that repeat applications of herbicide are necessary to control *L. vulgaris* (Lajeunesse 1999). These results do, however, speak to the importance of continued monitoring of *L. vulgaris*, or other NIS populations, even for more than one year following herbicide treatment. This is especially important in rangeland and forest situations, where remote populations of NIS may be identified and sprayed, but the location not permanently marked for follow-up monitoring or treatment.

Invasiveness Index as a Tool for Management

As discussed in Chapter 3, the Invasiveness Index can be a useful tool for assessing NIS population invasiveness. As demonstrated through this research, the Invasiveness Index captures the essence of the spatial and temporal population dynamics of a plant population through a simple annual count of stems within permanently marked

plots. Unlike λ, which can also be calculated from such counts, the Invasiveness Index provides information on both change in population density and area occupied. The Invasiveness Index also quantifies invasiveness within the range of -4 to +4, whereas λ can theoretically range from 0 to infinity. This research has also shown that the invasiveness of NIS populations varies depending on habitat suitability. Land managers can take advantage of this fact by calculating invasiveness values for populations in different environments, and then prioritizing management by environment based on these values.

CHAPTER 5

IMPACTS OF *LINARIA VULGARIS* AND DISTURBANCE ON NATIVE VEGETATION

Introduction

Non-indigenous species (NIS) are often cited as a major cause of plant extinctions and community change (Mack et al. 2000; Mooney and Cleland 2001; Hooper et al. 2005). There is still debate, however, about the relative importance of NIS compared to anthropogenic factors (Gurevitch and Padilla 2004; MacDougall and Turkington 2005) and disturbance in general. NIS can locally replace existing species, creating a structurally less complex plant community (Huenneke et al. 1990; Lavergne et al. 1999; Lambrinos 2000) while disturbance serves as a major force structuring plant communities (Gleason 1926; Connell 1978; Huston 1979; Pickett and White 1985).

Reported impacts of NIS on native plant communities are broad, including loss of native vegetation, reduced recruitment and growth rates of endemic plants and reduced biodiversity, as illustrated by the following examples. Non-native grasses such as cheatgrass (*Bromus tectorum*) have replaced native vegetation and altered the fire cycle in western United States deserts and shrublands (D'Antonio and Vitousek 1992). Seedling recruitment of a California endemic, Antioch Dunes evening primrose (*Oenothera deltoids*), was limited by the presence of a non-native grass (Thomson 2005). Similarly, Huenneke and Thompson (1995) found that seedlings and rosettes of the NIS teasel (*Dipsacus sylvestris*) had negative effects on the growth of the rare Mescalero thistle (*Cirsium vinaceum*). In a Mediterranean-type shrubland in California, invasion by

jubata grass (*Cortaderia jubata*) created a structurally less complex perennial grassland that was depauperate of native shrub species (Lambrinos 2000). In contrast to these findings, however, several authors have shown that NIS do not have a major impact on biodiversity (PlantyTabacchi et al. 1996; Lonsdale 1999; Sax et al. 2002; Gurevitch and Padilla 2004).

The effects of disturbance on plant communities are equally important. Disturbance is any discrete event in time, natural or otherwise, that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (Pickett and White 1985). More specifically, in terms of plant growth, disturbance can be thought of as a process that creates bare ground, loose soil, or light gaps which constitute microsites for new plant recruitment (Crawley 1997). Disturbance may also free up resources, reduce competition and create empty niches that other plants, including NIS can occupy (Elton 1958; Hobbs 1989; Rejmanek 1989; Hobbs and Huenneke 1992; Burke and Grime 1996).

It is difficult, however, to separate the effects of disturbance (especially habitat alteration) from those of NIS invasion as the two may be inextricably linked. Often the issue is not NIS causing the decline of native plants, but rather the decline of natives and the proliferation of NIS are both the result of anthropogenic disturbance (Gurevitch and Padilla 2004). These interrelated effects cannot be teased apart through observational studies where there is no control (i.e., no undisturbed but invaded areas for comparison).

Three common metrics for comparing plant communities are relative species abundance (RSA) distributions, species richness and diversity. Relative species

abundance distributions, also known as diversity or rank distributions, plot the dominance of a species (as number of individuals or percent cover) against the species rank (in terms of commonness). This plot provides a continuous distribution from dominant species through intermediate to rare species, and plots can be compared to examine temporal or spatial differences in communities (Whittaker 1965). Species richness is simply the number of different species that are present in an area. Knowing how many species are present is useful, but richness measures provide no information about how evenly species are distributed in the community. Diversity indices incorporate both richness and evenness. Two such diversity measures are the Simpson and the Shannon-Weiner indices. The Simpson index is a measure of the concentration of species in an area and is most influenced by the common species, while the Shannon-Weiner index is a measure of the uncertainty of species presence and is influenced by rare species (Dejong 1975).

This part of the research sought to understand how the NIS *Linaria vulgaris* impacts existing plant communities and how the plant communities respond to disturbances – specifically herbicide, digging, burning and clipping. Each of the metrics described above was used in this chapter to evaluate community differences and community changes initiated by disturbance.

Materials and Methods

Site Descriptions

This study was conducted at four sites within the Gallatin National Forest near West Yellowstone, Montana. The sites included an area that was logged in the mid

1980's (Clearcut), a site that burned in 1988 (Wildfire), a low-lying area adjacent to the South Fork Madison River and Hebgen Lake (Riparian) and a natural meadow (Meadow). These sites are described in detail in Chapter 2.

Plot Establishment

While this part of the research examined the effects of disturbance on the existing plant community, it was part of a larger study which evaluated the effects of disturbance on *L. vulgaris* population dynamics. Therefore, all plots were established within the interior, on the edge, or just outside of patches of *L. vulgaris*. Establishing plots on the edge and just outside of *L. vulgaris* patches made possible the assessment of the plant community with and without the presence of *L. vulgaris*. It should be noted that this study did not assess the effect of *L. vulgaris* on strictly native vegetation, as many of the plots were established in areas that were dominated by other NIS, particularly Kentucky bluegrass (*Poa pratensis*).

At the Clearcut, Wildfire, Riparian and Meadow Sites, there were 53, 53, 35, and 66 plots, respectively. All plots were 0.25 m^2, and were established in June 2004. More information regarding plot establishment is in Chapter 4 and a summary of plot information is provided in Table 4.1.

Experimental Treatments

Treatments included the application of the broadleaf herbicide Picloram (Tordon*K^{TM}) (Herbicide), digging (Dig) to represent disturbance by burrowing animals, burning (Burn), vegetation clipping (Clip) to simulate grazing and no treatment (Control).

Treatments were randomly assigned to plots and implemented in June 2004. More information regarding the treatments is presented in Chapter 4.

Plot Monitoring

Plots were monitored in June 2004 before any treatments were implemented. Plots were monitored again in the fall of 2004, and then in spring and fall of 2005 and 2006, and in the spring of 2007. At each monitoring period, the percent cover of each species, as well as percent cover of litter and bare ground was estimated to the nearest one percent for each plot.

Data Analysis

Measures of *L. vulgaris* Impact. Assessing *L. vulgaris* impact on the extant plant community was not directly possible without knowledge of the community before invasion (i.e., did *L. vulgaris* invasion change the community, or did some property of the community such as reduced richness facilitate invasion?). However, the experimental design was set up such that monitoring plots were placed in areas of *L. vulgaris* patches with different stem densities (interior, edge and just outside of patch). Thus, community differences in terms of richness and diversity, with respect to *L. vulgaris* density, were evaluated through ANOVA based on the plot positions. Also species richness and diversity were analyzed as functions of *L. vulgaris* cover through regression.

Measures of Site Differences. Several metrics, including RSA distributions, species richness and diversity and percent cover values were used to assess plant

community differences between sites. Relative species abundance distributions for each site, generated in R (version 2.3.1) with the package LabDSV (Roberts 2006), were used to compare species distributions and diversity between sites. Percent cover values from spring 2004 (prior to treatments) were used as the abundance measures for the RSA distributions, and data from all plots within a site – treatment combination were pooled.

Measures of site diversity, including the Simpson and Shannon-Wiener diversity indices, were also calculated in R with the package Vegan (Oksanen et al. 2005), using percent cover via the following formulas:

Simpson Diversity = D = $\sum p_i^2$

Shannon-Weiner Diversity = H = $-\sum[p_i \ln(p_i)]$

where: p_i is the proportion of the individuals in the ith species ($p_i = n_i/N$)
N is the total number of individuals sampled

Diversity values presented are the mean values from all plots at a site and within a given treatment. For the Simpson index, the presented values are 1-D, such that increasing values represent greater diversity.

Species lists, with species ranked by abundance, were compiled for each site using the spring 2004 pre-treatment data. Finally, analysis of variance (ANOVA) was performed to quantify site differences of percent bare ground, percent litter cover and percent plant cover (excluding *L. vulgaris*) within plots, and Tukey-Kramer multiple comparisons were used to examine site differences in these properties (S-PLUS 2000, Mathsoft, Inc.). R code generated for calculating diversity and RSA distributions is included in Appendix C.

Measures of Effects of Treatments on Plant Communities. Plant community changes were assessed by evaluating changes in the RSA distributions (based on log abundance), richness and Simpson's diversity at each site and for each treatment. Ranked species lists were used to track changes in the abundance of individual species prior to, and subsequent to the disturbances. Only data from spring counts were used for calculations because these data provided more reliable species identification and density results. The fall data were less consistent in terms of species percent cover and even species identification and presence because in some years drought or early frosts caused premature senescence of some species (relative to other years), and therefore could obscure community response differences.

Results

Impacts of *L. vulgaris* on Plant Community

Overall ANOVA showed differences between sites, so individual sites were evaluated separately. ANOVA results indicated that in spring 2004 prior to disturbance there were no significant differences in species richness between inside, edge and outside plots at the Clearcut, Wildfire and Riparian Sites ($P > 0.05$). At the Meadow Site, edge plots had greater richness than outside plots ($P = 0.002$), however, the difference was only one species, and this is accounted for by the fact that *L. vulgaris* was present in edge plots but generally not present in outside plots. ANOVA results also showed that there were no diversity differences between plot positions for the Clearcut and Wildfire Sites ($P > 0.05$). For the Riparian Site, diversity was lower in the interior plots (which were

dominated by *L. vulgaris*) than in edge or outside plots (P = 0.005) and in the Meadow Site, outside plots (where *L. vulgaris* presence was minimal) had the lowest diversity (P = 0.03).

ANOVA indicated significant differences in *L. vulgaris* cover by plot position. At the Clearcut and Wildfire Sites, *L. vulgaris* cover was higher in interior and edge plots than in outside plots (P = <0.001). At the Riparian and Meadow Sites, *L. vulgaris* cover was greatest in interior plots, followed by edge and then outside plots (P < 0.001).

Linear regression analysis suggested that species richness and diversity were related to *L. vulgaris* cover at some sites. The relationship between richness and *L. vulgaris* cover was positive at the Clearcut Site (P = 0.04, R^2 = 0.08) and negative at the Wildfire Site (P = 0.01, R^2 = 0.12). There was no relationship between *L. vulgaris* cover and species richness at the Riparian and Meadow Sites. Species diversity was negatively related to *L. vulgaris* cover at the Riparian Site (P = 0.01, R^2 = 0.17) and positively related at the Meadow Site (P < 0.001, R^2 = 0.20). There was no relationship between *L. vulgaris* cover and diversity at the Clearcut and Wildfire Sites.

Analysis of RSA distributions from spring 2004 for the four sites shows differences in species distributions and diversity (Figure 5.1). The Wildfire Site has the highest diversity as indicated by the curve being farthest to the right. The Meadow Site has the lowest as indicated by the placement of the curve to the lower left. All sites had relatively similar "tails" on the RSA curves, indicating a similar number of rare species. The Clearcut, Wildfire, Riparian and Meadow Sites had mean species richness values of 3.9, 5.7, 4.3 and 4.6, respectively (Table 5.1 and Figure 5.2). Note that the richness

values obtained from the RSA curves (i.e., species rank) are not site means, but rather represent the sum of all species at the site. Also, species present at less than one percent cover do not register on the RSA plot because log (<1) is a negative number.

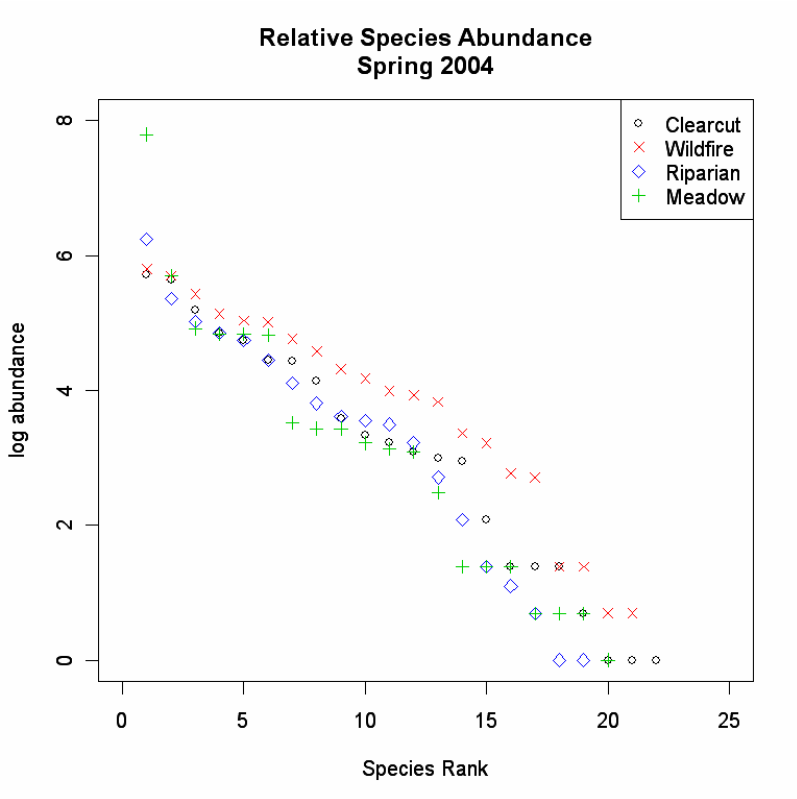

Figure 5.1. Relative species abundance distributions for all sites in spring 2004 (prior to any treatments).

Table 5.1. Richness and diversity values for all sites in spring 2004 (prior to any treatments). Standard deviations are in parentheses.

Site	Richness	Simpson Diversity	Shannon-wiener Diversity
Clearcut	3.9 (1.7)	0.49 (0.20)	0.91 (0.41)
Wildfire	5.7 (1.5)	0.62 (0.16)	1.26 (0.35)
Riparian	4.3 (1.5)	0.52 (0.20)	0.99 (0.42)
Meadow	4.6 (1.3)	0.41 (0.21)	0.81 (0.39)

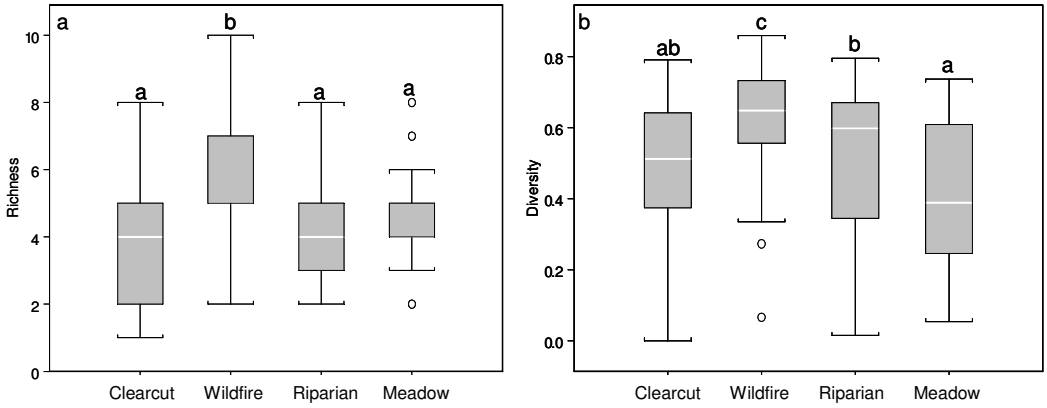

Figure 5.2. Species richness (a) and diversity (b) at each site in spring 2004 (prior to any treatments). Letters indicate significant differences ($\alpha = 0.05$) based on Tukey-Kramer method for multiple comparisons. N = 53, 53, 35 and 66 for Clearcut, Wildfire, Riparian and Meadow Sites, respectively.

The Simpson and Shannon-Wiener diversity indices showed site diversity patterns similar to those obtained from the RSA distributions (Table 5.1). Because the diversity trends are similar between sites, and because the RSA distributions do not indicate a long tail of rare species which would make the Shannon-Wiener index more appropriate, only the Simpson diversity values are presented for subsequent results.

Vegetation community differences were also apparent, based on the species lists. The top ten species, ranked by abundance (percent cover), for each site indicated that the Clearcut and Wildfire Sites had a mix of grasses and forbs, although the most dominant plant species at the Wildfire Site was moss. The Riparian Site was dominated by forbs while the dominant species at the Meadow Site was the non-native grass *Poa pratensis* (Table 5.2).

There are site differences in terms of percent cover of bare soil, vegetative cover and litter cover (Figure 5.3). The most bare soil was at the Wildfire (59 %) and Clearcut (54 %) Sites, followed by the Riparian (43 %) and then the Meadow (5 %) Sites. The pattern was reversed for vegetative cover (excluding *L. vulgaris*), with the Meadow Site (41 %) having significantly more vegetative cover than the Clearcut (10 %) Wildfire (25%) and the Riparian (25 %) Sites. Litter cover was also highest at the Meadow Site (44 %), followed by the Clearcut (22 %) and Riparian (27 %) Sites, and finally the Wildfire Site (9 %).

Effects of Treatments on Community Composition

Clearcut Site. At the Clearcut Site, both species diversity and richness declined after the Herbicide treatment and richness declined after digging (Figures 5.4a and 5.5a). Burning generally did not result in values different from the Control plots. Diversity and richness in herbicide plots increased after the initial decline, but did not return to pre-disturbance levels. Subsequent responses (after two years) to the Dig treatment were not different than in Control plots.

Relative species abundance distributions for all treatments and all years at the Clearcut Site are shown in Figure 5.6. The number as well as abundance of species declined after all treatments. Herbicide and Dig treatments resulted in precipitous drops in the number of species present while the Burn treatment resulted in a slightly lesser

Table 5.2. Ten most abundant species for all sites in spring 2004 (prior to any treatments).

Clearcut	Class[1]	Wildfire	Class	Riparian	Class	Meadow	Class
Pseudoroegneria spicatum	g, p	moss spp.	m, p	*Linaria vulgaris*	f, p	*Poa pratensis*	g, p
Linaria vulgaris	f, p	*Linaria vulgaris*	f, p	*Agoseris glauca*	f, p	*Linaria vulgaris*	f, p
bunchgrass spp.	g, p	*Eriogonum umbellatum*	f, p	*Erigeron speciosus*	f, p	*Erigeron* spp.	f, p
Poa pratensis	g, p	*Poa pratensis*	g, p	*Fragaria virginiana*	f, p	*Geranium viscosissimum*	f, p
Eriogonum umbellatum	f, p	*Collinsia parviflora*	f, a	*Carex* spp.	s, p	*Maianthemum stellatum*	f, p
Agoseris glauca	f, p	*Agoseris glauca*	f, p	*Achillea millefolium*	f, p	*Aster ciliolatus*	f, p
Antennaria microphylla	f, p	*Lupinus argenteus*	f, p	*Taraxacum officinale*	f, p	*Achillea millefolium*	f, p
Collinsia parviflora	f, a	*Carex* spp.	s, p	moss spp.	m, p	*Aster occidentalis*	f, p
Phlox spp.	f, p	*Elymus elymoides*	g, p	*Arnica* spp.	f, p	*Trifolium longipes*	f, p
Elymus elymoides	g, p	*Brassicaceae* spp.	f, p	*Collinsia parviflora*	f, a	*Carex* spp.	s, p

[1]g=grass, f=forb, m=moss, s=sedge, a=annual, p=perennial

decline. The number and abundance of species in the Burn treatment has increased over time, with spring 2007 numbers approaching the original ones, but the values have changed little for the Herbicide and Dig treatments.

The plant community responded differently to the different treatments. In the first year after treatment (spring 2005), herbicide application resulted in a shift from a grass (*P. spicatum* RSA = 4.01) and forb (*L. vulgaris* RSA = 3.93 and *E. umbellatum* RSA = 3.91) dominated community to one dominated by grasses (RSA of all grasses = 13.3 while RSA of all forbs = 1.61). Recovery was fairly rapid, however, with the forb *L. vulgaris* (RSA = 4.54) becoming dominant two years (spring 2006) after treatment, and other forbs including *A. glauca* (RSA = 1.79) and the annual plant *C. parviflora* (RSA = 0.69) appearing in the third year (spring 2007). The Dig treatment changed the community from a rich one (14 species) of mixed grasses (combined RSA = 11.94) and forbs (combined RSA = 19.15) to one containing just three forbs in spring 2005: *L. vulgaris* (RSA = 3.43), *A. ciliolatus* (RSA = 1.10) and *E. speciosus* (RSA = 0.69). This community shift persisted throughout the study period and only a few additional forbs (*A. glauca* RSA = 3.58 and *C. parviflora* RSA = 1.95) and a Carex species (RSA = 1.10) were present by spring 2007. Changes in Burn plots were similar to changes in the Control plots. Complete species lists with RSA values for each treatment and time are included in Appendix D.

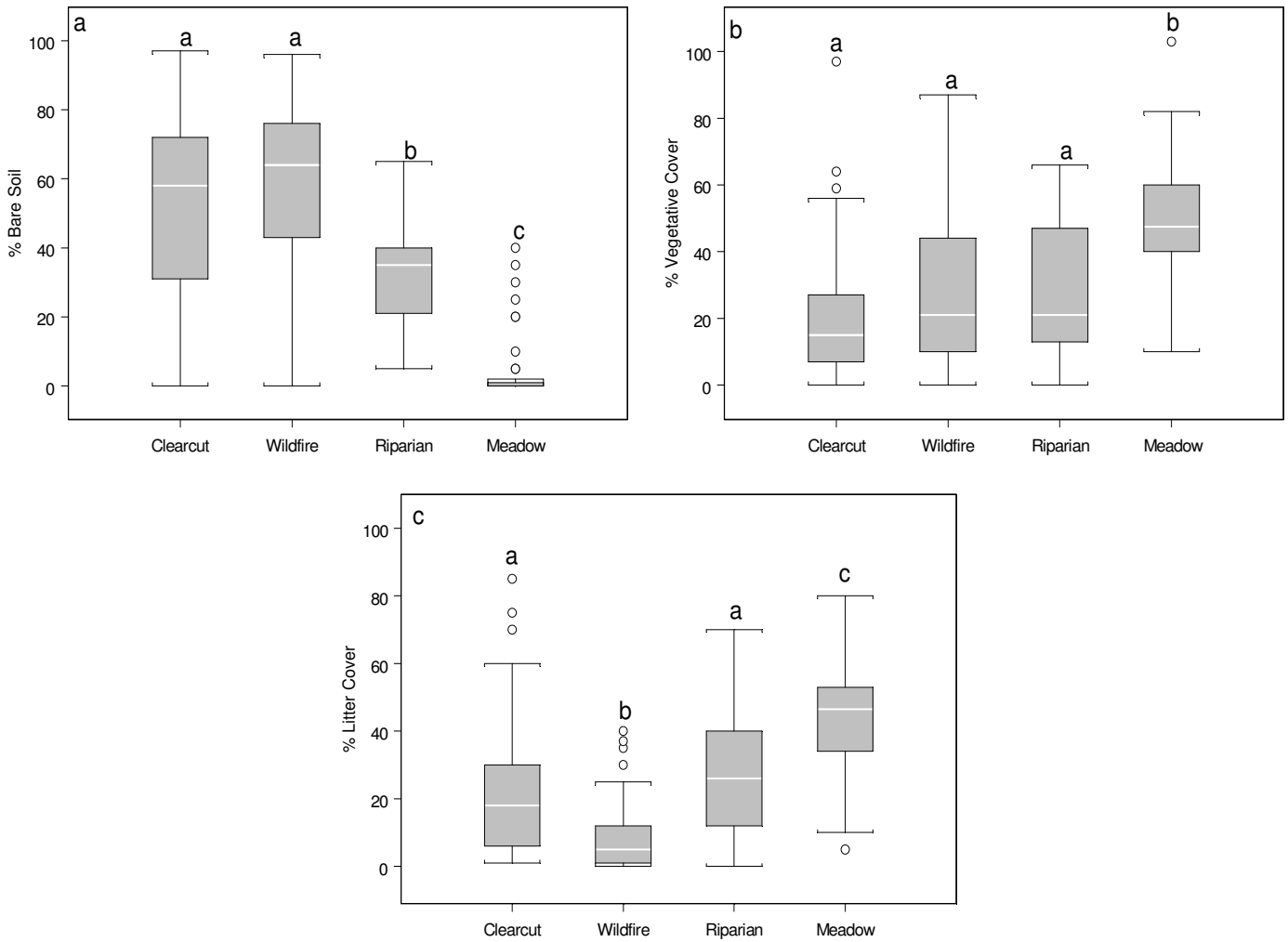

Figure 5.3. Spring 2004 values for % bare soil (a), % vegetative cover (b) and % litter cover (c) for all sites. Data are prior to any treatments at the sites. Box plots show median (central line of box, 50% of data (grey box), 95% of data (bars) and outliers (circles). Letters indicate significant differences (α=0.05) using Tukey-Kramer method for multiple comparisons. N = 53, 53, 35 and 66 for Clearcut, Wildfire, Riparian and Meadow Sites, respectively.

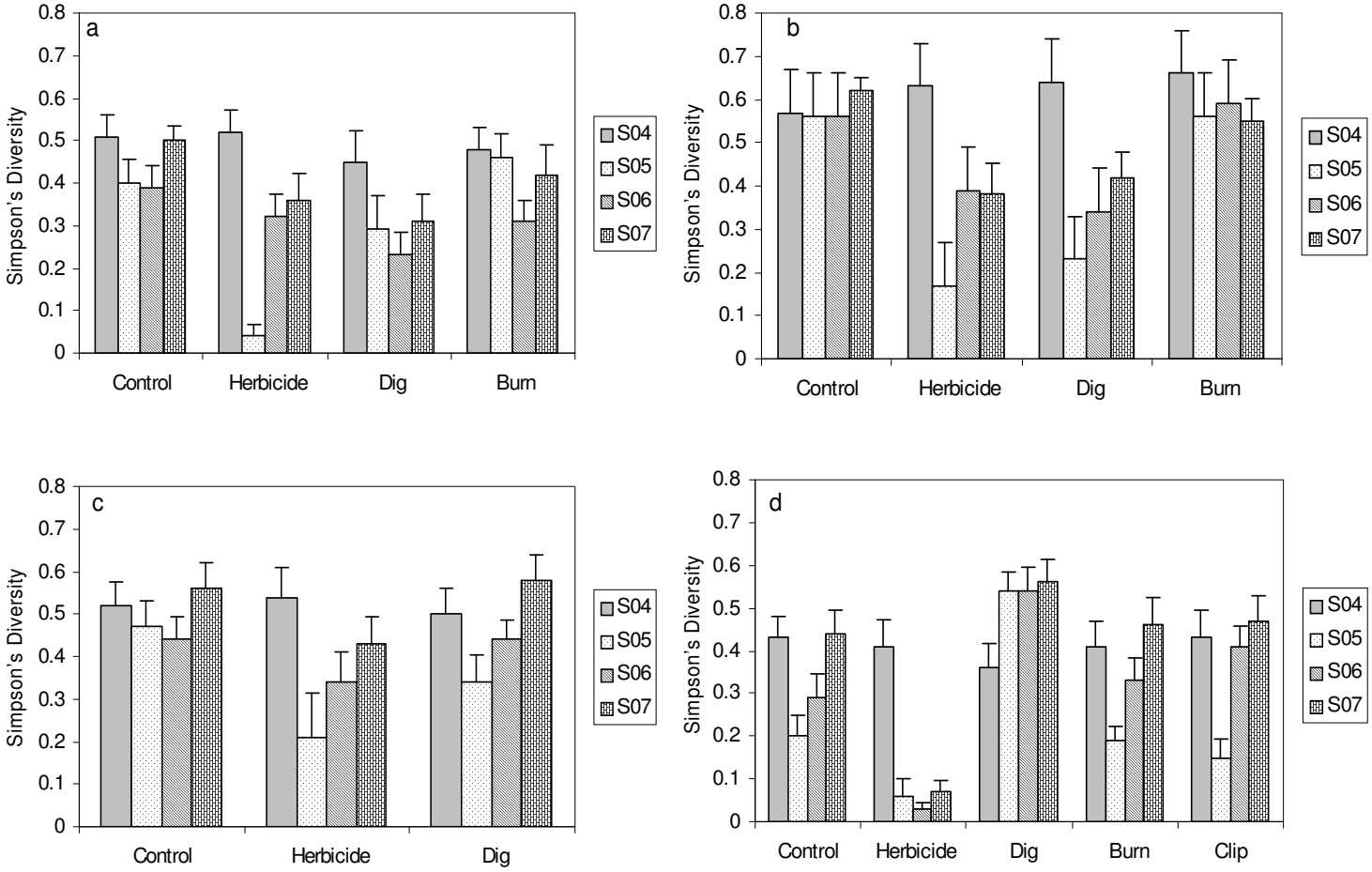

Figure 5.4. Simpson's diversity at (a) Clearcut Site, (b) Wildfire Site, (c) Riparian Site and (d) Meadow Site. S04 = spring 2004, S05 = spring 2005, S06 = spring 2006 and S07 = spring 2007. Error bars show standard error. For Clearcut and Wildfire control plots, N = 17. For Riparian control plots, N = 15. For Meadow control plots, N = 18. For other Riparian treatments, N=10. For all other treatments and sites, N = 12.

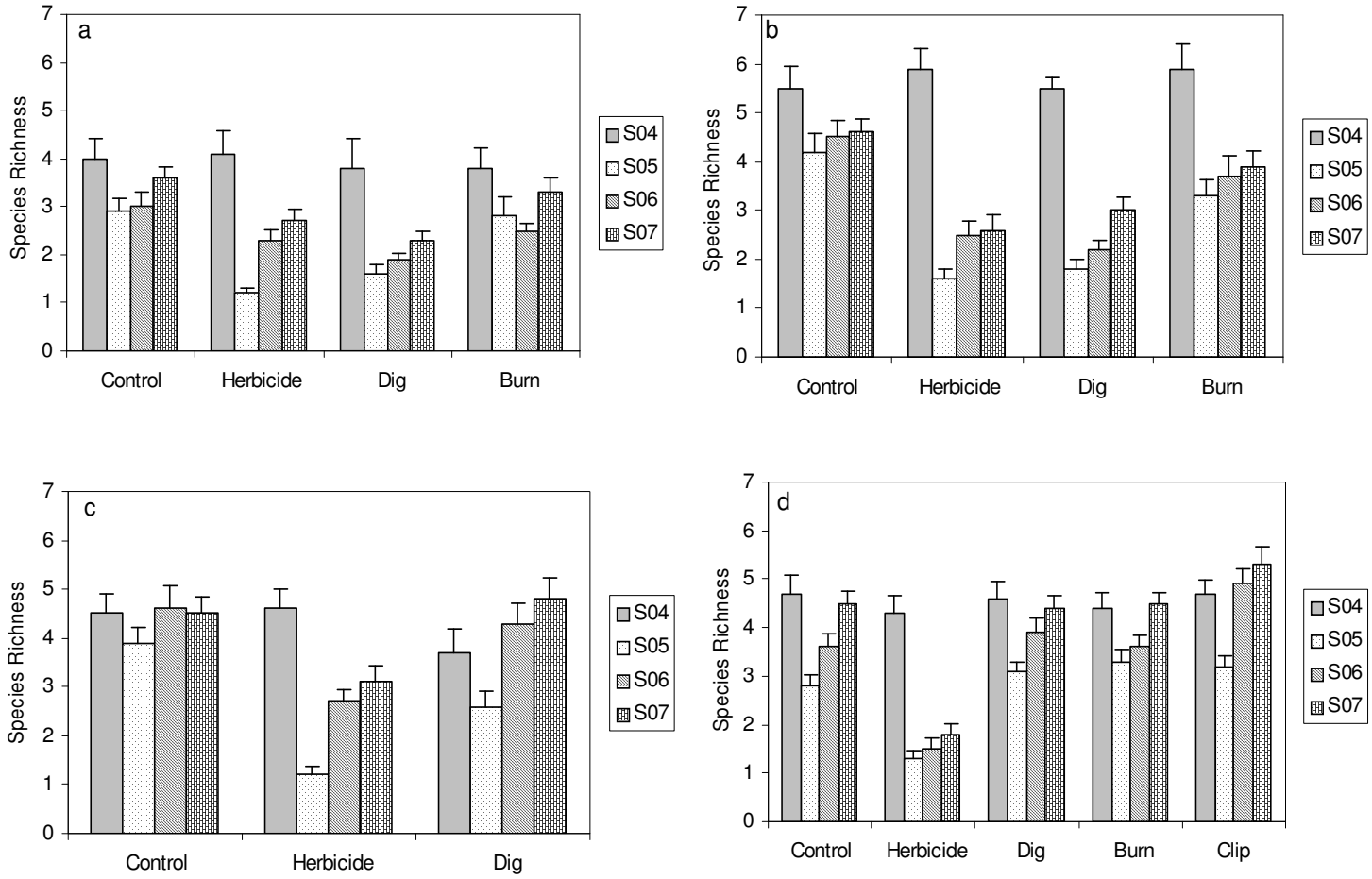

Figure 5.5. Species richness at (a) Clearcut Site, (b) Wildfire Site, (c) Riparian Site and (d) Meadow Site. S04 = spring 2004, S05 = spring 2005, S06 = spring 2006 and S07 = spring 2007. Error bars show standard error. For Clearcut and Wildfire control plots, N = 17. For Riparian control plots, N = 15. For Meadow control plots, N = 18. For other Riparian treatments, N=10. For all other treatments and sites, N = 12.

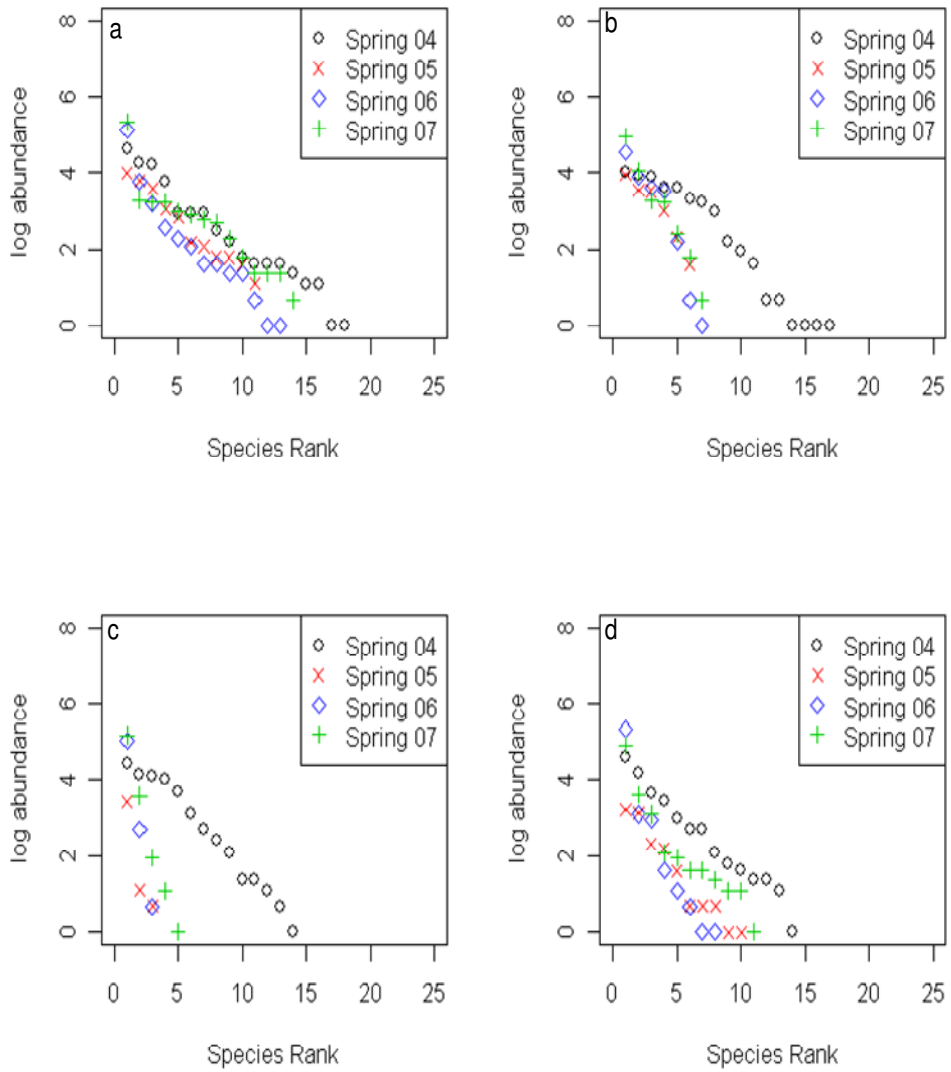

Figure 5.6. Relative species abundance distributions for (a) Control, (b) Herbicide, (c) Dig and (d) Burn treatments at Clearcut Site. The distributions for spring 2004 are prior to any treatments.

Wildfire Site. Herbicide application and digging greatly reduced diversity and richness while burning reduced richness and minimally reduced diversity in the first year after treatment (spring 2005) (Figures 5.4b and 5.5b). Diversity and richness in the Herbicide and Dig plots recovered to just over one half of their original levels in three years, but Burn plots had minimal recovery.

Relative species abundance curves indicated a decline in both species number and abundance following Herbicide and Dig treatments (Figure 5.7), but the RSA distributions for the burned plots were not different from the Control plots. Patterns of diversity recovery at the Wildfire Site were similar to the Clearcut Site with slow recovery in Herbicide and Dig treated plots.

Species composition at the Wildfire Site was changed by the treatments. In spring 2004, prior to herbicide treatment, the most dominant species were a moss (RSA = 4.93), *E. umbellatum* (RSA = 4.45) and *L. vulgaris* (RSA = 4.14). The Herbicide treatment reduced species richness (16 species in spring 2004 to 4 species in spring 2005 in all plots combined) and removed all forbs in spring 2005. In spring 2007, moss (RSA = 5.00) was still the most dominant species, *L. vulgaris* (RSA = 3.87) had returned as the second most dominant species, and three grasses (combined RSA = 10.45) followed. Digging also reduced the number of species (17 in spring 2004 to 4 in spring 2005), but did not change the dominant species, *L. vulgaris* (RSA = 4.13 in spring 2004 and 3.50 in spring 2005). By spring 2007, seven forb species were present with *L. vulgaris* (RSA = 4.63) and *A. glauca* (RSA = 3.66) being most dominant. Burning had a lesser effect on the number of species and the plant community, although some species including *R. tenerrima* (RSA =

1.79) and a *Penstemon* species (RSA = 0.69) that were originally scarcely abundant were removed from the community. Complete species lists with RSA values for all treatments and times are provided in Appendix D.

Riparian Site. Species diversity and richness at the Riparian Site were initially reduced by the Dig and Herbicide treatments, but then recovered in the second (spring 2006) and third (spring 2007) years (Figures 5.4c and 5.5c). In the case of the Dig treatment, diversity and richness after three years were higher than before treatments, and approximately equal to that of the control. Diversity in herbicide treated plots recovered, but not to pre-treatment levels.

Relative species abundance distributions were also altered after treatments. As shown on Figure 5.8, herbicide application and digging resulted in fewer species present at lower abundances. This is especially true for the Herbicide treatment, where overall species richness (all plots combined) was reduced from 15 to only three species in spring 2005, and by spring 2007, that number only increased to six species. The Dig treatment initially reduced the species richness from 14 to 9 (all plots combined), but richness increased back to the original number by spring 2007, although the abundance of the returning species was still less.

Herbicide treatment effectively removed nearly all forb species (combined RSA in spring 2004 = 24.34) in the first year such that only a small number of the annual *C. parviflora* (RSA = 0.00) were recorded in spring 2005 and *Carex spp.* (RSA = 2.83) was dominant. In subsequent years, plots treated with herbicide became dominated by *L. vulgaris* (RSA = 4.62 in spring 2007) and grasses (combined RSA = 6.78 in spring 2007).

Digging had little effect on long-term community composition, with *L. vulgaris* (RSA = 4.44 in spring 2007) and *F. virginiana* (RSA = 3.50 in spring 2007) remaining some of the most dominant species. See Appendix D for complete species lists with RSA values.

Meadow Site. At the Meadow Site, species diversity and richness in plots treated with herbicide declined and remained low through spring 2007 (Figures 5.4d and 5.5d). Species diversity in the Dig plots increased and remained elevated after treatment, but changes in species richness were generally not different from Control plots. Diversity and richness response in Burn and Clip plots were similar to Control plots. The cause of variation in diversity and richness in Control plots is unknown, but is likely related to the time of sampling (see Discussion).

Relative species abundance distribution patterns for the Meadow Site are similar to patterns from the other sites. All treatments, including Control, reduced the number and abundance of species in the first year (Figure 5.9). By spring 2007, species richness and abundance recovered to pre-disturbance levels in all plots except those treated with herbicide, where numbers remained very low. There was no apparent difference between Control, Dig, Burn and Clip treatments in the relative species abundance distributions.

Community response to treatments was varied. Herbicide application changed the plant community from being dominated in spring 2004 by *P. pratensis* (RSA = 6.14) and several forb species including *L. vulgaris* (RSA = 3.97), *Erigeron speciosus* (3.61), *Aster occidentalis* (RSA = 3.40) and *Geranium viscosissimum* (RSA = 3.30) to one dominated almost exclusively by *P. pratensis* (RSA = 5.75 in spring 2007) with the occasional forb (RSA = 3.47 for all forbs combined in spring 2007). The digging treatment, after one

year, transformed the community from a very rich one (13 species) dominated by *P. pratensis* (RSA = 6.06 in spring 2004) to a sparsely populated community (5 species) co-dominated by *L. vulgaris* (RSA = 2.94), *P. pratensis* (RSA = 2.89) and aster species (combined RSA = 3.81) in spring 2005. In subsequent years, more species returned and the community in spring 2007 resembled the original community with *P. pratensis* (RSA = 4.88), *A. occidentalis* (RSA = 3.95) and *L. vulgaris* (RSA = 3.87) being the most dominant species. After the Burn treatment the community changed little and by spring 2007, *P. pratensis* (RSA = 5.68) remained the dominant species, with *L. vulgaris* (RSA = 3.64), *Delphinium glaucum* (RSA = 2.83) and *A. ciliolatus* (RSA = 2.77) being the next most dominant ones. Clipping, simulating grazing, had little effect on community composition and *P. pratensis* (RSA = 5.56), *A. occindentalis* (RSA = 3.5), *L. vulgaris* (RSA = 3.22) and *Maianthemum stellatum* (RSA = 2.64) were generally the most dominant species in spring 2007. Complete species lists with RSA values for all treatments and time periods are included in Appendix D.

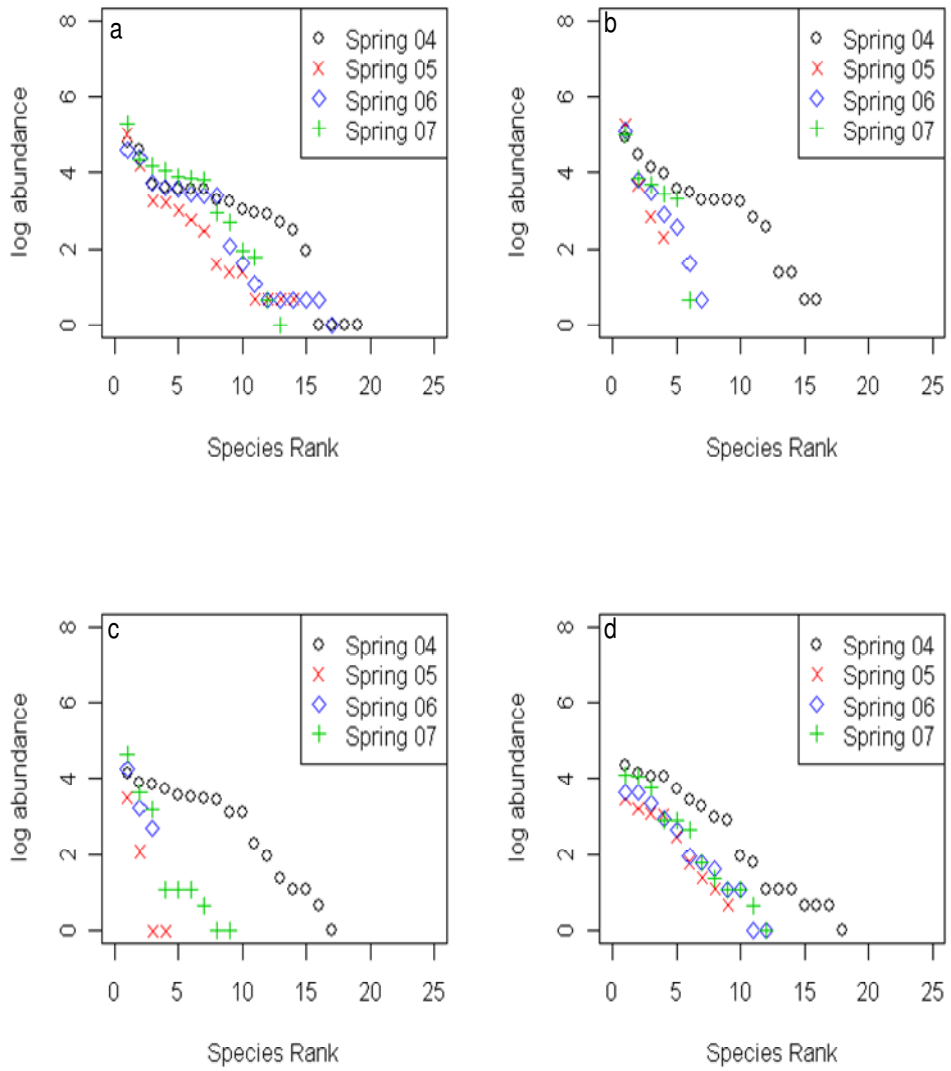

Figure 5.7. Relative species abundance distributions for (a) Control, (b) Herbicide, (c) Dig and (d) Burn treatments at Wildfire Site. The distributions for spring 2004 are prior to any treatments.

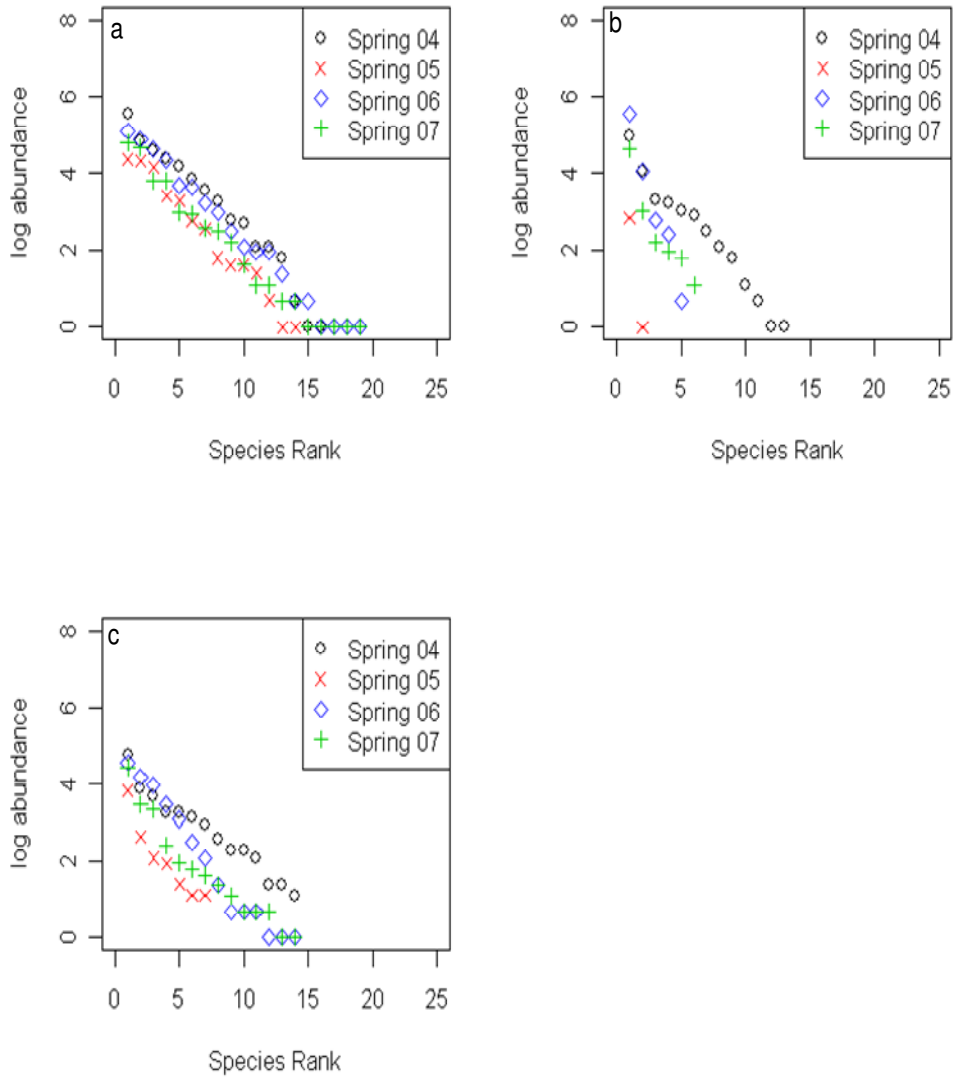

Figure 5.8. Relative species abundance distributions for (a) Control, (b) Herbicide and (c) Dig treatments at Riparian Site. The distributions for spring 2004 are prior to any treatments.

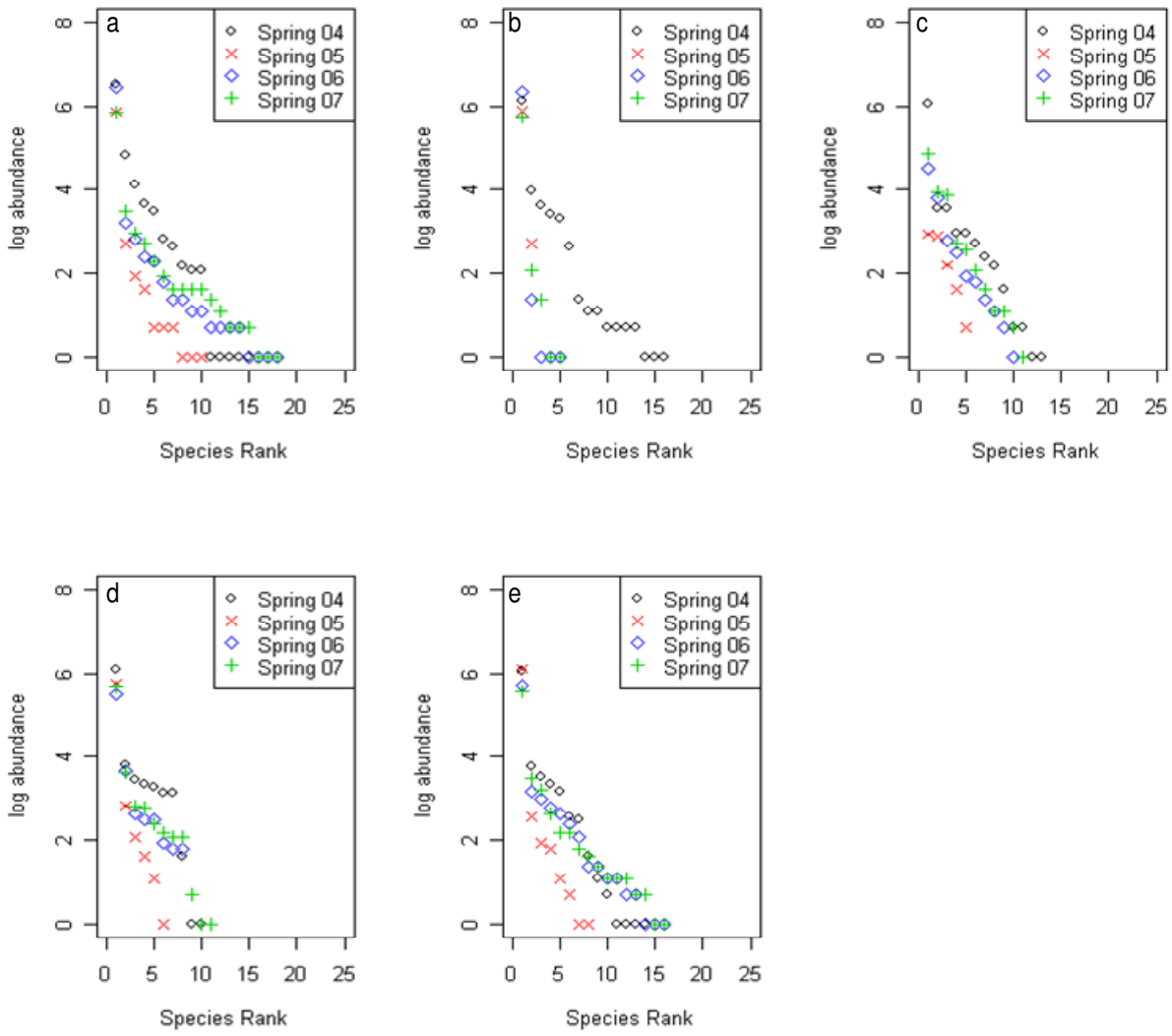

Figure 5.9. Relative species abundance distributions for (a) Control, (b) Herbicide, (c) Dig, (d) Burn and (e) Clip treatments at Meadow Site. The distributions for spring 2004 are prior to any treatments.

Discussion

Impacts of *L. vulgaris* on Plant Community

L. vulgaris impact on the plant community was minimal. At the Clearcut, Wildfire and Meadow Sites, values of diversity were not different in interior, edge or outside plots, while *L. vulgaris* cover was significantly greater in interior and edge plots, indicating that *L. vulgaris* did not suppress native species as NIS are often cited as doing (D'Antonio and Vitousek 1992; Mack et al. 2000; Mooney and Cleland 2001). In fact, richness values at the Meadow Site were slightly greater in interior and edge plots than in outside plots that lacked *L. vulgaris* presence. At the Riparian Site, diversity was lower in interior plots which had the highest *L. vulgaris* cover, but richness was not related to plot position or *L. vulgaris* cover.

Site Differences

Relative species abundance distributions, Simpson's diversity index and percent bare ground, vegetative cover and litter cover were all different across sites. Causes of the differentiation of vegetation between sites are likely differences in slope, aspect, elevation and soil properties (see Chapter 4). While there are clear site differences, some similarities between sites are apparent. The Clearcut and Wildfire Sites are most similar, with their RSA distributions being comparable, with 20 shared species, and no significant differences in percent bare soil or vegetative cover. By these same metrics, the Riparian Site is more similar to the Clearcut and Wildfire Sites than to the Meadow Site, although

the number of shared species is similar (16 shared with Clearcut and Wildfire Sites and 16 shared with Meadow Site).

Treatment Effects on Vegetation

There was a large degree of variation in the abundance of different species within the control plots at each site between years, as indicated by the RSA distributions and diversity values. The variation in abundance likely represents some true differences over time, but also was indicative of the fact that there were slight differences in annual spring sampling dates in terms of growing degree days and/or spring precipitation. While sampling always occurred in the last week of May or the first of June, differences in growing degree days or precipitation for that calendar day each year may have resulted in more or fewer species being present during sampling, or species being present in different relative abundances. This was especially apparent at the Meadow Site, where a few additional days of good growing conditions would make a large difference in terms of the percent cover classified as live *P. pratensis* rather than litter. Thus, the effects of treatments on vegetation were somewhat masked by the effects of different growing conditions at the time of measurement.

Herbicide. Herbicide reduced species richness and diversity the year after treatment. Species diversity recovered to a small degree at all sites except the Meadow Site, but species richness remained low, especially at the Meadow Site where only three species were present at more than one percent cover in spring 2007. The lack of recovery of species numbers at the Clearcut, Wildfire and Riparian Sites is indicative of the poor

soil quality and harsh growing conditions at these sites (see Chapter 4), and suggests that a disturbance that completely removes a group of species (e.g., dicotyledonous species in the case of the herbicide used) may reduce species richness for an extended time. At the Meadow Site, where soil and growing conditions are better (see Chapter 4) the lack of recovery is likely due to competition with the grass *P. pratensis* which was not affected by the herbicide (Rinella and Sheley 2005).

Dig and Burn. Digging reduced species richness the year after treatment at all sites, and diversity was reduced at all sites except the Meadow where it increased as a result of a more even distribution of species instead of being dominated by *P. pratensis*. Similar to the Herbicide treatment, species richness remained depressed at the Clearcut and Wildfire Sites. At the Riparian and Meadow Sites, however, with better growing conditions, the number of species recovered to pre-disturbance levels. Vegetation response to burning followed a similar pattern to the digging response with recovery of species richness and diversity the greatest at the Meadow Site.

Clip. Clipping did not elicit a response that was different from the Control in terms of richness and diversity, other than a slight increase in diversity in spring 2006. This lack of response was not surprising considering the nature of the disturbance – a single event where vegetation was merely clipped to just above ground level as opposed to the Burn and Dig treatments that destructively removed all vegetation, or severe overgrazing which would occur with repeated browsing and lack of vegetation recovery time.

General Conclusions / Management Implications

The disturbances of herbicide application, digging and burning generally reduced species richness and diversity. This seems to be in conflict with Connell's (1978) intermediate disturbance hypothesis which states that the highest diversity is in ecosystems that receive periodic disturbances. The aforementioned disturbances, however, certainly could not be considered intermediate in terms of intensity, as they removed all species from the plots (herbicide removed all forb species but not grasses). These high levels of disturbance, especially at sites with challenging growing conditions such as the Clearcut and Wildfire Sites, assured that recovery was slow and species richness and diversity may remain depressed for years. This places the community at higher risk for invasion by other NIS as low species richness and diversity in plant communities have been shown to increase the success of establishment by invading species (Knops et al. 1999, Levine 2000, van Ruijven et al. 2003, Fridley et al. 2007).

In terms of management, these results indicate that if high species richness and diversity are desired short-term outcomes, then herbicide, soil disturbance and burning should be avoided. If, however, the management goal is to increase forage for livestock, then a broadleaf selective herbicide such as Tordon K™ could be used as a tool to achieve this goal on sites where monocots comprise a large percentage of the cover. On sites with little monocot cover, use of such an herbicide will likely lead to species poor communities that are of low grazing value.

A final important aspect of the results was the difference in the magnitude of the effects of the NIS *L. vulgaris* versus the effects of disturbances on the extant plant

communities. Over the course of the study, there was little change in species richness, diversity or RSA in Control plots (no disturbance). In these plots, the dominance of *L. vulgaris* did not increase and other species were not displaced. In contrast, plots subject to disturbance experienced losses of species and often a species shift to dominance by *L. vulgaris*. This suggests that habitat alteration plays a much more significant role in community change and species loss than does the invasion by NIS (Gurevitch and Padilla 2004).

EPILOGUE

"...How interesting everything is! Every rock, mountain, stream, plant, lake, lawn, forest, garden, bird, beast, insect seems to call and invite us to come and learn something of its history and relationship...." John Muir

This Ph.D. dissertation was an attempt to understand the factors affecting the establishment and spread of *Linaria vulgaris* (yellow toadflax) and to develop a method for quantifying plant invasiveness. When reflecting on the process of completing this work, however, it becomes obvious that the dissertation represents more than these basic objectives. The work presented herein is the result of my transformation from an engineer to an ecologist. It reflects a change from a rigid, linear way of thinking to a more holistic, system-oriented frame of reference where the above quote by John Muir aptly describes my philosophy and love of ecology. Regardless of this love, though, I must admit that ecology is complex – unbelievably complex. This is even true (especially true?) for someone with an engineering background steeped in quantitative approaches to problem solving. In a typical engineering problem (e.g., determining the size of rebar required in a concrete beam supporting a bridge deck), there is a single, tested method for determining a single, acceptable answer. In ecology, there are no typical problems, and there is generally no single approach in ecological studies that is correct. Furthermore, there is often not a correct answer. It depends on the question; the year; the environment. It depends on any number of uncontrollable stochastic factors that virtually ensure that the answer will be somewhat different with each repetition of the experiment. This uncertainty and unpredictability in nature challenges us as ecologists. Challenge and complexity, however, do not equate to futility. It is these difficulties that

inspire us to ask more questions, to refine these questions and to seek an understanding of the environments that surround us.

General Summary

Through my research, I have investigated four separate but related topics, with the intent of providing land managers with information that will change the way in which NIS are perceived and improve their management. The research topics can be summarized as follows: (1) assessing the effects of disturbance size and propagule pressure on the colonization success of *L. vulgaris*, (2) evaluating the differing degrees of *L. vulgaris* invasiveness across different environments and developing a method for quantifying invasiveness, (3) evaluating the effects of disturbances on *L. vulgaris* invasiveness in different environments and (4) measuring the impacts of *L. vulgaris* and disturbance on plant communities.

The first study revealed that *L. vulgaris* colonization success was positively correlated with disturbance size and propagule pressure, but was rare and likely occurred at the sites in the past as episodic events, dependent upon environmental conditions. The second study developed methodology to quantify NIS invasiveness and demonstrated that invasiveness of *L. vulgaris* populations varied across environments. The third part of the research showed that the disturbances of digging and burning generally caused increased *L. vulgaris* invasiveness in the short term, but had minimal long-term effects; clipping had minimal effects; and herbicide application reduced invasiveness initially, but at some sites subsequently led to increased invasiveness. Lastly, plant community data indicated

that *L. vulgaris* impacts on other vegetation were minimal, but the experimental disturbance treatments changed communities in terms of species richness, diversity and community composition.

Future Research

The foremost area for additional research lies in testing the implementation and applicability of the method for calculating invasiveness on other NIS. The methodology was developed in particular for *L. vulgaris*, but more generally for other perennial species with clonal growth and / or short seed dispersal distances. Thus, to evaluate its usefulness, the method should be tested on other similar species, with *Euphorbia esula* being an ideal candidate. Adaptation of the method to assess invasiveness of NIS with longer dispersal distances should also be a priority. Species such as *Cirsium arvense* and to a lesser degree, *Centaurea maculosa,* would be good candidates for this. Testing the method on these species could be accomplished with a combination of surveys and adaptive sampling techniques, both prior to plot establishment to locate existing populations, and in subsequent years of monitoring to locate new ones.

An additional subject for research would be an expanded evaluation of the effects of grazing on *L. vulgaris* invasiveness. Results from the clipping experiments indicated that this disturbance had little effect on *L. vulgaris*. I would not, however, conclude that grazing has no effect. The clipping treatment was intended to represent a single, intense grazing episode. Actual grazing patterns (at least by cattle) would likely be quite different than the clipping treatment though, with repeated grazing, selective

consumption of more palatable species, and less disturbance to *L. vulgaris*. Monitoring plots established within and outside exclosures in grazed *L. vulgaris* infested pasture or rangeland would be the most simplistic, and realistic way to test the effects of livestock grazing.

Additional opportunities for future research are in the study of NIS growth differences in their invaded and native ranges. This topic is underrepresented in the literature, and provides an important potential avenue for understanding how NIS species growth is affected by subtle environmental differences. Of primary interest is the question, "Why is the species invasive here, but not there?" This question has of course been researched in terms of the "enemy release" and "evolution of increased competitive ability" hypotheses. Less work has been done on the effects of differing environmental factors such as soil chemistry and climate. Also of interest would be the historical distribution of the species from a paleoecological perspective. Several potential questions include: (1) what percent of its historical native range does the species currently occupy? (2) is the current range smaller/larger as a result of long-term climate change? and (3) how does the invaded range's climate compare to historical native range's climate?

Unsolicited Advice

At this point I will offer some unsolicited advice to my current graduate student colleagues and to future graduate students, and indeed to anyone involved in ecological research. Some of this same advice was given to me at the outset of my research, much

of it was learned the hard way, and unfortunately, not all of it was followed. It is certainly valuable though, and could potentially save days, weeks or even months of frustration.

- Understand how you will analyze your data before you ever enter the field to collect it. Data are useless without a plan to analyze it, and knowing that plan before the data are collected may pre-empt numerous problems in the future. Foremost, understanding your data analysis will help assure you that the experimental design is sound, and that the data are being collected properly. It will also help you devise an expedient method of collecting and storing your data (i.e., data sheets and files).
- A corollary of the above is to make sure that you are collecting the right data to be able to reject or fail to reject your null hypothesis. In other words, know what your question is and make sure that your data collection scheme will provide the information needed to explicitly test your hypotheses. Additionally, it is essential that you perform a power test so that you know how many replications are necessary to provide the statistical power necessary to reject a null hypothesis.
- Learn to program in R (or your language of choice). Knowing how to write code to perform statistical analysis and graphing gives you complete control over your data analysis and figure generation. R has extraordinary capabilities beyond statistics as well. It is an invaluable tool for modelling and performing ecological analysis. There are two excellent books written by the ecologist Michael J.

Crawley that can prove to be enormously valuable: *Statistics, An Introduction using R* (Crawley 2005) and *The R Book* (Crawley 2007).

- Start writing early. Every paragraph written early in the process, whether it is literature review, methods, data analysis or results will be a gift to you later.

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APPENDICES

APPENDIX A

R SCRIPT FOR CALCULATING INVASIVENESS

```
#Script to calculate Invasiveness of Linaria vulgaris for all treatments at all sites
#Erik Lehnhoff
#12/29/2006
data=read.table("allstemdata.txt", header=T)
attach(data)

#make subsets of Wildfire data
wf = subset(data, Site == "Wildfire")
wfcont = subset(wf, Treat == "C")
wfcontE = subset(wfcont, Pos == "E")
wfcontO = subset(wfcont, Pos == "O")
wfcontC = subset(wfcont, Pos == "I") #these are Center plots
wfcont=cbind(wfcontE,wfcontO)
wfcont<<-wfcont[,c(-2,-3,-14,-15)] #removes unneeded columns.
wfburn = subset(wf, Treat == "B")
wfburnE = subset(wfburn, Pos == "E")
wfburnO = subset(wfburn, Pos == "O")
wfburn=cbind(wfburnE,wfburnO)
wfburn<<-wfburn[,c(-2,-3,-14,-15)] #removes unneeded columns.
wfdig = subset(wf, Treat == "D")
wfdigE = subset(wfdig, Pos == "E")
wfdigO = subset(wfdig, Pos == "O")
wfdig=cbind(wfdigE,wfdigO)
wfdig<<-wfdig[,c(-2,-3,-14,-15)] #removes unneeded columns.
wfherb = subset(wf, Treat == "H")
wfherbE = subset(wfherb, Pos == "E")
wfherbO = subset(wfherb, Pos == "O")
wfherb=cbind(wfherbE,wfherbO)
wfherb<<-wfherb[,c(-2,-3,-14,-15)] #removes unneeded columns.

wfcontfall=wfcont[-(1:4),] #this removes entire rows with missing values so the
                           #invasiveness index will run properly.  this is only
                           #for FALL data for wildfire control plots
#make subsets of Clearcut data
cc = subset(data, Site == "Clearcut")
cccont = subset(cc, Treat == "C")
cccontE = subset(cccont, Pos == "E")
cccontO = subset(cccont, Pos == "O")
cccontI = subset(cccont, Pos == "I")
cccont=cbind(cccontE,cccontO)
cccont<<-cccont[,c(-2,-3,-14,-15)] #removes unneeded columns.
ccburn = subset(cc, Treat == "B")
ccburnE = subset(ccburn, Pos == "E")
ccburnO = subset(ccburn, Pos == "O")
```

```
ccburn=cbind(ccburnE,ccburnO)
ccburn<<-ccburn[,c(-2,-3,-14,-15)] #removes unneeded columns.
ccdig = subset(cc, Treat == "D")
ccdigE = subset(ccdig, Pos == "E")
ccdigO = subset(ccdig, Pos == "O")
ccdig=cbind(ccdigE,ccdigO)
ccdig<<-ccdig[,c(-2,-3,-14,-15)] #removes unneeded columns.
ccherb = subset(cc, Treat == "H")
ccherbE = subset(ccherb, Pos == "E")
ccherbO = subset(ccherb, Pos == "O")
ccherb=cbind(ccherbE,ccherbO)
ccherb<<-ccherb[,c(-2,-3,-14,-15)] #removes unneeded columns.

#make subsets of Meadow data
mw = subset(data, Site == "Meadow")
mwcont = subset(mw, Treat == "C")
mwcontE = subset(mwcont, Pos == "E")
mwcontO = subset(mwcont, Pos == "O")
mwcontI = subset(mwcont, Pos == "I")
mwcont=cbind(mwcontE,mwcontO)
mwcont<<-mwcont[,c(-2,-3,-14,-15)] #removes unneeded columns.
mwburn = subset(mw, Treat == "B")
mwburnE = subset(mwburn, Pos == "E")
mwburnO = subset(mwburn, Pos == "O")
mwburn=cbind(mwburnE,mwburnO)
mwburn<<-mwburn[,c(-2,-3,-14,-15)] #removes unneeded columns.
mwdig = subset(mw, Treat == "D")
mwdigE = subset(mwdig, Pos == "E")
mwdigO = subset(mwdig, Pos == "O")
mwdig=cbind(mwdigE,mwdigO)
mwdig<<-mwdig[,c(-2,-3,-14,-15)] #removes unneeded columns.
mwherb = subset(mw, Treat == "H")
mwherbE = subset(mwherb, Pos == "E")
mwherbO = subset(mwherb, Pos == "O")
mwherb=cbind(mwherbE,mwherbO)
mwherb<<-mwherb[,c(-2,-3,-14,-15)] #removes unneeded columns.
mwclip = subset(mw, Treat == "K")
mwclipE = subset(mwclip, Pos == "E")
mwclipO = subset(mwclip, Pos == "O")
mwclip=cbind(mwclipE,mwclipO)
mwclip<<-mwclip[,c(-2,-3,-14,-15)] #removes unneeded columns.

#make subsets of Riparian data
rp = subset(data, Site == "Riparian")
```

```
rpcont = subset(rp, Treat == "C")
rpcontE = subset(rpcont, Pos == "E")
rpcontO = subset(rpcont, Pos == "O")
rpcontI = subset(rpcont, Pos == "I")
rpcont=cbind(rpcontE,rpcontO)
rpcont<<-rpcont[,c(-2,-3,-14,-15)] #removes unneeded columns.
rpburn = subset(rp, Treat == "B")
rpburnE = subset(rpburn, Pos == "E")
rpburnO = subset(rpburn, Pos == "O")
rpburn=cbind(rpburnE,rpburnO)
rpburn<<-rpburn[,c(-2,-3,-14,-15)] #removes unneeded columns.
rpdig = subset(rp, Treat == "D")
rpdigE = subset(rpdig, Pos == "E")
rpdigO = subset(rpdig, Pos == "O")
rpdig=cbind(rpdigE,rpdigO)
rpdig<<-rpdig[,c(-2,-3,-14,-15)] #removes unneeded columns.
rpherb = subset(rp, Treat == "H")
rpherbE = subset(rpherb, Pos == "E")
rpherbO = subset(rpherb, Pos == "O")
rpherb=cbind(rpherbE,rpherbO)
rpherb<<-rpherb[,c(-2,-3,-14,-15)] #removes unneeded columns.

##1=spr04->spr05, 2=fall04->fall05, 3=spr05->spr06, 4=fall05->fall06

inv = function(pop,yr) #user imputs population (this is Site and Treatment) and year for
        analysis
{
 table<<-pop #define table as the data from population chosen
 if(yr==1)
   {
    stems<<-table[,c(4,14,7,17)]
   }
   else if(yr==2)
   {
    stems<<-table[,c(6,16,8,18)]
   }
   else if(yr==3)
   {
    stems<<-table[,c(7,17,9,19)]
   }
   else if(yr==4)
   {
    stems<<-table[,c(8,18,10,20)]
   }
```

```
dndtint=stems[,3]-stems[,1]
dndtint=as.matrix(dndtint)
dndtedge=stems[,4]-stems[,2]
dndnedge=as.matrix(dndtedge)
stems<<-cbind(stems,dndtint,dndtedge)
colnames(stems)=c("int1","edge1","int2","edge2","int dn/dt", "edge dn/dt")

Q=dim(stems)[1] #number of rows

int1=0
edge1=0
int2=0
edge2=0
posintdndt=0 #interior dn/dt > 0
negintdndt=0 #interior dn/dt < 0
posedgedndt=0 #edge dn/dt > 0
negedgedndt=0 #edge dn/dt < 0

for (i in 1:Q)
{
  if(stems[i,1]>0)
  {
    int1=int1+1
  }

  if(stems[i,2]>0)
  {
    edge1=edge1+1
  }

  if(stems[i,3]>0)
  {
    int2=int2+1
  }

  if(stems[i,4]>0)
  {
    edge2=edge2+1
  }

  if(stems[i,5]>0)
  {
    posintdndt=posintdndt+1
```

```
    }

    if(stems[i,5]<0)
    {
      negintdndt=negintdndt+1
    }

    if(stems[i,6]>0)
    {
      posedgedndt=posedgedndt+1
    }

    if(stems[i,6]<0)
    {
      negedgedndt=negedgedndt+1
    }
  }

  pint1 = int1/Q #proportion of interior cells occupied in '02
  pedge1 = edge1/Q #proportion of edge cells occupied in '02
  pint2 = int2/Q #proportion of interior cells occupied in '05
  pedge2 = edge2/Q #proportion of edge cells occupied in '05
  pposintdndt = posintdndt/Q #proportion of interior cells with positive growth rate
  pnegintdndt = negintdndt/Q #proportion of interior cells with negative growth rate
  pposedgedndt = posedgedndt/Q #proportion of interior cells with positive growth rate
  pnegedgedndt = negedgedndt/Q #proportion of interior cells with negative growth rate

  intinv = pint2-pint1+pposintdndt-pnegintdndt #interior invasiveness = change in
          #proportion of cells occupied from year 1 - year 2 + prop. with pos. growth rate -
           prop.
          #with negative growth rate
  edgeinv = pedge2-pedge1+pposedgedndt-pnegedgedndt

  ii=intinv+edgeinv #total invasiveness = interior invasiveness + edge invasiveness

  print("Interior Invasiveness Index")
  print(intinv)
  print("Edge Invasiveness Index")
  print(edgeinv)
  print("Total Invasiveness Index")
  print(ii)
}
####END OF INVASIVENESS CALCULATIONS###
```

APPENDIX B

TABLES OF MEAN λ, $\delta N/\delta T$ AND INVASIVENESS VALUES

Mean *L. vulgaris* λ values for all sites, treatments and years. Standard deviations are in parentheses.

Site	Treatment[1]	S04-S05	F04-F05	S05-S06	F05-F06
Clearcut	C	3.5 (6.1)	2.9 (3.5)	5.7 (6.6)	1.7 (1.0)
	H	0.6 (0.4)	1.5 (1.5)	12.4 (12.2)	7.6 (6.4)
	D	6.8 (10.2)	2.9 (2.9)	5.0 (7.5)	2.1 (2.4)
	B	8.1 (13.0)	1.9 (2.0)	4.9 (6.8)	1.5 (1.2)
Wildfire	C	2.8 (3.1)	3.0 (2.4)	2.2 (2.8)	1.2 (0.9)
	H	0.3 (0.3)	1.3 (1.2)	4.1 (7.5)	1.7 (1.9)
	D	4.3 (7.2)	1.7 (1.9)	2.3 (2.9)	1.9 (1.8)
	B	4.4 (6.4)	1.2 (1.3)	2.3 (3.2)	1.6 (1.5)
Riparian	C	2.6 (3.0)	2.2 (2.2)	2.3 (2.9)	1.9 (1.9)
	H	0.3 (0.4)	3.6 (3.3)	18.8 (20.8)	3.0 (2.7)
	D	2.9 (4.6)	1.2 (0.9)	3.2 (6.3)	3.5 (6.2)
Meadow	C	0.6 (0.8)	1.5 (1.5)	2.7 (2.4)	1.1 (0.8)
	H	0.6 (0.4)	1.7 (2.6)	1.1 (0.4)	1.0 (0.4)
	D	6.8 (8.1)	1.7 (2.2)	4.0 (9.6)	1.7 (2.4)
	B	1.6 (1.7)	1.5 (1.6)	1.2 (1.1)	0.9 (0.7)
	K	0.6 (0.6)	1.4 (1.6)	3.5 (2.6)	1.2 (1.2)

[1]C=control, H=herbicide, D=dig, B=burn, K=clip

Mean *L. vulgaris* δN/δt values for all sites, treatments and years. Standard deviations are in parentheses.

Site	Treatment[1]	S04-S05	F04-F05	S05-S06	F05-F06
Clearcut	C	1.6 (9.6)	1.5 (6.9)	6.1 (11.0)	1.9 (6.3)
	H	-4.3 (5.0)	0.5 (1.6)	11.4 (12.2)	7.7 (6.6)
	D	9.5 (15.0)	3.4 (8.3)	5.3 (13.3)	1.6 (9.0)
	B	7.8 (14.5)	-0.9 (11.6)	8.3 (15.8)	2.0 (6.6)
Wildfire	C	2.0 (8.1)	3.1 (5.4)	2.7 (8.3)	-1.6 (5.1)
	H	-5.9 (4.8)	0.3 (1.2)	3.1 (7.5)	0.9 (2.1)
	D	7.1 (9.8)	-0.5 (7.1)	3.0 (8.4)	0.9 (6.1)
	B	8.3 (8.9)	-2.4 (7.6)	-1.9 (11.7)	-1.0 (4.9)
Riparian	C	4.5 (15.1)	1.5 (7.3)	4.4 (15.7)	0.3 (7.4)
	H	-11.1 (12.5)	2.9 (3.5)	17.8 (20.8)	3.8 (3.4)
	D	8.6 (14.1)	-3.6 (10.3)	-7.9 (18.2)	2.4 (9.7)
Meadow	C	-4.2 (4.7)	-0.1 (4.0)	2.6 (3.5)	-1.2 (3.7)
	H	-2.4 (3.4)	0.7 (2.6)	0.1 (0.4)	-0.7 (2.6)
	D	14.7 (19.7)	-1.1 (8.8)	-5.4 (25.0)	-4.0 (11.7)
	B	0.7 (4.6)	-0.3 (5.2)	-1.6 (4.2)	-2.3 (4.1)
	K	-3.2 (4.7)	-1.9 (5.4)	2.5 (3.0)	-1.2 (3.8)

[1]C=control, H=herbicide, D=dig, B=burn, K=clip

Invasiveness Index Values

Site	Treatment[1]	S04-S05	F04-F05	S05-S06	F05-F06
Clearcut	C	1.00	1.29	1.79	1.04
	H	-2.00	0.79	3.25	2.92
	D	1.42	1.54	1.04	0.50
	B	1.25	0.33	1.00	0.29
Wildfire	C	1.25	1.75	0.79	-0.45
	H	-3.33	0.42	1.25	0.75
	D	1.42	0.13	0.96	0.50
	B	1.54	-0.54	0.71	0.50
Riparian	C	1.13	1.00	0.54	0.63
	H	-3.00	1.80	3.60	2.00
	D	1.30	-0.25	-1.20	0.65
Meadow	C	-2.04	0.08	2.13	-0.38
	H	-2.25	0.42	0.25	-0.25
	D	1.75	0.50	-0.17	-0.08
	B	-0.08	0.46	0.00	-0.71
	K	-2.25	-0.08	2.75	-0.29

[1]C=control, H=herbicide, D=dig, B=burn, K=clip

APPENDIX C

R SCRIPT FOR CALCULATING RELATIVE SPECIES ABUNDANCE DISTRIBUTIONS AND SPECIES DIVERSITY

```
#Import data table and convert to a data frame
native<-read.table("NativeVeg.txt", header=T)
attach(native)
native<-data.frame(native)
library(vegan)
library(labdsv)

#make subsets of yearly data
S04 = subset(native, Year == "S04")
S05 = subset(native, Year == "S05")
F05 = subset(native, Year == "F05")
S06 = subset(native, Year == "S06")
F06 = subset(native, Year == "F06")
S07 = subset(native, Year == "S07")

#make subsets of Wildfire data
 #Spring 04 #No plots had been treated yet; the "Treat"
          #is the treatment that plots subsequently received.
 s04wf = subset(S04, Site == "WF")
 s04wfe = subset(s04wf, Pos == "E") #these three subsets (e, o & i) are
 s04wfo = subset(s04wf, Pos == "O") #for all plots because no treatments
 s04wfi = subset(s04wf, Pos == "I") #yet performed.
 s04wfcont = subset(s04wf, Treat == "C")
 s04wfcontE = subset(s04wfcont, Pos == "E")
 s04wfcontO = subset(s04wfcont, Pos == "O")
 s04wfcontI = subset(s04wfcont, Pos == "I")
 s04wfburn = subset(s04wf, Treat == "B")
 s04wfburnE = subset(s04wfburn, Pos == "E")
 s04wfburnO = subset(s04wfburn, Pos == "O")
 s04wfdig = subset(s04wf, Treat == "D")
 s04wfdigE = subset(s04wfdig, Pos == "E")
 s04wfdigO = subset(s04wfdig, Pos == "O")
 s04wfherb = subset(s04wf, Treat == "H")
 s04wfherbE = subset(s04wfherb, Pos == "E")
 s04wfherbO = subset(s04wfherb, Pos == "O")
 #Spring 05
 s05wf = subset(S05, Site == "WF")
 s05wfcont = subset(s05wf, Treat == "C")
 s05wfcontE = subset(s05wfcont, Pos == "E")
 s05wfcontO = subset(s05wfcont, Pos == "O")
 s05wfcontI = subset(s05wfcont, Pos == "I")
 s05wfburn = subset(s05wf, Treat == "B")
 s05wfburnE = subset(s05wfburn, Pos == "E")
 s05wfburnO = subset(s05wfburn, Pos == "O")
```

```
s05wfdig = subset(s05wf, Treat == "D")
s05wfdigE = subset(s05wfdig, Pos == "E")
s05wfdigO = subset(s05wfdig, Pos == "O")
s05wfherb = subset(s05wf, Treat == "H")
s05wfherbE = subset(s05wfherb, Pos == "E")
s05wfherbO = subset(s05wfherb, Pos == "O")
#Fall 05
f05wf = subset(F05, Site == "WF")
f05wfcont = subset(f05wf, Treat == "C")
f05wfcontE = subset(f05wfcont, Pos == "E")
f05wfcontO = subset(f05wfcont, Pos == "O")
f05wfcontI = subset(f05wfcont, Pos == "I")
f05wfburn = subset(f05wf, Treat == "B")
f05wfburnE = subset(f05wfburn, Pos == "E")
f05wfburnO = subset(f05wfburn, Pos == "O")
f05wfdig = subset(f05wf, Treat == "D")
f05wfdigE = subset(f05wfdig, Pos == "E")
f05wfdigO = subset(f05wfdig, Pos == "O")
f05wfherb = subset(f05wf, Treat == "H")
f05wfherbE = subset(f05wfherb, Pos == "E")
f05wfherbO = subset(f05wfherb, Pos == "O")
#Spring 06
s06wf = subset(S06, Site == "WF")
s06wfcont = subset(s06wf, Treat == "C")
s06wfcontE = subset(s06wfcont, Pos == "E")
s06wfcontO = subset(s06wfcont, Pos == "O")
s06wfcontI = subset(s06wfcont, Pos == "I")
s06wfburn = subset(s06wf, Treat == "B")
s06wfburnE = subset(s06wfburn, Pos == "E")
s06wfburnO = subset(s06wfburn, Pos == "O")
s06wfdig = subset(s06wf, Treat == "D")
s06wfdigE = subset(s06wfdig, Pos == "E")
s06wfdigO = subset(s06wfdig, Pos == "O")
s06wfherb = subset(s06wf, Treat == "H")
s06wfherbE = subset(s06wfherb, Pos == "E")
s06wfherbO = subset(s06wfherb, Pos == "O")
#Fall 06
f06wf = subset(F06, Site == "WF")
f06wfcont = subset(f06wf, Treat == "C")
f06wfcontE = subset(f06wfcont, Pos == "E")
f06wfcontO = subset(f06wfcont, Pos == "O")
f06wfcontI = subset(f06wfcont, Pos == "I")
f06wfburn = subset(f06wf, Treat == "B")
f06wfburnE = subset(f06wfburn, Pos == "E")
```

```
f06wfburnO = subset(f06wfburn, Pos == "O")
f06wfdig = subset(f06wf, Treat == "D")
f06wfdigE = subset(f06wfdig, Pos == "E")
f06wfdigO = subset(f06wfdig, Pos == "O")
f06wfherb = subset(f06wf, Treat == "H")
f06wfherbE = subset(f06wfherb, Pos == "E")
f06wfherbO = subset(f06wfherb, Pos == "O")
#Spring 07
s07wf = subset(S07, Site == "WF")
s07wfcont = subset(s07wf, Treat == "C")
s07wfcontE = subset(s07wfcont, Pos == "E")
s07wfcontO = subset(s07wfcont, Pos == "O")
s07wfcontI = subset(s07wfcont, Pos == "I")
s07wfburn = subset(s07wf, Treat == "B")
s07wfburnE = subset(s07wfburn, Pos == "E")
s07wfburnO = subset(s07wfburn, Pos == "O")
s07wfdig = subset(s07wf, Treat == "D")
s07wfdigE = subset(s07wfdig, Pos == "E")
s07wfdigO = subset(s07wfdig, Pos == "O")
s07wfherb = subset(s07wf, Treat == "H")
s07wfherbE = subset(s07wfherb, Pos == "E")
s07wfherbO = subset(s07wfherb, Pos == "O")

#make subsets of Clearcut data
#Spring 04 #No plots had been treated yet; the "Treat"
        #is the treatment that plots subsequently received.
s04cc = subset(S04, Site == "CC")
s04cce = subset(s04cc, Pos == "E") #these three subsets (e, o & i) are
s04cco = subset(s04cc, Pos == "O") #for all plots because no treatments
s04cci = subset(s04cc, Pos == "I") #yet performed.
s04cccont = subset(s04cc, Treat == "C")
s04cccontE = subset(s04cccont, Pos == "E")
s04cccontO = subset(s04cccont, Pos == "O")
s04cccontI = subset(s04cccont, Pos == "I")
s04ccburn = subset(s04cc, Treat == "B")
s04ccburnE = subset(s04ccburn, Pos == "E")
s04ccburnO = subset(s04ccburn, Pos == "O")
s04ccdig = subset(s04cc, Treat == "D")
s04ccdigE = subset(s04ccdig, Pos == "E")
s04ccdigO = subset(s04ccdig, Pos == "O")
s04ccherb = subset(s04cc, Treat == "H")
s04ccherbE = subset(s04ccherb, Pos == "E")
s04ccherbO = subset(s04ccherb, Pos == "O")
#spring 05
```

```
s05cc = subset(S05, Site == "CC")
s05cccont = subset(s05cc, Treat == "C")
s05cccontE = subset(s05cccont, Pos == "E")
s05cccontO = subset(s05cccont, Pos == "O")
s05cccontI = subset(s05cccont, Pos == "I")
s05ccburn = subset(s05cc, Treat == "B")
s05ccburnE = subset(s05ccburn, Pos == "E")
s05ccburnO = subset(s05ccburn, Pos == "O")
s05ccdig = subset(s05cc, Treat == "D")
s05ccdigE = subset(s05ccdig, Pos == "E")
s05ccdigO = subset(s05ccdig, Pos == "O")
s05ccherb = subset(s05cc, Treat == "H")
s05ccherbE = subset(s05ccherb, Pos == "E")
s05ccherbO = subset(s05ccherb, Pos == "O")
#fall 05
f05cc = subset(F05, Site == "CC")
f05cccont = subset(f05cc, Treat == "C")
f05cccontE = subset(f05cccont, Pos == "E")
f05cccontO = subset(f05cccont, Pos == "O")
f05cccontI = subset(f05cccont, Pos == "I")
f05ccburn = subset(f05cc, Treat == "B")
f05ccburnE = subset(f05ccburn, Pos == "E")
f05ccburnO = subset(f05ccburn, Pos == "O")
f05ccdig = subset(f05cc, Treat == "D")
f05ccdigE = subset(f05ccdig, Pos == "E")
f05ccdigO = subset(f05ccdig, Pos == "O")
f05ccherb = subset(f05cc, Treat == "H")
f05ccherbE = subset(f05ccherb, Pos == "E")
f05ccherbO = subset(f05ccherb, Pos == "O")
#spring 06
s06cc = subset(S06, Site == "CC")
s06cccont = subset(s06cc, Treat == "C")
s06cccontE = subset(s06cccont, Pos == "E")
s06cccontO = subset(s06cccont, Pos == "O")
s06cccontI = subset(s06cccont, Pos == "I")
s06ccburn = subset(s06cc, Treat == "B")
s06ccburnE = subset(s06ccburn, Pos == "E")
s06ccburnO = subset(s06ccburn, Pos == "O")
s06ccdig = subset(s06cc, Treat == "D")
s06ccdigE = subset(s06ccdig, Pos == "E")
s06ccdigO = subset(s06ccdig, Pos == "O")
s06ccherb = subset(s06cc, Treat == "H")
s06ccherbE = subset(s06ccherb, Pos == "E")
s06ccherbO = subset(s06ccherb, Pos == "O")
```

```
#fall 06
f06cc = subset(F06, Site == "CC")
f06cccont = subset(f06cc, Treat == "C")
f06cccontE = subset(f06cccont, Pos == "E")
f06cccontO = subset(f06cccont, Pos == "O")
f06cccontI = subset(f06cccont, Pos == "I")
f06ccburn = subset(f06cc, Treat == "B")
f06ccburnE = subset(f06ccburn, Pos == "E")
f06ccburnO = subset(f06ccburn, Pos == "O")
f06ccdig = subset(f06cc, Treat == "D")
f06ccdigE = subset(f06ccdig, Pos == "E")
f06ccdigO = subset(f06ccdig, Pos == "O")
f06ccherb = subset(f06cc, Treat == "H")
f06ccherbE = subset(f06ccherb, Pos == "E")
f06ccherbO = subset(f06ccherb, Pos == "O")
#spring 07
s07cc = subset(S07, Site == "CC")
s07cccont = subset(s07cc, Treat == "C")
s07cccontE = subset(s07cccont, Pos == "E")
s07cccontO = subset(s07cccont, Pos == "O")
s07cccontI = subset(s07cccont, Pos == "I")
s07ccburn = subset(s07cc, Treat == "B")
s07ccburnE = subset(s07ccburn, Pos == "E")
s07ccburnO = subset(s07ccburn, Pos == "O")
s07ccdig = subset(s07cc, Treat == "D")
s07ccdigE = subset(s07ccdig, Pos == "E")
s07ccdigO = subset(s07ccdig, Pos == "O")
s07ccherb = subset(s07cc, Treat == "H")
s07ccherbE = subset(s07ccherb, Pos == "E")
s07ccherbO = subset(s07ccherb, Pos == "O")

#make subsets of Meadow data
#spring 04 #No plots had been treated yet; the "Treat"
        #is the treatment that plots subsequently received.
s04mw = subset(S04, Site == "MW")
s04mwe = subset(s04mw, Pos == "E") #these three subsets (e, o & i) are
s04mwo = subset(s04mw, Pos == "O") #for all plots because no treatments
s04mwi = subset(s04mw, Pos == "I") #yet performed.
s04mwcont = subset(s04mw, Treat == "C")
s04mwcontE = subset(s04mwcont, Pos == "E")
s04mwcontO = subset(s04mwcont, Pos == "O")
s04mwcontI = subset(s04mwcont, Pos == "I")
s04mwburn = subset(s04mw, Treat == "B")
s04mwburnE = subset(s04mwburn, Pos == "E")
```

```
s04mwburnO = subset(s04mwburn, Pos == "O")
s04mwdig = subset(s04mw, Treat == "D")
s04mwdigE = subset(s04mwdig, Pos == "E")
s04mwdigO = subset(s04mwdig, Pos == "O")
s04mwherb = subset(s04mw, Treat == "H")
s04mwherbE = subset(s04mwherb, Pos == "E")
s04mwherbO = subset(s04mwherb, Pos == "O")
s04mwclip = subset(s04mw, Treat == "K")
s04mwclipE = subset(s04mwclip, Pos == "E")
s04mwclipO = subset(s04mwclip, Pos == "O")
#spring 05
s05mw = subset(S05, Site == "MW")
s05mwcont = subset(s05mw, Treat == "C")
s05mwcontE = subset(s05mwcont, Pos == "E")
s05mwcontO = subset(s05mwcont, Pos == "O")
s05mwcontI = subset(s05mwcont, Pos == "I")
s05mwburn = subset(s05mw, Treat == "B")
s05mwburnE = subset(s05mwburn, Pos == "E")
s05mwburnO = subset(s05mwburn, Pos == "O")
s05mwdig = subset(s05mw, Treat == "D")
s05mwdigE = subset(s05mwdig, Pos == "E")
s05mwdigO = subset(s05mwdig, Pos == "O")
s05mwherb = subset(s05mw, Treat == "H")
s05mwherbE = subset(s05mwherb, Pos == "E")
s05mwherbO = subset(s05mwherb, Pos == "O")
s05mwclip = subset(s05mw, Treat == "K")
s05mwclipE = subset(s05mwclip, Pos == "E")
s05mwclipO = subset(s05mwclip, Pos == "O")
#fall 05
f05mw = subset(F05, Site == "MW")
f05mwcont = subset(f05mw, Treat == "C")
f05mwcontE = subset(f05mwcont, Pos == "E")
f05mwcontO = subset(f05mwcont, Pos == "O")
f05mwcontI = subset(f05mwcont, Pos == "I")
f05mwburn = subset(f05mw, Treat == "B")
f05mwburnE = subset(f05mwburn, Pos == "E")
f05mwburnO = subset(f05mwburn, Pos == "O")
f05mwdig = subset(f05mw, Treat == "D")
f05mwdigE = subset(f05mwdig, Pos == "E")
f05mwdigO = subset(f05mwdig, Pos == "O")
f05mwherb = subset(f05mw, Treat == "H")
f05mwherbE = subset(f05mwherb, Pos == "E")
f05mwherbO = subset(f05mwherb, Pos == "O")
f05mwclip = subset(f05mw, Treat == "K")
```

```
f05mwclipE = subset(f05mwclip, Pos == "E")
f05mwclipO = subset(f05mwclip, Pos == "O")
#spring 06
s06mw = subset(S06, Site == "MW")
s06mwcont = subset(s06mw, Treat == "C")
s06mwcontE = subset(s06mwcont, Pos == "E")
s06mwcontO = subset(s06mwcont, Pos == "O")
s06mwcontI = subset(s06mwcont, Pos == "I")
s06mwburn = subset(s06mw, Treat == "B")
s06mwburnE = subset(s06mwburn, Pos == "E")
s06mwburnO = subset(s06mwburn, Pos == "O")
s06mwdig = subset(s06mw, Treat == "D")
s06mwdigE = subset(s06mwdig, Pos == "E")
s06mwdigO = subset(s06mwdig, Pos == "O")
s06mwherb = subset(s06mw, Treat == "H")
s06mwherbE = subset(s06mwherb, Pos == "E")
s06mwherbO = subset(s06mwherb, Pos == "O")
s06mwclip = subset(s06mw, Treat == "K")
s06mwclipE = subset(s06mwclip, Pos == "E")
s06mwclipO = subset(s06mwclip, Pos == "O")
#fall 06
f06mw = subset(F06, Site == "MW")
f06mwcont = subset(f06mw, Treat == "C")
f06mwcontE = subset(f06mwcont, Pos == "E")
f06mwcontO = subset(f06mwcont, Pos == "O")
f06mwcontI = subset(f06mwcont, Pos == "I")
f06mwburn = subset(f06mw, Treat == "B")
f06mwburnE = subset(f06mwburn, Pos == "E")
f06mwburnO = subset(f06mwburn, Pos == "O")
f06mwdig = subset(f06mw, Treat == "D")
f06mwdigE = subset(f06mwdig, Pos == "E")
f06mwdigO = subset(f06mwdig, Pos == "O")
f06mwherb = subset(f06mw, Treat == "H")
f06mwherbE = subset(f06mwherb, Pos == "E")
f06mwherbO = subset(f06mwherb, Pos == "O")
f06mwclip = subset(f06mw, Treat == "K")
f06mwclipE = subset(f06mwclip, Pos == "E")
f06mwclipO = subset(f06mwclip, Pos == "O")
#spring 07
s07mw = subset(S07, Site == "MW")
s07mwcont = subset(s07mw, Treat == "C")
s07mwcontE = subset(s07mwcont, Pos == "E")
s07mwcontO = subset(s07mwcont, Pos == "O")
s07mwcontI = subset(s07mwcont, Pos == "I")
```

```
s07mwburn = subset(s07mw, Treat == "B")
s07mwburnE = subset(s07mwburn, Pos == "E")
s07mwburnO = subset(s07mwburn, Pos == "O")
s07mwdig = subset(s07mw, Treat == "D")
s07mwdigE = subset(s07mwdig, Pos == "E")
s07mwdigO = subset(s07mwdig, Pos == "O")
s07mwherb = subset(s07mw, Treat == "H")
s07mwherbE = subset(s07mwherb, Pos == "E")
s07mwherbO = subset(s07mwherb, Pos == "O")
s07mwclip = subset(s07mw, Treat == "K")
s07mwclipE = subset(s07mwclip, Pos == "E")
s07mwclipO = subset(s07mwclip, Pos == "O")

#make subsets of Riparian data
#Spring 04 #No plots had been treated yet; the "Treat"
        #is the treatment that plots subsequently received.
s04rp = subset(S04, Site == "RP")
s04rpe = subset(s04rp, Pos == "E") #these three subsets (e, o & i) are
s04rpo = subset(s04rp, Pos == "O") #for all plots because no treatments
s04rpi = subset(s04rp, Pos == "I") #yet performed.
s04rpcont = subset(s04rp, Treat == "C")
s04rpcontE = subset(s04rpcont, Pos == "E")
s04rpcontO = subset(s04rpcont, Pos == "O")
s04rpcontI = subset(s04rpcont, Pos == "I")
s04rpburn = subset(s04rp, Treat == "B")
s04rpburnE = subset(s04rpburn, Pos == "E")
s04rpburnO = subset(s04rpburn, Pos == "O")
s04rpdig = subset(s04rp, Treat == "D")
s04rpdigE = subset(s04rpdig, Pos == "E")
s04rpdigO = subset(s04rpdig, Pos == "O")
s04rpherb = subset(s04rp, Treat == "H")
s04rpherbE = subset(s04rpherb, Pos == "E")
s04rpherbO = subset(s04rpherb, Pos == "O")
#spring 05
s05rp = subset(S05, Site == "RP")
s05rpcont = subset(s05rp, Treat == "C")
s05rpcontE = subset(s05rpcont, Pos == "E")
s05rpcontO = subset(s05rpcont, Pos == "O")
s05rpcontI = subset(s05rpcont, Pos == "I")
s05rpburn = subset(s05rp, Treat == "B")
s05rpburnE = subset(s05rpburn, Pos == "E")
s05rpburnO = subset(s05rpburn, Pos == "O")
s05rpdig = subset(s05rp, Treat == "D")
s05rpdigE = subset(s05rpdig, Pos == "E")
```

```
s05rpdigO = subset(s05rpdig, Pos == "O")
s05rpherb = subset(s05rp, Treat == "H")
s05rpherbE = subset(s05rpherb, Pos == "E")
s05rpherbO = subset(s05rpherb, Pos == "O")
#fall 05
f05rp = subset(F05, Site == "RP")
f05rpcont = subset(f05rp, Treat == "C")
f05rpcontE = subset(f05rpcont, Pos == "E")
f05rpcontO = subset(f05rpcont, Pos == "O")
f05rpcontI = subset(f05rpcont, Pos == "I")
f05rpburn = subset(f05rp, Treat == "B")
f05rpburnE = subset(f05rpburn, Pos == "E")
f05rpburnO = subset(f05rpburn, Pos == "O")
f05rpdig = subset(f05rp, Treat == "D")
f05rpdigE = subset(f05rpdig, Pos == "E")
f05rpdigO = subset(f05rpdig, Pos == "O")
f05rpherb = subset(f05rp, Treat == "H")
f05rpherbE = subset(f05rpherb, Pos == "E")
f05rpherbO = subset(f05rpherb, Pos == "O")
#spring 06
s06rp = subset(S06, Site == "RP")
s06rpcont = subset(s06rp, Treat == "C")
s06rpcontE = subset(s06rpcont, Pos == "E")
s06rpcontO = subset(s06rpcont, Pos == "O")
s06rpcontI = subset(s06rpcont, Pos == "I")
s06rpburn = subset(s06rp, Treat == "B")
s06rpburnE = subset(s06rpburn, Pos == "E")
s06rpburnO = subset(s06rpburn, Pos == "O")
s06rpdig = subset(s06rp, Treat == "D")
s06rpdigE = subset(s06rpdig, Pos == "E")
s06rpdigO = subset(s06rpdig, Pos == "O")
s06rpherb = subset(s06rp, Treat == "H")
s06rpherbE = subset(s06rpherb, Pos == "E")
s06rpherbO = subset(s06rpherb, Pos == "O")
#fall 06
f06rp = subset(F06, Site == "RP")
f06rpcont = subset(f06rp, Treat == "C")
f06rpcontE = subset(f06rpcont, Pos == "E")
f06rpcontO = subset(f06rpcont, Pos == "O")
f06rpcontI = subset(f06rpcont, Pos == "I")
f06rpburn = subset(f06rp, Treat == "B")
f06rpburnE = subset(f06rpburn, Pos == "E")
f06rpburnO = subset(f06rpburn, Pos == "O")
f06rpdig = subset(f06rp, Treat == "D")
```

```
f06rpdigE = subset(f06rpdig, Pos == "E")
f06rpdigO = subset(f06rpdig, Pos == "O")
f06rpherb = subset(f06rp, Treat == "H")
f06rpherbE = subset(f06rpherb, Pos == "E")
f06rpherbO = subset(f06rpherb, Pos == "O")
#spring 07
s07rp = subset(S07, Site == "RP")
s07rpcont = subset(s07rp, Treat == "C")
s07rpcontE = subset(s07rpcont, Pos == "E")
s07rpcontO = subset(s07rpcont, Pos == "O")
s07rpcontI = subset(s07rpcont, Pos == "I")
s07rpburn = subset(s07rp, Treat == "B")
s07rpburnE = subset(s07rpburn, Pos == "E")
s07rpburnO = subset(s07rpburn, Pos == "O")
s07rpdig = subset(s07rp, Treat == "D")
s07rpdigE = subset(s07rpdig, Pos == "E")
s07rpdigO = subset(s07rpdig, Pos == "O")
s07rpherb = subset(s07rp, Treat == "H")
s07rpherbE = subset(s07rpherb, Pos == "E")
s07rpherbO = subset(s07rpherb, Pos == "O")

#######################################################################

#Calculate Simpson's and Shannon's diversity (data table arranged with
#species in columns and plots in rows)

div=function(pop) #enter "div(population_name" to calculate diversity)
{
  values<<-pop[,7:63]
  simpson<<-mean(diversity(values, index="simpson"))
  print("Simpson Diversity =")
  print(simpson)
  shannon=mean(diversity(values, index="shannon"))
  print("Shannon Diversity =")
  print(shannon)
}

#######################################################################

#function to calculate RSA for a treatment

#s06mwcont<-s06mwcont[-9,]#remove NAs from data set
#s07mwcont<-s07mwcont[-7,]
#s07rpcont<-s07rpcont[-7,]#remove NAs from data set
```

```
rsa=function(pop1,pop2,pop3,pop4)
{
  tmp1<<-pop1[,7:63]
  mask0<<-apply(tmp1>0,2,sum)#masks 0 abundant species
  tmp1<<-tmp1[,mask0>0]
  tmp1<<-apply(tmp1,2,sum)
  tmp1.log<<-log(sort(floor(tmp1),decreasing=TRUE))

  tmp2<<-pop2[,7:63]
  mask0<<-apply(tmp2>0,2,sum)#masks 0 abundant species
  tmp2<<-tmp2[,mask0>0]
  tmp2<<-apply(tmp2,2,sum)
  tmp2.log<<-log(sort(floor(tmp2),decreasing=TRUE))

  tmp3<<-pop3[,7:63]
  mask0<<-apply(tmp3>0,2,sum)#masks 0 abundant species
  tmp3<<-tmp3[,mask0>0]
  tmp3<<-apply(tmp3,2,sum)
  tmp3.log<<-log(sort(floor(tmp3),decreasing=TRUE))

  tmp4<<-pop4[,7:63]
  mask0<<-apply(tmp4>0,2,sum)#masks 0 abundant species
  tmp4<<-tmp4[,mask0>0]
  tmp4<<-apply(tmp4,2,sum)
  tmp4.log<<-log(sort(floor(tmp4),decreasing=TRUE))

  write.table(tmp1.log,file="tmp1_species.txt")
  write.table(tmp2.log,file="tmp2_species.txt")
  write.table(tmp3.log,file="tmp3_species.txt")
  write.table(tmp4.log,file="tmp4_species.txt")
}

#Make plots of RSA.  Need to manually change plot titles and legends to correspond
#with the populations selected
yrange<-range(0,8) #manually change y and x ranges to get all data on graph
xrange<-range(0,25)
#par(mfrow=c(2,3))
plot(tmp1.log,type="p",xlim=xrange,ylim=yrange,pch=1,col=1,main="Relative Species
Abundance Meadow Site, Clip Treatment",xlab="Species Rank",ylab="log abundance")
points(tmp2.log,col=2,pch=4)
points(tmp3.log,col=4,pch=5)
points(tmp4.log,col=3,pch=3)
legend("topright",c("Spring 04","Spring 05","Spring 06","Spring 07"),pch=c(1,4,5,3),
 col=c(1,2,4,3))
```

APPENDIX D

SPECIES LISTS AND RELATIVE ABUNDANCE VALUES

FOR ALL SITES, TREATMENTS AND SAMPLING PERIODS

Clearcut Site, Control Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Linaria vulgaris	4.62	*Pseudoroegneria spicatum*	3.99	*Linaria vulgaris*	5.12	*Linaria vulgaris*	5.36
Poa pratensis	4.28	*Poa pratensis*	3.81	*Pseudoroegneria spicatum*	3.76	*Pseudoroegneria spicatum*	3.30
Pseudoroegneria spicatum	4.20	Moss spp.	3.58	*Poa pratensis*	3.18	*Agoseris glauca*	3.22
Bunchgrass spp.	3.78	Bunchgrass spp.	3.04	*Erigeron speciosus*	2.56	*Poa pratensis*	3.22
Agoseris glauca	2.94	*Linaria vulgaris*	2.83	*Elymus elymoides*	2.30	Moss spp.	3.00
Antennaria microphylla	2.94	*Erigeron speciosus*	2.20	Moss spp.	2.08	*Collinsia parviflora*	2.89
Moss spp	2.94	*Antennaria microphylla*	2.08	*Aster ascendens*	1.61	*Elymus elymoides*	2.77
Collinsia parviflora	2.48	*Aster ciliolatus*	1.79	*Eriogonum umbellatum*	1.61	*Eriogonum umbellatum*	2.71
Eriogonum umbellatum	2.20	*Elymus elymoides*	1.79	*Collinsia parviflora*	1.39	*Antennaria microphylla*	2.30
Collomia linearis	1.79	*Eriogonum umbellatum*	1.61	Phlox spp.	1.39	*Aster ciliolatus*	1.79
Elymus elymoides	1.61	*Collinsia parviflora*	1.10	*Geranium viscosissimum*	0.69	Bunchgrass spp.	1.39
Erigeron speciosus	1.61	*Achillea millefolium*	0.00	*Achillea millefolium*	0.00	*Carex* spp.	1.39
Phlox spp.	1.61			*Collomia linearis*	0.00	*Phlox* spp.	1.39
Aster ciliolatus	1.39					*Achillea millefolium*	0.69
Carex spp.	1.10						
Senecio spp.	1.10						
Achillea millefolium	0.00						
Aster occidentalis	0.00						

Clearcut Site, Herbicide Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Pseudoroegneria spicatum	4.01	*Pseudoroegneria spicatum*	3.95	*Linaria vulgaris*	4.54	*Linaria vulgaris*	4.98
Linaria vulgaris	3.93	*Poa pratensis*	3.56	*Pseudoroegneria spicatum*	3.89	*Elymus elymoides*	4.08
Eriogonum umbellatum	3.91	Bunchgrass spp.	3.53	*Poa pratensis*	3.61	*Carex spp.*	3.26
Bunchgrass spp.	3.61	Moss spp.	3.00	*Elymus elymoides*	3.53	*Pseudoroegneria spicatum*	3.22
Poa pratensis	3.61	*Elymus elymoides*	2.30	*Carex* spp.	2.20	Moss spp.	2.40
Phlox spp.	3.33	*Eriogonum umbellatum*	1.61	Moss spp.	0.69	*Agoseris glauca*	1.79
Agoseris glauca	3.22			*Erigeron speciosus*	0.00	*Collinsia parviflora*	0.69
Elymus elymoides	3.00						
Collinsia parviflora	2.20						
Erigeron speciosus	1.95						
Collomia linearis	1.61						
Antennaria microphylla	0.69						
Cirsium arvense	0.69						
Achillea millefolium	0.00						
Carex spp.	0.00						
Taraxacum officinale	0.00						
Viola spp.	0.00						
Lupinus argenteus	0.00						

Clearcut Site, Dig Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Pseudoroegneria spicatum	4.43	*Linaria vulgaris*	3.43	*Linaria vulgaris*	5.00	*Linaria vulgaris*	5.15
Linaria vulgaris	4.16	*Aster ciliolatus*	1.10	*Erigeron speciosus*	2.71	*Agoseris glauca*	3.58
Bunchgrass spp.	4.11	*Erigeron speciosus*	0.69	*Collinsia parviflora*	0.69	*Collinsia parviflora*	1.95
Antennaria microphylla	4.01					*Carex* spp.	1.10
Eriogonum umbellatum	3.69					*Achillea millefolium*	0.00
Agoseris glauca	3.09						
Poa pratensis	2.71						
Collinsia parviflora	2.40						
Achillea millefolium	2.08						
Collomia linearis	1.39						
Erigeron speciosus	1.39						
Phlox spp.	1.10						
Elymus elymoides	0.69						
Senecio spp.	0.00						

Clearcut Site, Burn Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Pseudoroegneria spicatum	4.58	*Pseudoroegneria spicatum*	3.22	*Linaria vulgaris*	5.32	*Linaria vulgaris*	4.89
Linaria vulgaris	4.17	*Linaria vulgaris*	3.14	*Pseudoroegneria spicatum*	3.09	*Agoseris glauca*	3.61
Bunchgrass spp.	3.64	Bunchgrass spp.	2.30	*Erigeron speciosus*	2.94	*Elymus elymoides*	3.09
Collinsia parviflora	3.43	*Erigeron speciosus*	2.20	*Eriogonum umbellatum*	1.61	*Eriogonum umbellatum*	2.08
Agoseris glauca	3.00	*Aster ciliolatus*	1.61	*Aster ciliolatus*	1.10	*Collinsia parviflora*	1.95
Achillea millefolium	2.71	*Antennaria microphylla*	0.69	*Collinsia parviflora*	0.69	*Antennaria microphylla*	1.61
Eriogonum umbellatum	2.71	*Eriogonum umbellatum*	0.69	*Achillea millefolium*	0.00	*Penstemon* spp.	1.61
Antennaria microphylla	2.08	*Moss* spp.	0.69	*Elymus elymoides*	0.00	*Pseudoroegneria trichophorum*	1.39
Erigeron speciosus	1.79	*Achillea millefolium*	0.00			*Aster ciliolatus*	1.10
Collomia linearis	1.61	*Elymus elymoides*	0.00			*Carex* spp.	1.10
Carex spp.	1.39					*Achillea millefolium*	0.00
Poa pratensis	1.39						
Aster occidentalis	1.10						
Elymus elymoides	0.00						
Lupinus argenteus	0.00						

Wildfire Site, Control Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Moss spp.	4.81	Moss spp.	5.01	Moss spp.	4.61	Moss spp.	5.29
Linaria vulgaris	4.58	*Carex spp.*	4.20	*Linaria vulgaris*	4.39	*Linaria vulgaris*	4.36
Poa pratensis	3.69	*Eriogonum umbellatum*	3.26	*Erigeron speciosus*	3.74	*Agoseris glauca*	4.19
Collinsia parviflora	3.61	*Linaria vulgaris*	3.22	*Eriogonum umbellatum*	3.61	*Calamagrostis rubescens*	4.04
Eriogonum umbellatum	3.58	*Erigeron speciosus*	3.00	*Elymus elymoides*	3.58	*Pinus contortus*	3.91
Lupinus argenteus	3.58	*Pseudoroegneria spicatum*	2.77	*Pinus contortus*	3.43	*Lupinus argenteus*	3.87
Elymus elymoides	3.56	*Pinus contortus*	2.48	*Calamagrostis rubescens*	3.40	*Eriogonum umbellatum*	3.81
Carex spp.	3.30	*Lupinus argenteus*	1.61	*Maianthemum stellatum*	3.40	*Elymus elymoides*	2.94
Pinus contortus	3.22	*Aster ciliolatus*	1.39	*Lupinus argenteus*	2.08	*Aster ciliolatus*	2.71
Erigeron speciosus	3.04	*Collinsia parviflora*	1.39	*Achillea millefolium*	1.61	*Achillea millefolium*	1.95
Mustard spp.	2.94	*Achillea millefolium*	0.69	*Arabis* spp.	1.10	*Carex* spp.	1.79
Agoseris glauca	2.89	*Elymus elymoides*	0.69	*Pseudoroegneria spicatum*	0.69	*Arabis* spp.	0.69
Bunchgrass spp.	2.71	*Mustard* spp.	0.69	*Aster ascendens*	0.69	*Collinsia parviflora*	0.00
Collomia linearis	2.48	*Taraxacum officinale*	0.69	*Geranium viscosissimum*	0.69		
Achillea millefolium	1.95	*Arabis* spp.	0.00	*Poa pratensis*	0.69		
Pseudoroegneria spicatum	0.00			*Taraxacum officinale*	0.69		
Arabis spp.	0.00			*Agoseris glauca*	0.00		
Rorippa tenerrima	0.00						
Taraxacum officinale	0.00						

Wildfire Site, Herbicide Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Moss spp.	4.93	Moss spp.	5.28	Moss spp.	5.11	Moss spp.	5.00
Eriogonum umbellatum	4.45	*Pseudoroegneria spicatum*	3.66	*Pseudoroegneria spicatum*	3.81	*Linaria vulgaris*	3.87
Linaria vulgaris	4.14	*Carex* spp.	2.83	*Poa pratensis*	3.50	*Pseudoroegneria spicatum*	3.69
Collinsia parviflora	3.97	*Elymus elymoides*	2.30	*Calamagrostis rubescens*	2.89	*Calamagrostis rubescens*	3.43
Agoseris glauca	3.58			*Linaria vulgaris*	2.56	*Elymus elymoides*	3.33
Elymus elymoides	3.50			*Elymus elymoides*	1.61	*Cirsium arvense*	0.69
Poa pratensis	3.30			*Aster ascendens*	0.69		
Carex spp.	3.26						
Lupinus argenteus	3.26						
Pseudoroegneria spicatum	3.22						
Mustard spp.	2.83						
Collomia linearis	2.56						
Achillea millefolium	1.39						
Rorippa tenerrima	1.39						
Bunchgrass spp.	0.69						
Erigeron speciosus	0.69						

Wildfire Site, Dig Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Linaria vulgaris	4.13	*Linaria vulgaris*	3.50	*Linaria vulgaris*	4.25	*Linaria vulgaris*	4.63
Eriogonum umbellatum	3.89	*Erigeron speciosus*	2.08	*Erigeron speciosus*	3.22	*Agoseris glauca*	3.66
Poa pratensis	3.85	*Collinsia parviflora*	0.00	*Lupinus argenteus*	2.71	*Lupinus argenteus*	3.18
Moss spp.	3.71	Moss spp.	0.00			*Aster ciliolatus*	1.10
Lupinus argenteus	3.58					*Collinsia parviflora*	1.10
Agoseris glauca	3.53					Moss spp.	1.10
Collinsia parviflora	3.50					*Arabis* spp.	0.69
Bunchgrass spp.	3.43					*Elymus elymoides*	0.00
Erigeron speciosus	3.09					*Macaeranthera canescens*	0.00
Mustard spp.	3.09						
Collomia linearis	2.30						
Elymus elymoides	1.95						
Rorippa tenerrima	1.39						
Achillea millefolium	1.10						
Carex spp.	1.10						
Antennaria microphylla	0.69						
Arabis spp.	0.00						

Wildfire Site, Burn Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Linaria vulgaris	4.34	*Linaria vulgaris*	3.47	*Eriogonum umbellatum*	3.64	*Eriogonum umbellatum*	4.11
Agoseris glauca	4.14	*Erigeron speciosus*	3.22	*Linaria vulgaris*	3.64	*Linaria vulgaris*	4.04
Eriogonum umbellatum	4.06	*Eriogonum umbellatum*	3.09	*Erigeron speciosus*	3.37	*Agoseris glauca*	3.76
Poa pratensis	4.04	*Carex* spp.	3.04	*Calamagrostis rubescens*	2.94	*Calamagrostis rubescens*	2.89
Carex spp.	3.74	Moss spp.	2.48	Moss spp.	2.64	*Lupinus argenteus*	2.89
Collinsia parviflora	3.43	*Achillea millefolium*	1.79	*Lupinus argenteus*	1.95	Moss spp.	2.64
Moss spp.	3.30	*Taraxacum officinale*	1.39	*Pseudoroegneria spicatum*	1.79	*Elymus elymoides*	1.79
Lupinus argenteus	3.00	*Pseudoroegneria spicatum*	1.10	*Achillea millefolium*	1.61	*Collinsia parviflora*	1.39
Collomia linearis	2.89	*Elymus elymoides*	0.69	*Elymus elymoides*	1.10	*Arabis* spp.	1.10
Mustard spp.	1.95	*Aster ciliolatus*	0.00	*Poa pratensis*	1.10	*Aster ciliolatus*	1.10
Rorippa tenerrima	1.79	*Collinsia parviflora*	0.00	*Arabis* spp.	0.00	*Achillea millefolium*	0.69
Pseudoroegneria spicatum	1.10			*Aster ascendens*	0.00	*Macaeranthera canescens*	0.00
Bunchgrass spp.	1.10						
Taraxacum officinale	1.10						
Achillea millefolium	0.69						
Arabis spp.	0.69						
Penstemon spp.	0.69						
Erigeron speciosus	0.00						

Riparian Site, Control Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Linaria vulgaris	5.56	*Linaria vulgaris*	4.36	*Fragaria virginiana*	5.09	*Fragaria virginiana*	4.79
Agoseris glauca	4.84	*Fragaria virginiana*	4.34	*Linaria vulgaris*	4.87	*Linaria vulgaris*	4.76
Erigeron speciosus	4.62	*Aster ciliolatus*	4.16	*Poa pratensis*	4.63	*Aster ascendens*	3.83
Fragaria virginiana	4.38	Moss spp.	3.43	*Aster occidentalis*	4.36	*Phleum pratense*	3.81
Carex spp.	4.19	*Achillea millefolium*	3.30	*Carex* spp.	3.69	*Viola* spp.	3.00
Achillea millefolium	3.87	Bunchgrass spp.	2.77	*Erigeron speciosus*	3.66	Bunchgrass spp.	2.94
Moss spp.	3.56	*Erigeron speciosus*	2.56	*Stellaria* spp.	3.22	*Penstemon* spp.	2.56
Antennaria microphylla	3.26	*Antennaria microphylla*	1.79	Moss spp.	3.00	*Lupinus argenteus*	2.48
Taraxacum officinale	2.77	*Agoseris glauca*	1.61	*Achillea millefolium*	2.48	*Antennaria microphylla*	2.20
Collinsia parviflora	2.71	*Carex* spp.	1.61	*Collomia linearis*	2.08	*Potentilla gracilis*	1.61
Arnica spp.	2.08	*Potentilla gracilis*	1.39	*Collinsia parviflora*	1.95	*Agoseris glauca*	1.10
Lupinus argenteus	2.08	*Stellaria* spp.	0.69	*Geum macrophyllum*	1.95	*Poa pratensis*	1.10
Penstemon spp.	1.79	*Lupinus argenteus*	0.00	*Aster ascendens*	1.39	*Epilobium angustifolium*	0.69
Elymus elymoides	0.69	*Taraxacum officinale*	0.00	*Lupinus argenteus*	0.69	*Taraxacum officinale*	0.69
Cirsium arvense	0.00			*Maianthemum stellatum*	0.69	*Achillea millefolium*	0.00
Geum macrophyllum	0.00			*Geranium viscosissimum*	0.00	*Arabis* spp.	0.00
				Rorippa tenerrima	0.00	*Arnica* spp.	0.00
				Senecio spp.	0.00	*Stellaria* spp.	0.00
				Taraxacum officinale	0.00	*Eriogonum umbellatum*	0.00

Riparian Site, Herbicide Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Linaria vulgaris	4.96	*Carex* spp.	2.83	*Poa pratensis*	5.53	*Linaria vulgaris*	4.62
Agoseris glauca	4.06	Moss spp.	0.00	*Linaria vulgaris*	4.06	Bunchgrass spp.	3.04
Achillea millefolium	3.33	*Collinsia parviflora*	0.00	*Carex* spp.	2.77	*Penstemon* spp.	2.20
Carex spp.	3.22			*Collinsia parviflora*	2.40	*Phleum pratense*	1.95
Arnica spp.	3.04			*Collomia linearis*	0.69	*Poa pratensis*	1.79
Taraxacum officinale	2.89					*Carex* spp.	1.10
Potentilla gracilis	2.48						
Fragaria virginiana	2.08						
Penstemon spp.	1.79						
Antennaria microphylla	1.10						
Cirsium arvense	0.69						
Collinsia parviflora	0.00						
Rorippa tenerrima	0.00						
Geum macrophyllum	0.00						
Lupinus argenteus	0.00						

Riparian Site, Dig Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Linaria vulgaris	4.75	*Linaria vulgaris*	3.85	*Poa pratensis*	4.54	*Linaria vulgaris*	4.44
Erigeron speciosus	3.91	*Taraxacum officinale*	2.64	*Linaria vulgaris*	4.19	*Fragaria virginiana*	3.50
Fragaria virginiana	3.69	*Aster ciliolatus*	2.08	*Carex* spp.	3.97	Bunchgrass spp.	3.37
Agoseris glauca	3.30	*Carex* spp.	1.95	*Fragaria virginiana*	3.50	*Viola* spp.	2.40
Taraxacum officinale	3.30	*Erigeron speciosus*	1.39	*Erigeron speciosus*	3.09	*Lupinus argenteus*	1.95
Carex spp.	3.14	*Agoseris glauca*	1.10	*Aster occidentalis*	2.48	*Agoseris glauca*	1.79
Collinsia parviflora	2.94	*Fragaria virginiana*	1.10	*Rorippa tenerrima*	2.08	*Achillea millefolium*	1.61
Potentilla gracilis	2.56	*Collinsia parviflora*	0.00	*Geum macrophyllum*	1.39	*Phleum pratense*	1.39
Achillea millefolium	2.30	*Lupinus argenteus*	0.00	*Achillea millefolium*	0.69	*Poa pratensis*	1.10
Moss spp.	2.30			*Collinsia parviflora*	0.69	*Carex* spp.	0.69
Arnica spp.	2.08			*Lupinus argenteus*	0.69	*Mustard* spp.	0.69
Antennaria microphylla	1.39			*Aster ciliolatus*	0.00	*Taraxacum officinale*	0.69
Phleum pratense	1.39			*Collomia linearis*	0.00	*Antennaria microphylla*	0.00
Penstemon spp.	1.10			*Taraxacum officinale*	0.00	*Potentilla gracilis*	0.00
						Geum macrophyllum	0.00

Meadow Site, Control Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Poa pratensis	6.51	*Poa pratensis*	5.87	*Poa pratensis*	6.45	*Poa pratensis*	5.85
Linaria vulgaris	4.83	*Bunchgrass spp.*	2.71	*Linaria vulgaris*	3.22	*Linaria vulgaris*	3.50
Aster ciliolatus	4.11	*Aster ciliolatus*	1.95	*Aster ciliolatus*	2.83	*Trifolium longipes*	2.94
Maianthemum stellatum	3.66	*Erigeron speciosus*	1.61	*Maianthemum stellatum*	2.40	*Aster occidentalis*	2.71
Erigeron speciosus	3.50	*Achillea millefolium*	0.69	*Geum macrophyllum*	2.30	*Maianthemum stellatum*	2.30
Agoseris glauca	2.83	*Geranium viscosissimum*	0.69	*Trifolium longipes*	1.79	*Cirsium arvense*	1.95
Achillea millefolium	2.64	*Linaria vulgaris*	0.69	*Aster ascendens*	1.39	*Achillea millefolium*	1.61
Trifolium longipes	2.20	*Delphinium glaucum*	0.00	*Potentilla gracilis*	1.39	*Agoseris glauca*	1.61
Collomia linearis	2.08	*Frasera speciosa*	0.00	*Achillea millefolium*	1.10	*Epilobium angustifolium*	1.61
Geranium viscosissimum	2.08	*Rorippa tenerrima*	0.00	*Epilobium angustifolium*	1.10	*Galium* spp.	1.61
Aster occidentalis	0.00	*Zigadenus elegans*	0.00	*Aster occidentalis*	0.69	*Phleum pratense*	1.39
Carex spp.	0.00			*Carex* spp.	0.69	*Potentilla gracilis*	1.10
Collinsia parviflora	0.00			*Frasera speciosa*	0.69	*Aster ciliolatus*	0.69
Galium spp.	0.00			*Zigadenus elegans*	0.69	*Geranium viscosissimum*	0.69
Zigadenus elegans	0.00			*Stellaria* spp.	0.00	*Tragopogon dubius*	0.69
Arnica spp.	0.00			*Collinsia parviflora*	0.00	*Collinsia parviflora*	0.00
				Delphinium glaucum	0.00	*Viola* spp.	0.00
				Elymus elymoides	0.00	*Zigadenus elegans*	0.00
				Erigeron speciosus	0.00	*Delphinium glaucum*	0.00

Meadow Site, Herbicide Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Poa pratensis	6.64	*Poa pratensis*	5.88	*Poa pratensis*	6.35	*Poa pratensis*	5.75
Linaria vulgaris	3.97	Bunchgrass spp.	2.71	*Aster ascendens*	1.39	*Aster occidentalis*	2.08
Erigeron speciosus	3.61	*Aster ciliolatus*	0.00	*Linaria vulgaris*	0.00	*Linaria vulgaris*	1.39
Aster occidentalis	3.40			*Maianthemum stellatum*	0.00	*Maianthemum stellatum*	0.00
Geranium viscosissimum	3.30			*Trifolium longipes*	0.00	*Viola* spp.	0.00
Aster ciliolatus	2.64						
Geum macrophyllum	1.39						
Carex spp.	1.10						
Trifolium longipes	1.10						
Achillea millefolium	0.69						
Agoseris glauca	0.69						
Maianthemum stellatum	0.69						
Mustard	0.69						
Collinsia parviflora	0.00						
Galium spp.	0.00						
Zigadenus elegans	0.00						
Collomia linearis	0.00						

Meadow Site, Dig Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Poa pratensis	6.06	*Linaria vulgaris*	2.94	*Linaria vulgaris*	4.50	*Poa pratensis*	4.88
Geranium viscosissimum	3.56	*Poa pratensis*	2.89	*Poa pratensis*	3.81	*Aster occidentalis*	3.95
Linaria vulgaris	3.56	*Aster ciliolatus*	2.20	*Aster ascendens*	2.77	*Linaria vulgaris*	3.87
Erigeron speciosus	2.94	*Aster occidentalis*	1.61	*Delphinium glaucum*	2.48	*Trifolium longipes*	2.71
Maianthemum stellatum	2.94	*Senecio* spp.	0.69	*Aster ciliolatus*	1.95	*Collinsia parviflora*	2.56
Carex spp.	2.71			*Trifolium longipes*	1.79	*Polygonum* spp.	2.08
Aster ciliolatus	2.40			*Epilobium angustifolium*	1.39	*Geranium viscosissimum*	1.61
Trifolium longipes	2.20			*Maianthemum stellatum*	1.10	*Galium* spp.	1.10
Achillea millefolium	1.61			*Carex* spp.	0.69	*Maianthemum stellatum*	1.10
Agoseris glauca	0.69			*Rorippa tenerrima*	0.00	*Epilobium angustifolium*	0.69
Collinsia parviflora	0.69					*Carex* spp.	0.00
Collomia linearis	0.00					*Antennaria microphylla*	0.00
Phleum pratense	0.00					*Potentilla gracilis*	0.00

Meadow Site, Burn Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Poa pratensis	6.09	*Poa pratensis*	5.76	*Poa pratensis*	5.49	*Poa pratensis*	5.68
Linaria vulgaris	3.81	*Aster ciliolatus*	2.83	*Delphinium glaucum*	3.66	*Linaria vulgaris*	3.64
Maianthemum stellatum	3.47	*Linaria vulgaris*	2.08	*Aster ascendens*	2.64	*Delphinium glaucum*	2.83
Geranium viscosissimum	3.33	*Geranium viscosissimum*	1.61	*Geranium viscosissimum*	2.48	*Aster occidentalis*	2.77
Aster ciliolatus	3.26	*Delphinium glaucum*	1.10	*Linaria vulgaris*	2.48	*Trifolium longipes*	2.40
Delphinium glaucum	3.14	Bunchgrass spp.	0.00	*Trifolium longipes*	1.95	*Geranium viscosissimum*	2.20
Erigeron speciosus	3.14	*Trifolium longipes*	0.00	*Aster ciliolatus*	1.79	*Cirsium arvense*	2.08
Trifolium longipes	1.61			*Maianthemum stellatum*	1.79	*Maianthemum stellatum*	2.08
Carex spp.	0.00					*Tragopogon dubius*	0.69
Collomia linearis	0.00					*Epilobium angustifolium*	0.00
						Zigadenus elegans	0.00

Meadow Site, Clip Plots. Species lists and relative species abundance (log).

Spring 2004	RSA	Spring 2005	RSA	Spring 2006	RSA	Spring 2007	RSA
Poa pratensis	6.07	*Poa pratensis*	6.11	*Poa pratensis*	5.72	*Poa pratensis*	5.56
Linaria vulgaris	3.76	*Aster ciliolatus*	2.56	*Aster ascendens*	3.18	*Aster occidentalis*	3.50
Maianthemum stellatum	3.53	Bunchgrass spp.	1.95	*Maianthemum stellatum*	3.00	*Linaria vulgaris*	3.22
Geranium viscosissimum	3.33	*Achillea millefolium*	1.79	*Linaria vulgaris*	2.77	*Maianthemum stellatum*	2.64
Erigeron speciosus	3.18	*Geranium viscosissimum*	1.10	*Aster occidentalis*	2.64	*Delphinium glaucum*	2.20
Achillea millefolium	2.56	*Linaria vulgaris*	0.69	*Delphinium glaucum*	2.40	*Geranium viscosissimum*	2.20
Aster ciliolatus	2.48	*Aster occidentalis*	0.00	*Geranium viscosissimum*	2.08	*Achillea millefolium*	1.79
Carex spp.	1.61	Moss spp.	0.00	*Achillea millefolium*	1.39	*Potentilla gracilis*	1.61
Trifolium longipes	1.10	*Delphinium glaucum*	0.00	*Aster ciliolatus*	1.39	*Trifolium longipes*	1.39
Zigadenus elegans	0.69			*Potentilla gracilis*	1.10	*Stellaria* spp.	1.10
Agoseris glauca	0.00			*Trifolium longipes*	1.10	*Cirsium arvense*	1.10
Collomia linearis	0.00			*Stellaria* spp.	0.69	*Epilobium angustifolium*	1.10
Phleum pratense	0.00			*Cirsium arvense*	0.69	*Galium* spp.	0.69
Potentilla gracilis	0.00			*Elymus elymoides*	0.00	*Myosotis asitica*	0.69
				Epilobium angustifolium	0.00	*Lupinus argenteus*	0.00
				Lupinus argenteus	0.00	*Tragopogon dubius*	0.00
				Erigeron speciosus	0.00		
				Zigadenus elegans	0.00		

APPENDIX E

PATHWAYS TO DATA AND R SCRIPT FILES

Data can be found in:
\\Seedbank\d\Experiments\Data\WYellowstone\Lehnhoff\Dissertation

\Chapter1-Lit_Review
    Endnote File
    Figure

\Chapter2-Size_Propagule
    \Seeds
        All seed collection data
    \temp_precip.xls
        Historical temperature and precipitation data
    \VSVDs
        \VSVD2005
            \2005_VS_VD_Results.xls
                2005 stem count data
        \VSVD2006
            \2006_VS_VD_Results.xls
                2006 stem count data
        \VSVD2007
            \2007_VS_VD_Results.xls
                2007 stem count data

\Chapter3-Invasiveness
    \Charles_Sites_Data.xls
        Raw stem count data for Ridge, Valley and Forest for all years
    \lambda_and_invasiveness.xls
        Calculated values of lambda and invasiveness
    \MeanData.xls
        Values of invasiveness, % sand, annual solar radiation and precipitation
    \soil_sample_data.xls
        Soil analysis data for Ridge, Valley and Forest Sites
    \R\calculate_lambdas
        R script for calculating population lambdas
    \R\Inv_Mod_01-02.txt
        R script for calculating population invasiveness (years 2001-2002)
    \R\Inv_Mod_02-03.txt
        R script for calculating population invasiveness (years (2002-2003)
    \R\Inv_Mod_03-04.txt
        R script for calculating population invasiveness (years 2003-2004)
    \R\Inv_Mod_04-05.txt
        R script for calculating population invasiveness (years 2004-2005)

\R\Inv_Mod_05-06.txt
R script for calculating population invasiveness (years 2005-2006)

\Chapter4-Effects_Disturbance
\density.xls
Stem count data for all years and treatments at Clearcut, Wildfire, Riparian and Meadow Sites
\data_for_stats.xls
Stem count data for all years and treatments at Clearcut, Wildfire, Riparian and Meadow Sites arranged for statistical analysis
\soil_sample_results.xls
Soil analysis data for Clearcut, Wildfire, Riparian and Meadow Sites
\INV.txt
R script for calculating invasiveness

\Chapter5-Native_Veg
\NativeVeg.xls
Percent cover of all species in all plots at Clearcut, Wildfire, Riparian and Meadow Sites for all sampling events
\Native_Analysis.txt
R script for calculating species richness and diversity and relative species abundance