

EVALUATING AND MONITORING INVASIVE PLANT PROCESSES

by

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ABSTRACT

Non-indigenous plant species (NIS) are a concern for both natural area land managers and the public. These species are perceived negatively despite the fact that the processes and impacts related to NIS are not fully understood. Also, control is generally conducted without understanding NIS population ecology. As a result, few NIS populations have been successfully controlled.

We studied the population ecology of NIS in natural areas. First, *Linaria vulgaris* was monitored at different spatial scales over three years to determine its invasiveness, and also to determine which life history states drove this invasiveness. An invasive population was one that increased in density and/or spatial extent over time. We found that not all study populations were invasive, that invasiveness varied across spatial scales and habitats, and that invasiveness at one spatial scale did not necessarily correspond with invasiveness at another. This invasiveness was driven primarily by vegetative spread. Relative population invasiveness was then evaluated using an invasiveness index, a tool for prioritizing management.

Next, we explored the contribution of NIS propagule pressure with distance from a road to NIS colonization of a natural grassland. Roads are the major vector for NIS propagule movement into natural areas, and NIS occurrence decreases rapidly with distance from roads. Two species with different colonization strategies, *Cirsium arvense*, and *Bromus inermis* were studied. *Bromus inermis* seed rain and seed bank decreased both with distance from the road and established patches. *Cirsium arvense* seed rain decreased with distance from established patches, but not the road. Soil water and conditions for emergence were studied using surrogate NIS to see if emergence varied with distance from the road. Soil water only varied with distance from the road in June; and soils were otherwise uniformly moist or dry. Surrogate NIS emergence did not vary with distance from the road or varying soil water. Finally, seed predation was studied to determine if whether it varied with distance from the road or between four different species. Seed predation varied with distance from the road and also between species for two of the four species.

REVIEW OF LITERATURE

Introduction

Managers of natural areas are faced with a huge challenge when confronting the increasing number and abundance of non-indigenous species (NIS). Within U.S. national forests and parks the management of NIS and the preservation of biodiversity are mandated by law (U.S. Congress 1872; U.S. National Park Service 1996). However, according to the U.S. General Accounting Office (1998) and a coalition of leading environmental groups (Wilderness Society 2004), funding for public lands management has not kept pace with the increasing pressures and needs on these lands. To face the challenge of NIS and to do more with less, land managers need better tools for estimating NIS invasiveness and impact, thus more efficiently prioritizing and implementing management.

The human population is now over 6.3 billion worldwide and is expected to reach 9 billion by 2050 (U.S. Census Bureau 2004). As a result of the current population, an estimated 83% of the earth's terrestrial surface has been directly altered or fragmented by human processes such as road construction, conversion to farmland, resource extraction, urbanization and the movement of species from their regions of origin to new continents and regions (Sanderson et al. 2002). Individual habitats have been altered to different extents. For example, in the U.S.A. alone 99% of tall grass prairies and 53% of wetlands have been converted to human use (Dahl and Johnson 1991; Swengel and Swengel 1995).

Non-indigenous species are a significant component of this human-induced global change, although the magnitude of the biotic costs of NIS to ecological systems is just beginning to be assessed (Mack 1981; Vitousek et al. 1997; Walker and Steffen 1997). Pimental et al. (1999) estimated that 17,000 plant species are native to the U.S. and that in the last 500 years, many thousands of non-indigenous plant species have been introduced. Of the introduced plant species, approximately 5000 have become established and approximately 500 are causing environmental and economic problems (Pimental et al. 1999). In Britain, Crawley (1997) recorded the proportion causing problems to be even smaller. Of the approximately 23,550 NIS that were found and able to grow wild in Britain, only 5% became naturalized and only 0.1% were a problem. According to Pimental et al. (1999), invasive species in the U.S. cause economic and environmental damages totaling over \$138 billion per year, with agricultural weed control and crop losses costing approximately \$34 billion per year. Culotta (1991) described the global spread and the extent of ecological change wrought by NIS as the biological homogenization of the world flora.

While the number and abundance of NIS is much lower in protected areas than in the surrounding human-dominated landscapes (Usher 1988; Pauchard et al. 2003), NIS still represent a significant threat to the ecosystems and biodiversity in these areas (MacDonald et al. 1989; Lonsdale 1999; Stohlgren et al. 1999; Olliff et al. 2001). This is because indigenous plant communities, including communities within protected natural areas and communities that lack obvious human disturbance, are susceptible to invasion by NIS (Cronk and Fuller 1995; Tilman 1997 a; Stohlgren et al. 1999; Weaver et al.

2001; Pauchard et al. 2003). Exotic flora represent an estimated 19% of the U.S. flora (Lonsdale 1999). Within the Northern Rocky Mountains, 29 NIS are common invaders of indigenous vegetation communities (Weaver et al. 2001). NIS comprise 15% of the flora in Yellowstone National Park (Whipple 2001).

Non-indigenous species may degrade natural habitats by displacing indigenous species and altering community composition, and also by altering natural disturbance regimes such as fire frequency (Vitousek et al. 1997; Davis et al. 2000; Mack et al. 2000). NIS may also alter successional processes through changes in soil nutrients, biogeochemical cycles, organic matter and biota; and these changes can lead to feedbacks which allow for further disruptions and further weed invasion (Wardle 2002). The loss of indigenous seed banks and seed sources can lead to a change in species composition away from indigenous plant communities (D'Antonio and Vitousek 1992). This change in species composition can result in further negative feedbacks, as a recent study suggests that affiliate indigenous species can be lost when species upon which they depend are lost (Koh et al. 2004).

Some impacts of NIS are well documented in the scientific literature, such as the displacement of temperate bunchgrass communities by downy brome (*Bromus tectorum*) in the sage-steppe of the intermountain west of the U. S. (Mack 1989; D'Antonio and Vitousek 1992). The enduring perception of the negative impacts of NIS is the basis for costly, uncoordinated, and - especially in natural areas - largely unsuccessful management programs (Simberloff 1996; Hulme 2003). Simberloff (2003) argued that when NIS are discovered they should be immediately attacked by whatever means are

known to be effective. Williamson (1996) criticized such an approach to controlling NIS by stating that definitions of a pest species are most often socio-economically and not ecologically based. Mack et al. (2000) further stated that in many cases, assumptions about impacts are not supported with sufficiently rigorous quantitative experimentation. Cousens and Mortimer (1995) stated that more research is needed in order to improve our understanding of NIS spatial and temporal dynamics in agricultural systems. These observations also apply to natural systems, where far fewer studies have been performed and significantly less is known.

The studies presented here began with the idea that the invasiveness and impact of NIS may vary among species and in space and time. The impacts may also vary among different plant communities (Rew et al. 2002). Lessons from conservation biology indicate that an organism's demographics, including fecundity, germination, establishment and death rates, can determine survival, abundance and dispersal within and among habitats (Bullock et al. 1994; Meekins and McCarthy 2001). These demographics can vary among different populations and years.

Patterns of Plant Establishment as Related to NIS

Many biological and environmental processes work together to determine patterns in plant communities, even in communities with NIS. Facilitation, inter- and intra-specific competition and allelopathy influence plant patterns (Mack and Harper 1997). Other determinators include soil and environmental heterogeneity, reproduction strategy and seed dispersal, safe-sites, disturbance, and stochastic processes (Greig-Smith 1979;

Barot et al. 1999). Abiotic and biotic heterogeneity of the environment are often essential to the coexistence of species and the spatial and temporal distributions of species are descriptions of patterns of diversity (Levin 1992).

Patterns of invasion can include random diffusion (Skellam 1951), advance along a united front (phalanx) and sporadic advance (guerilla) (Lovett-Doust 1981). A common pattern for the spread of NIS is that they spread outward from a point of initial introduction (Rejmánek 1989). Early in the invasion when population densities are low, NIS are often clustered in patches around the points of introduction, with their distribution becoming more dispersed as the individual patches grow together (Pauchard et al. 2003).

Clustered patterns result when reproduction is vegetative and when individual patches grow along a front that is clustered around the parent plant (Cousens and Mortimer 1995). Parent plants and flowers are often spatially clustered, so both seed dispersal and germination are also often clustered (Rabinowitz and Rapp 1980). High environmental heterogeneity can also result in clustered plant distributions both within a species and across a landscape (Begon et al. 1986). Competition for soil resources or the heterogeneous distribution of these resources have been shown to result in random distributions (Barbour and Diaz 1973). Species that reproduce by seed are more likely to spread randomly or in discretely dispersed patches than species more dependent upon vegetative reproduction (Thompson 1958). In terms of random patterns, while individual organisms or plants do not move randomly, the movement and mortality of large numbers of individuals may be indistinguishable from a random distribution (Barot et al. 1999).

Local population dynamics and spatial dynamics can be sensitive to different factors, so determining the scale for the study of invasion is necessary for understanding the long-term fate of populations across the landscape (D'Antonio et al. 2004). Smaller-scale point patterns can influence patterns over larger scales. Also, dispersal patterns can vary for seedlings and adults of the same species. As an example of this, the palm tree *Borassus aethiopum* grows in the humid savanna of West Africa (Barot et al. 1999). Its seedlings were found to have an aggregated distribution because the plant's seeds have a short dispersal distance (5 m to 12 m) from the mother tree. However, adult plants had a random distribution that reflected the dispersal of nutrient rich patches (termite mounds) and inter-specific competition at scales larger than 5 m to 12 m.

Density Dependence and Competition

The number of individuals in an established plant population is determined by the numbers of births, deaths, immigrants and emigrants, and also by regulation from density dependent processes (Watkinson 1997). Because of density dependence, rates of population growth slow with time and a maximum population size is eventually reached, albeit with variation of the maximum population size. Density dependence can act to regulate individual plant and also plant population size by decreasing the number of seeds produced per plant and also the number of plants surviving to reproduction (Meekins and McCarthy 2001). Small plants are thought to be more sensitive to density effects than larger plants (Watkinson 1997). However, for small or recently established NIS populations, low population density can increase the probability that a population will go

extinct (Meekins and McCarthy 2001). Population densities are usually low along the invading front (a good reason for investigating differences in plant densities at the patch interior versus edge) and reproduction is frequently inhibited in sparse or small populations (Travis and Dytham 2002). An understanding of density dependent effects can be confounded by spatial heterogeneity, seed production, predation and other factors (Watkinson 1997).

Tilman (1997 b) stated that, in order to coexist, an inferior competitor must either have greater longevity or be a superior colonist. Individual plants that have a high relative growth rate are thought to have superior competitive ability (Callaway and Walker 1997). The life stage of the plant, whether it is a seed, seedling, pre-reproductive adult or reproductive adult, may also affect interactions between individual plants or plant species (Callaway and Walker 1997).

Three hypotheses have been put forth to explain why NIS are better competitors than indigenous species. One reason for this, suggested by Callaway and Aschehoug (2000), is that NIS may have evolved in a more competitive environment. Another hypothesis, the escape from enemies' hypothesis, posits that NIS exhibit enhanced performance following introduction to a new region (Lawton and Brown 1986). This is because having escaped from natural enemies, i.e. their competitors, pathogens and predators, NIS have more resources available for growth and reproduction than indigenous species. Finally, NIS may be able to out-compete indigenous populations in the short-term because short-term indigenous species performance may be constrained by

long-term adaptations to long-term periodic disturbances such as drought or fire (Reiman and Clayton 1997).

Burke and Grime (1996) divided invasive plant characteristics into two groups: those that respond to disturbance (smaller-seeded species that grew faster and were better able to capture and use resources), and those that are able to invade closed, established perennial communities (generally larger-seeded species which were slower growing and better able to resist competition from established plants). Cousins and Mortimer (1995) also found that species which invade established, closed, perennial communities have larger seeds, more even distributions, and longer persistence in the seed bank than those that do not. Bazazz (1986) found that species that respond to disturbance generally have small seeds, rapid growth and high resource demands, as well as phenotypic plasticity, prostrate growth form and ground-level buds.

Theories of Non-Indigenous Species Invasion

Several ideas are particularly important to providing a context for understanding NIS invasion of natural areas. When discussing NIS as they relate to community invasibility, it is important to observe that most NIS fail to become established (Williamson 1996). Also, the populations of any species in a community must be invasive to some degree ($\lambda > 1.0$ where λ is the rate of population growth) if that species is to persist within a community (Crawley 1997).

Dispersal between suitable environments was once limited by natural barriers, such as oceans, deserts and mountain ranges, and time, allowing for the differential

development of plant species and communities. Humans have recently broken down many of these barriers to natural species dispersal (Vitousek et al. 1997). Different forms of human transport have either intentionally or unintentionally removed such barriers for many species. Due to this breakdown, current rates of exotic species invasion occurs at ten times the rate of historic climate-driven Holocene plant migration (Mack 1989; Vitousek 1992). Present-day plant community associations in the Northern Rocky Mountains have a relatively short history. The paleoecological record reveals continual change in plant community composition over time, mediated by climate change and its resulting effects on fire frequency and the physical and biotic environment (Whitlock and Millspaugh 2001). These researchers hypothesized that due to human influence on the rate of climate change, future climate change might occur with unprecedented speed, requiring plant species to migrate at unprecedented rates just to keep pace. For some species this migration may no longer be possible in our human-altered and fragmented landscapes.

The debate between proponents of Hubbell's unified neutral theory of biodiversity and biogeography (2001) and Elton's (1958) classic community assembly theory provides a theoretical basis for thinking about how plant species colonize new areas. Hubbell's theory is based on the assumptions that all species are transient, few examples of true community equilibrium are present in nature, and that species assemblages are determined by chance, individual plant survival, random migration, random speciation, disturbance and niche assembly rules. One study supporting Hubbell's theory (Levine 2000) showed that invasion is mostly a function of propagule pressure. Elton's more

established community assembly theory (1958) stated that species are competitive in particular niches and that niche assembled communities are at stable equilibrium.

MacArthur and Wilson (1967) built upon this with their dispersal assembly theory which assumed that all species have equal potential for colonization, that history and random dispersal create communities, and that late arriving species are less successful. Davis et al. (2000) supported the community assembly theory by showing that invasion is influenced by fluctuating resource availability, species frequency is related to resource availability, and that population fluctuations are caused by disturbance.

The following theories have been put forth to specifically explain NIS invasion. McEvoy et al. (1993) described an “activation hypothesis” where recruitment of individual plants from the seed bank is dependent upon localized disturbance. Lonsdale (1999) proposed that invasion is based upon ecosystem properties, frequency of disturbance, propagule pressure and specific properties of the invasive species. Davis et al. (2000) state that invasion is a function of fluctuating resource availability and that these fluctuations are caused by disturbance.

One current question in ecology asks whether more diverse habitats are more invulnerable than less diverse habitats. Elton’s classic view (1958), later supported by Tilman (1997 a), was that plant communities that are rich in species and/or functional groups are more resistant to invasion. In communities with a greater number of functional groups, the spectrum of available resources would be more completely used and thus fewer resources would be available for invaders. Contrarily, Stohlgren et al. (1999) argued that species rich areas are more invaded than species poor areas and that

this may be a function of resource availability. Belnap and Phillips (2001) showed that fertile sites, or sites with more silt and a more continuous cover of living and dead plant material, had higher soil moisture and more safe sites for germination, and thus were more susceptible to invasion.

Invasiveness can vary across different plant community types. Riparian areas are more invaded than adjacent uplands (Stohlgren et al. 1998; Levine 2000). In the northern range of Yellowstone National Park, plant communities dominated by grasses, forbs and shrubs were more often invaded than forests (Weaver et al. 2001, Rew et al. 2002). Also in the Northern Rockies, Weaver et al. (2001) found that invasion of undisturbed habitats declined from grasslands and open forests to moist forests and alpine. Whichever theory or combination of theories is eventually accepted, these studies have shown that invasion is a complex process that can be affected by propagule pressure, species distribution, population demographics, disturbance, resource competition and chance.

Monitoring

As the ecological and economic impacts of NIS continue to increase, the question is raised as to how to best apply science to the regulation and management of invasive plants (D'Antonio et al. 2004). This study is based upon the basic tenets of integrated pest management (IPM). These tenets include an initial inventory or survey to find out where NIS populations exist within a management area. Monitoring is performed to determine which NIS are actually invasive in which habitats (consistently increasing in spatial and/or spatial extent), to assess the impact of NIS on indigenous plant

communities and to evaluate the need for and effectiveness of management efforts (Haber 1997; Rew et al. in press a). There is little in the scientific literature regarding protocols for monitoring the spatial and temporal dynamics of non-indigenous plant populations, although a variety of sources do mention the need for monitoring (Haber 1997; Wooten and Renwyck 2001). Nor, are there many studies which have quantified invasiveness on a patch scale.

Anthropogenic Disturbance

Disturbance is believed to influence the spread of NIS and human disturbance has been shown to create conditions that are favorable for exotic species invasion (Rejmánek 1989; Hobbs 1991; D'Antonio and Vitousek 1992). Disturbing the soil surface may break dormancy by bringing seeds to the surface and exposing them to light. Seed bank numbers generally decline with increasing frequency of disturbance due to increased germination (Cousens and Mortimer 1995). Disturbance can also support seedling emergence and early growth by providing space, aerated soil, light and nutrients, and reducing competition for limiting resources from the existing community (Froud-Williams et al. 1984). The invasion of NIS is especially enhanced when disturbance differs from the natural disturbance regimes (Hobbs and Huenneke 1992).

The presence of a road alters light availability, soil texture, soil compaction, chemistry, and increases water runoff in adjacent areas (Rejmánek 1989; Hobbs 1991; D'Antonio and Vitousek 1992). NIS spread can be facilitated when roadside materials differ from the native soils (Greenburg et al. 1997). Soil compaction inhibits plant

growth in laboratory studies and also to decrease vegetation cover and change species composition relative to uncompacted soils (Prose et al. 1987). Repeated disturbance along road margins from routine road maintenance procedures includes periodic grading, mowing and snow plowing, plus soil compaction and plant community disturbance from maintenance and other vehicles. Roads also represent a primary driver of habitat fragmentation, another serious threat to our remaining wildlands (Brothers and Springarn 1992; Reed et al. 1996). This fragmentation can increase the ratio of non-forest to forest, and forest edge to forest interior, and can thus provide both points of entry and means of dispersal for NIS propagules (Spellerberg 1998). These effects have led some researchers to suggest that roadless areas should be preserved to act as refuges for indigenous plant diversity against NIS invasion (Gelbard and Harrison 2003).

Seed Dispersal and Vehicles

Cousens and Mortimer (1995) stated that successful NIS are those that are able to disperse because of association with human-managed habitats, and that they dominate and persist because of their wide habitat tolerance and their rapid rate of increase. Propagule pressure may be the most important factor for predicting whether or not a NIS will become established (Davis et al. 2000; Kolar and Lodge 2001). With regard to propagule pressure from vehicles, non-indigenous species have been found attached to vehicles, though at low densities (Clifford 1959; Schmidt 1989; Lonsdale and Lane 1994). In an Australian nature reserve, an average of 2.51 viable seeds were found per vehicle (Lonsdale and Lane 1994). The number of NIS seeds carried by each vehicle varied greatly (from 0.9 to 8,000 seeds) depending upon where and in what season the

study was performed, and whether the vehicle had been driven on paved versus gravel roads (Clifford 1959; Schmidt 1989; Lonsdale and Lane 1994; Hodkinson and Thompson 1997). Higher numbers of seeds were found to be attached on cars driven on unpaved roads than on paved roads (Hodkinson and Thompson 1997). The seeds were present in soil attached to the cars, and more soils were attached to cars driven on unpaved roads. In an English study on urban roads, a seasonal difference was found in the numbers of seeds found on vehicles, with an average of 0.9 seeds in June, and 2.2 seeds in October (Hodkinson and Thompson 1997).

High visitor numbers in protected natural areas is correlated with high NIS invasion rates (MacDonald et al. 1989). In a California study, when roads were improved and vehicle traffic increased, the rate of introduction of NIS increased and the scale of road-associated disturbance also increased (Gelbard and Harrison, 2003). Improved roads generally have higher traffic and higher NIS richness than non-improved roads, possibly because of more frequent disturbance and higher vehicle traffic (Parendes and Jones 2000; Gelbard and Belnap 2003).

There is some information regarding the variation in occurrence and frequency of NIS on the landscape, and several studies demonstrate the potential role of roads as conduits of NIS dispersal. However, few studies evaluate which road related processes assist NIS invasion. Few studies have quantified whether an individual NIS is equally invasive across the environments in which it is found, or have quantified the relative invasiveness of different species. The following two studies were intended to address these issues. In the first study, the invasiveness of a NIS was evaluated at three different

scales; metapopulation, population/patch and within patch over a three year period. In the second study, seed establishment, propagule pressure from seed rain and the seed bank, and seed predation with were evaluated against distance from road, soil moisture, and competition from existing NIS and indigenous vegetation. Yellow toadflax (*Linaria vulgaris* P. Mill) was the species of interest for the invasiveness study, and smooth brome (*Bromus inermis* Leyss), Canada thistle (*Cirsium arvense* (L.) Scop) and two pseudo-NIS, radish (*Raphanus sativa*) and spring wheat (*Triticum aestivum*) were evaluated in the second study.

Hulme (2003) states, with regard to the invasion of NIS into natural areas, that we are “winning the science battles but losing the conservation war”. This is because, while we are beginning to understand the processes of NIS invasion of natural areas, we have had little success in preventing or controlling these invasions at the wider landscape level. The aim of this project is to increase our understanding of the demographics and also the temporal dynamics of individual NIS populations. This will be achieved by testing which ecological processes are driving the observed dynamics, at appropriate scales. A second question addressed here concerns the role of propagule pressure from roads as it relates to NIS invasion of indigenous plant communities. Increased understanding of this problem could allow managers to better forecast and manage future NIS invasion from roads. Our overriding aim with the studies outlined here, and other associated studies, is to better inform land managers as to which species are likely to invade which habitats and should be prioritized for management, thus making the most of limited management dollars.

This may be challenging however, as NIS can demonstrate a phenotypic plasticity that allows for rapid adjustment to different habitats (Sakai et al. 2001).

Three stories are told in this thesis. In Chapter 1, a literature review of plant population ecology is presented as it relates to NIS in natural areas and the specific objectives of this study. In Chapter 2, an experiment is described where we monitored the demographics and temporal dynamics of yellow toadflax to determine invasiveness. In Chapter 3, a second experiment is presented where we quantified the role of NIS propagule pressure on occurrence and establishment with distance from a road. Descriptions of the species of interest are provided below.

Study Species

Linaria vulgaris P. Mill

Problem Description

Yellow toadflax was selected for monitoring at the patch scale because its clonal growth and primarily short-distance dispersal cause it to form discrete patches (Nadeau and King 1991; Saner et al. 1995). Thus patch boundaries are relatively easy to discern. Yellow toadflax presents a challenge for land managers because it invades a variety of upland plant communities, including those that lack obvious human disturbance (Pauchard et al. 2003). This species is especially invasive in grasslands (Saner et al. 1995) where its prolific vegetative reproduction and potentially high seed production

allow for rapid spread and high persistence (Saner et al. 1995). As examples of vegetative spread, a patch in one Canadian study was observed to increase 418 % in a single season and a second one-acre patch was observed to expand to cover 85 acres (an 8500% increase) over a five-year period (Zimmerman 1996).

Yellow toadflax can be an aggressive weed in rangelands where it replaces useful herbs and grasses (Jeanneret and Shroeder 1991; Saner et al. 1995). It is avoided by cattle and native browsers (Mitich 1993; Saner et al. 1995), and contains a glucoside that is mildly poisonous to livestock (Morishita 1991). It is a particular problem in zero and minimum till agriculture in the northern plains (McClay 1992), and high yellow toadflax densities (180 stems m⁻²) have reduced forage crops-seed yields by 33% in Alberta (Saner et al. 1995). Yellow toadflax has been used as a garden ornamental, in folk medicine, as a dye, as an insecticide, and, for soil stabilization (Mitich 1993; Saner et al. 1995).

Yellow toadflax is listed as a weed in the U.S. Europe, Russia, New Zealand and Canada (Saner et al. 1995). In the U.S., it is on the state noxious weed lists of Colorado, Idaho, Nevada, New Mexico, Oregon, South Dakota, Washington and Wyoming (USDA 2004). Montana is not on the USDA list but it will be added soon as it is listed as a Category 1 noxious weed in the Montana County Weed List (Montana Department of Agriculture 2003). Category 1 noxious weeds are currently established in many counties, are capable of rapid spread, and have the potential to render land unfit for or greatly limit beneficial uses.

Yellow toadflax is a species of concern for both the Gallatin National Forest and Yellowstone National Park. This species is listed as a Priority III exotic plant on the

Yellowstone National Park Exotic Plant Priority List (Olliff et al. 2001). Priority III species are those that are aggressive widespread, deleterious invaders where control efforts are projected to have high cost and low effectiveness.

Origin and Distribution

Yellow toadflax is indigenous to the steppes of southeastern Europe and southwestern Asia (Saner et al. 1995; Zouher 2001). Other names include common toadflax, butter and eggs and wild snapdragon. This species is usually associated with sandy or gravelly soils, and disturbed but also undisturbed open habitats where it commonly occurs along roadsides and railroads, in pastures, cultivated fields, and range lands and clearcuts (Arnold 1982; Saner et al. 1995).

The plant arrived in New England over 300 years ago as an ornamental (Saner et al. 1995; Nechols 1995) and is still widely used as an ornamental throughout the world (Mitich 1993). It now occurs in all U.S. states (except Hawaii) and all Canadian Provinces, spread as both an ornamental and garden escapee (Saner et al. 1995; USDA 2004). It was reportedly introduced to West Yellowstone area homesteads and stage stations in the late 1800's as an ornamental (Lamont, personal communication). In this area it has since been observed on National Forest lands at elevations from 1900 m to 2200 m on both disturbed lands and undisturbed lands. In the Colorado Rockies, yellow toadflax has been documented at elevations exceeding 3000 m (Saner et al. 1995).

Morphology and Development

Yellow toadflax is a perennial herb that grows to heights of 0.2 m to 0.8 m. Its morphology is variable depending upon environmental factors such as soil type, shading or grazing (Saner et al. 1995). The plant has an average lifespan of 3.8 years, although individual plants can live up to five years (Robocker 1968). The leaves are pale green, soft, alternate, linear or linear-lanceolate and sessile (Morishita 1991). Leaves are generally 25 mm long by 2 – 4 mm wide and are crowded on the stem. The stems are hairless and are sometimes branched near the top of the plant (Morishita 1991). The taproot can be over 1 m deep and roots can extend laterally for several meters (Saner et al. 1995).

Flowers are 20 mm - 30 mm long with 4 stamens and 1 pistil, 5 united, bright-yellow petals, a hairy orange throat, and a slender, 20 mm - 30 mm spur at the base of the corolla (Saner et al. 1995). The primary pollinators are bumblebees and halictid bees (Zimmerman 1996). Yellow toadflax adaptations believed to increase attractiveness to insect pollinators include long-lived individual inflorescences, high flower-nectar sugar content, showy flowers, and pattern of 15 - 20 flowers in a vertical inflorescence with temporally staggered blooming (Arnold 1982). In Alberta, Canada, flowers appear in mid July, seed capsules form in the first week of August, and seeds begin to be shed in the second week of August (Nadeau and King 1991). The latter is similar to the timing of flowering and seed production I observed during this study.

A closely related species, *Linaria dalmatica*, commonly known as Dalmatian toadflax and broad-leaved toadflax, is also a problem weed throughout North America and in the Rocky Mountains, including nearby Yellowstone National Park (USDA 2004). It can be differentiated from *L. vulgaris* by its broader, clasping, lance-shaped leaves and its larger (30 mm - 40 mm), paler yellow flowers. Twelve other species of *Linaria* have been introduced to the United States, but these species are much less common than *L. vulgaris* and *L. dalmatica* (USDA, NRCS 2004).

Reproduction and Dispersal

Yellow toadflax reproduces from seeds and creeping rhizomes (Nechols 1995). It is considered self-incompatible, although a small proportion of seeds can develop without cross pollination (Arnold 1982). Seeds form in brown, 8 mm - 12 mm long, egg-shaped capsules that are located on the ends of branched stems (Nadeau et al. 1992; Saner et al. 1995). Seed production varies greatly and is low when compared with other self-incompatible perennials (Arnold 1982). In an Alberta wheat competition study, an average of 165 seeds were produced per stem in the presence of a seed predator and an average of 824 were produced per stem without the predator (Darwent et al. 1975). In a Saskatchewan study, 5584 seeds per stem were recorded in the absence of seed predators (Zilke and Coupland 1954).

Seeds are persistent up to 8 years in cultivated seed banks, but seed viability is not particularly high and seedling emergence rates are low when compared with other species (Carder 1963; Roberts 1986; Nadeau et al. 1992). One study found seed viability, using

the tetrazolium test, to be 40%, and seedling emergence, following 8 weeks of cold stratification, to be between 0.13% and 0.23% (Nadeau and King 1991). In one field study, a flush of emergence occurred in April after sowing, followed by a smaller late season flush (Roberts 1986). Over five years the emergence rates were 0, 8.4%, 4.4%, 2.2%, 1.9% and 1.2%, with emergence only occurring after soil disturbance.

While the seeds are small and have wings that may aid dispersal, seed dispersal is primarily short distance, with 80% and 90% of seeds falling within 0.5 m of the parent plant, and following a negative polynomial function (Nadeau and King 1991; Saner et al. 1995). Long distance dispersal is aided by human, wind, water and animal vectors (Saner et al. 1995).

Vegetative reproduction is important to this species because of its low seedling establishment (Nadeau and King 1991). Vegetative reproduction from root buds can begin as early as 2 - 3 weeks after germination. Root fragments as short as 10 mm in length will establish (Zimmerman 1996). In the first year alone, 90 to 100 secondary shoots can be produced per plant (Raul 1937 in Saner et al. 1995). The large, deep root system allows for efficient water use and makes damage to the plant from grazing, shallow cultivation or chemical control difficult, and can allow this plant to persist and spread in hostile environments (Saner et al. 1995). Ramets can produce their own roots and become independent within a year (Zimmerman 1996). In agriculture, tillage can result in the significant dispersal of infestations through ramet production (Darwent, 1975). Patches can reach densities of 300 stems m⁻² and can expand vegetatively up to

2 m per year in cultivated land (Bakshi and Coupland 1960; Nadeau et al. 1992; Saner et al. 1995).

A Canadian study which compared genet versus ramet growth found that differential growth could influence respective competitive ability and their susceptibility to management techniques (Nadeau et al. 1992). While the number of shoots produced was the same for both genets and ramets, genets were smaller for the first few weeks of growth and root pieces from genets had to be older to produce daughter shoots, indicating that genets were not as competitive as ramets.

Management in Wildlands

In both wildlands and agriculture, chemical control is the primary method utilized to control yellow toadflax, with glyphosate, amitrole, diquat and picloram most often used for spot treatment (Saner et al. 1995). In agricultural situations, yellow toadflax is resistant to 2, 4-D, 2, 4-DB and MCPA (Warren 1957 in Saner et al. 1995). Tordon and 2-4 D are currently being used to control yellow toadflax in the Gallatin National Forest (Lamont personal communication). While not completely effective, Tordon has been observed by their personnel to be most effective against yellow toadflax. According to some studies, long-term control of yellow toadflax cannot be accomplished using herbicide treatments alone (Lajeunesse et al. 1993).

Five insect species have been approved by the USDA-APHIS-PPQ for release as biological controls for yellow toadflax and these insects have had varying success in controlling the plant (Saner et al. 1995; McEvoy and Coombs 1999; USDA 2004). One problem is that while these insects may limit reproduction from seed, this success can be negated by the vegetative vigor with which the species reproduces. A combination of the stem and bud-feeding beetle, *Brachypterolus pulicarius* and the bud, stem and leaf-feeding weevil, *Gymnaetron antirrhini*, accompanied with improved tillage practices, restricted the rate of spread and seriousness of yellow toadflax as a weed in the prairies of Alberta, Canada (Darwent et al. 1975; Saner et al. 1995). In another Canadian study, the presence of these two species reduced seed rain within 0.5 m of the parent plant from 210,000 seeds m⁻² to 1410 seeds m⁻² in consecutive growing seasons (Nadeau and King 1991). Both *Brachypterolus pedicarius* and *Gymnaetron antirrhini* have been documented on *L. vulgaris* in Yellowstone National Park, (Olliff et al. 2001), and I observed *Gymnaetron antirrhini* at both study sites.

Mowing and tillage prevent seed production and promoting root starvation (Saner et al. 1995). For example, a tillage frequency of every three to four weeks reduced toadflax on agricultural lands (Darwent et al. 1975).

Replanting of vigorous indigenous species, especially grasses, may help to control yellow toadflax, although this idea needs more research (Nadeau et al. 1992; Saner et al. 1995). Grass competition in conjunction with chemical control (2, 4-D) has been found to control yellow toadflax (Carder 1963). Burning is not recommended, as it may

decrease competition from indigenous species and increase the invasive potential of yellow toadflax (Zouher 2001).

Bromus inermis Leyss.

Problem Description

Smooth brome is an example of a NIS that has both positive and negative attributes. Smooth brome is a very important forage grass in North America, and cultivars adapted to specific environments are available (Wasser 1982). This species has also been widely planted on road margins within the region for erosion control (Marlow personal communication). Smooth brome has been found to be invasive within natural areas where it may displace indigenous species because of the formation of dense sod (Sather 2004). This species may be invasive in grassland and other habitats in the Northern Rocky Mountains that do not have human disturbance (Weaver et al. 2001). In the northern range of Yellowstone National Park, its frequency decreased rapidly with increasing distance from roads and trails (Rew et al. 2002). Smooth brome is eaten by deer and elk (Hobbs et al. 1981), although its seeds have been found to be avoided by deer mice (Everett et al. 1978).

Origin and Distribution

Smooth brome was introduced to the U.S. by the California Experiment Station in 1884 for its potential as a drought resistant forage grass (Kennedy 1899 in Sather 2004). It is a widely cultivated forage grass that is now common in pastures and on roadsides

across Canada and in every state except Alabama, Georgia, Florida and Hawaii (USDA 2002). Smooth brome is a common invader of disturbed prairie, especially those with a history of overgrazing and/or fire exclusion, throughout the Great Plains (Masters and Vogel 1989). It now dominates and persists in many native grasslands and old fields (Boggs 1984). Weaver et al. (2001), in an investigation of NIS in fifteen Northern Rocky Mountain environments, found that smooth brome invaded a wide range of environments including moist grassland, forests and mountain meadows. In nearby Yellowstone National Park, it was found to be very common along roadsides and trails (Rew et al. 2002).

A closely-related indigenous species, *B. carinatus*, is a indigenous, cool season, perennial bunchgrass that is also present at the site. *B. pumpellianus*, another indigenous species that is reported to be present in the region was not found at the site, but is thought to cross with *B. inermis* (Elliot 1949 in Sather 2004). An annual brome species, *B. tectorum* has altered Great Basin shrub-steppe fire regimes and nutrient cycles, drastically altering plant community composition (Mack, 1981; Whisenant 1990).

Morphology and Development

Smooth brome is a strongly rhizomatous, sod-forming perennial that grows to a height of 1.5 m. Due to cloning, smooth brome is a long-lived species and plantings have persisted for at least 60 years (McKone 1985). Leaves are flat, lacerate, 100 mm - 150 mm long and 3 mm - 10 mm wide (Hitchcock and Cronquist 1994). Ligules are truncate and from 0.5 mm - 2.5 mm long. The plant can be vegetatively identified by a "V" or

"W" in the middle of the leaf and also because it is the only grass in our region with a sealed sheath. Spikelets are 6 -8 flowered, 25 mm long, narrowly oblong and pale green to slightly purple-tinged. Lemmas are mucronate or short awned (1 mm) (Hitchcock and Cronquist 1994). Each floret has 1 ovule and produces 1 seed (McKone 1985). Seeds are 10 mm long, 2.5 mm wide and less than 1 mm thick.

Reproduction and Dispersal

Smooth brome is a wind pollinated and self-incompatible perennial that reproduces by seed, rhizomes, and tillers (McKone 1985). It can produce 156 to 10,080 viable seeds per plant (Lowe and Murphy 1955). Its seeds may be transported short distances by wind, water, and also by ants (Kramer 1975).

Management in Wildlands

Spring burning is a commonly used control method in grasslands (Cosby 1972 in Sather 2004). Mowing at the boot stage may also be effective (Lawrence and Ashford 1964 in Sather 2004). In one study on Nebraska rangelands, a variety of chemical treatments were tested. Spring application of glyphosate at 1.12 kg/ha was found to be most effective (Rayburn et al. 1981). Other chemicals that have been used to control smooth brome include atrazine, pronamide, imazapyr, bromacil and simazine (Butterfield et al. 1996). No research has been done to develop potential biological controls because of the extensive use of smooth brome as a forage grass (Butterfield et al. 1996).

Cirsium arvense (L.) Scop.

Problem Description

Canada thistle, a member of the Asteraceae family, is also known as California thistle, creeping thistle and field thistle (Morishita 1999). Canada thistle is a strong competitor that can significantly reduce crop yields (Mamolos and Kalburtji 2001). Wildlife use of Canada thistle is thought to be light (Hobbs et al. 1981). The spiny leaved plant is unpalatable to grazers and dense infestations can displace desirable forage species (Morishita 1999). However, it is known to be a minor part of the winter and spring diet of mule deer (Kufeld et al. 1973). Its spiny leaves can limit human use of recreation areas (Morishita 1999). The only known beneficial use for this species is as a source of nectar for honeybees (Morishita 1999).

In wildlands, Canada thistle invades prairies, grasslands and riparian areas where it can displace indigenous species (Sachion and Zimdahl 1980). In the Northern Rocky Mountains, it is present in natural areas that lack obvious human disturbance (Weaver et al. 2001).

Origin and Distribution

Originally from southeastern Europe, North Africa and the eastern Mediterranean, Canada thistle now occurs in the middle latitudes (30° to 68°) throughout temperate regions of the world (Morishita 1999). The species came to North America in the 17th century as either a seed contaminant or as a contaminant in ship packing material. Canada thistle spread through New England, leading to the enactment of control

legislation in 1795 in Vermont and 1831 in New York (Moore 1975). It has since been declared noxious in at least 35 states and 6 Canadian provinces (Moore 1975).

This species grows in a variety of habitats ranging from upland grasslands and prairies to wetlands and riparian areas (Morishita 1999). It invades both disturbed and undisturbed areas, and does best in open, sunny sites (Moore 1975). In Yellowstone National Park, Canada thistle occurs at elevations ranging from 1,820 m to 2,400 m, in areas with a canopy of less than 20% (Allen and Hansen 1999). Another study in the Northern Rocky Mountains, found that Canada thistle was most likely to be a dominant species at the lower-montane forest margin (Weaver et al. 2001). Fifteen indigenous *Cirsium* species and one other non-indigenous *Cirsium* (*Cirsium vulgare*) are also present in this region (Hitchcock and Cronquist 1994).

Morphology and Development

Stems are erect, from 0.3 m to 1.2 m tall, and are often branched at maturity (Moore 1975; Morishita 1999). The leaves spiny and are 20 mm to 200 mm long with crinkly leaf edge (Morishita 1999). *Cirsium arvense* morphology varies with different environmental conditions (Nadeau and Vanden Born 1989).

Unlike other *Cirsium* species, male and female flowers are produced on separate plants (Hitchcock and Cronquist 1994). The plant generally produces 32 to 69 pink to purple flower heads per shoot, and 84 to 131 florets per flower head (Bakker 1960; Moore 1975; Morishita 1999). The flowers are 12.5 mm in diameter and are discoid with tubular flowers and many bracts (Morishita 1999). At the study site, flowers were produced in July and August.

Reproduction and Dispersal

The species is pollinated by insects, primarily honeybees (Donald 1994; Morishita 1999). Male and female plants must be located within a few hundred meters of each other for insect pollination and seed set to occur (Lalonde and Rothberg 1994).

Canada thistle seeds are a brownish achene with a feathery, loosely attached pappus (Terpstra 1986). Seeds are from 2.5 mm - 3.2 mm long, 1mm in diameter and average 1.08 mg (Terpstra 1986). Different studies show great differences in *C. arvensis* seed production (Kay, 1985; Lalonde and Roitberg, 1994), ranging from 0 to 40,000 per plant (see review by Heimann and Cussans 1996). Hobbs and Mooney (1986) found that seed production averaged 1300 seeds m⁻², and seed rain averaged 80 ± 50 seeds m⁻². Seed viability for the season after seed production has been shown to be as high as 84% (Haderlie et al. 1991). Seeds generally stay viable for less than 5 years in the seed bank, and most germinate during the first year (Donald 1994). Depth of burial is important to the duration of seed viability. Bakker (1960) found that seeds buried at a depth of 10 mm remained viable for less than a season, while 35 % - 39 % of seeds buried 0.4 m deep remained viable after 30 months.

The literature is mixed with regard to the question of the importance of seed dispersal by wind. Some workers have found wind dispersal to be relatively insignificant, and that most seeds land near the parent plant (Bakker 1960, Morishita 1999). Other workers have found that the pappus attached to the seed can enable the seed

to be transported by wind for several hundred meters to several kilometers (Wood and Del Moral 2000).

Seedlings require adequate light and are sensitive to competition (Moore 1975 Donald 1994), and seedling emergence and establishment varies with disturbance. Amor and Harris (1974) reported no seedling establishment from seed artificially sown in undisturbed pastures, whereas 7 % - 13 % of seeds sown on bare soil emerged, and 78 % - 93 % of emerging seedlings became established.

The plant also reproduces vegetatively through an extensive root system (Lalonde and Rothberg 1994; Morishita 1999), and horizontal stems can extend 6 m in one season (Morishita 1999). The species can reproduce from root fragments as short as 6 mm long (Nadeau and Vanden Born 1989).

Management in Wildlands

Once established, Canada thistle is very difficult to control, especially in natural areas (Donald 1994). While many insects have been found to feed on this species in Canada, no biocontrol agents have yet been found to control this species (Moore 1975). The response to burning is mixed, although repeated late-spring burning can be effective (Smith 1985). Application of roundup and 2, 4-D to individual plants has been found to be effective (Sather 1987; Hutchison 1992). Mowing and pulling several times a year has been found to be effective in controlling this species (Hutchison 1992).

Study Area Climate

Climate data for the period of 1948 to 2003 comes from the Hebgen Dam weather station, located at 44° 52'N, 111° 20'W (Western Regional Climate Center 2004). This weather station was located 15 km from site 1, 18 km from site 2 and 7 km from site 3. Over this 55-year period the mean annual precipitation was 720.6 mm, much of it as winter snow. The mean growing season precipitation over that period (April through September) was 330 mm. May and June were the wettest months of the year and July, August and September were the driest. The 55 year monthly mean precipitation and that of 2001, 2002 and 2003 are provided in Fig 1.1. This study took place during the fourth, fifth and sixth consecutive years of a drought. The mean annual precipitation for 2001, 2002 and 2003 was 81%, 73% and 83% of normal respectively. The mean growing season precipitation for 2001, 2002 and 2003 was 87%, 89% and 74% of normal respectively.

The mean annual temperature was 2.4 °C, with an average January low of -11.1 °C and an average July high of 15.2 °C. The average frost-free season is short, generally lasting only the 88 days from June 15 to September 11. The 55-year mean growing season temperatures and those of the study years 2001, 2002 and 2003 are provided in Figure 1.2. The mean annual temperatures for 2001 and 2003 were 38% and 59% higher than normal respectively, and the mean annual temperature was 15% lower than normal in 2002. The mean growing season temperatures for 2001, 2002 and 2003 were 14%, 0.4% and 13% higher than normal respectively.

Figure 1.1. Growing season precipitation recorded at the Hebgen Dam weather station from 1948 - 2003. Mean annual precipitation over this time was 720.6 mm.

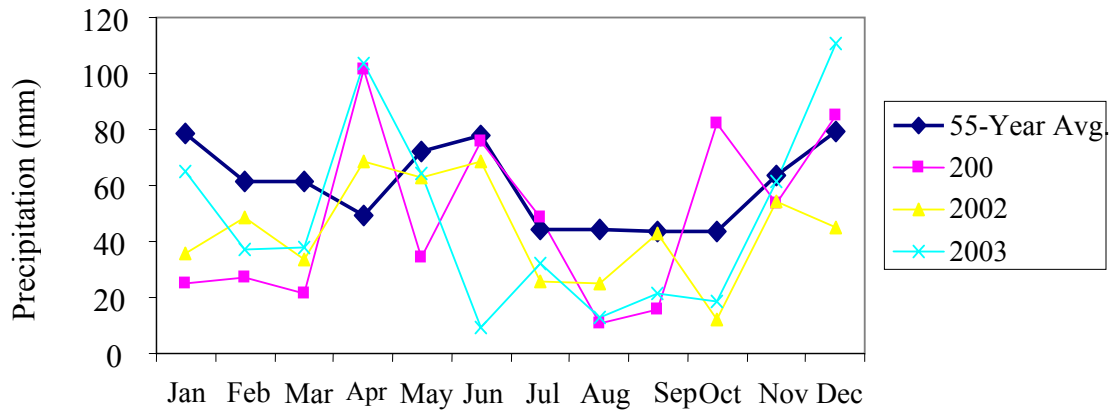
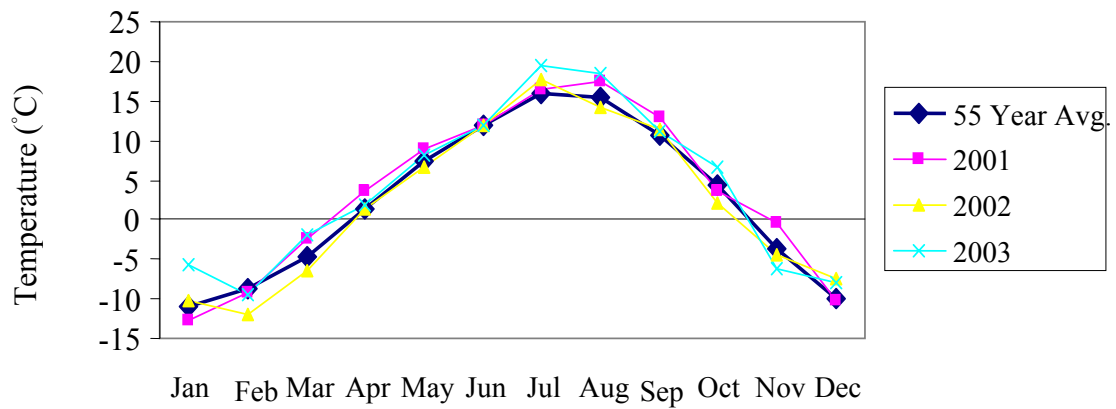


Figure 1.2. Growing season temperature recorded at the Hebgen Dam weather station from 1948 - 2003. Mean annual temperature was 2.4 °C.



Definitions:

Here follow definitions which are used throughout this thesis:

Habitat – and Environment are used interchangeably. These are here defined as the areas in which plants live, characterized by similar physical features, growing conditions and dominant vegetation.

Invasive Plant Population – a non-indigenous plant population that is consistently increasing in density (number of vegetative shoots per unit area) and/or spatial extent over time, $\delta N/\delta t > 0$ and/or $\delta n/\delta t > 0$. N is population density and n is number of occupied cells in a grid placed over the study community. There is no implication of ecosystem impact of a population designated as invasive (Rejmánek et al. 2002).

Metapopulation – discrete sets of patches of the same species in the same environment close enough to permit interbreeding. For example, the three yellow toadflax patches at each study site were assumed to be part of the same metapopulation.

Non-Indigenous Plant Species (NIS) - a non-indigenous plant species introduced on purpose or accidentally by man to an area (Hulme 2003). Smooth brome (*Bromus inermis*) is an example of a NIS that is not designated as a weed, as it is an important and widely planted forage species that is invasive in natural areas (Weaver et al. 2001).

Noxious Weed – a non-indigenous plant species that is designated by law (county, state or federal noxious weed lists) or is listed by a land management agency as a species that interferes with some management objective.

Patch – a population with distinct boundaries that is separated from other patches. In this study, we defined separate patches as being at least 2.0 m from the nearest plant of the same species. Also, we defined distinct patches as distinct populations.

Plant Community – a mix of plant populations (more than one species) sharing a habitat.

Plant Population – a group of individuals of a single species in an area linked by parenthood or mating, or as individuals in an area circumscribed for the purpose of study (Watkinson 1997), here we most generally use the word population to describe an individual patch.

Spatial Population Growth Rate – the change in the number of sub-sampled areas occupied by NIS within and surrounding the population from t to $t + 1 = \delta n / \delta t$, thus

$$\delta n = n_{t+1} - n_t.$$

Temporal Population Growth Rate – the change in population density (N) over the change in time (t) = $\delta N / \delta t$, thus $\delta N = N_{t+1} - N_t$.

Weed – in natural areas, a non-indigenous plant that interferes with management objectives and threatens to displace indigenous plant species and plant communities. The

word “weed” should be replaced by NIS as “weed” has so many connotations, often without a scientific basis, that its meaning is often lost or muddled.

MONITORING THE DEMOGRAPHICS AND THE SPATIAL AND TEMPORAL
DYNAMICS OF YELLOW TOADFLAX (*Linaria vulgaris*) POPULATIONS TO
DETERMINE INVASIVENESS

Introduction

Managers of natural areas are faced with the problems of rising human demands upon the lands they oversee and concurrent decreases in funding and staff for achieving their management objectives (US GAO 1998; Wilderness Society 2004). Simultaneously, the diversity and cover of non-indigenous species (NIS) is increasing in natural areas, leading some researchers to hypothesize that this may result in the disappearance of some indigenous plant communities and the extinction of some indigenous plant species and their dependent wildlife (Mack 1989; D'Antonio and Vitousek 1992). Natural area land managers need to increase their understanding of the population demographics and the spatial and temporal dynamics of weed populations to determine the invasiveness and impacts of a particular NIS and also for prioritizing its management (Rew et al. in press b).

We hypothesize that the invasiveness of yellow toadflax (*Linaria vulgaris* L., Scrophulariaceae) populations vary depending upon the environment in which it exists. The response of these species to the environment, and the specific life history and dispersal traits that drive their invasion are critical as knowledge for the design of management plans. We also hypothesized that a determination of invasiveness depends

upon the scale at which invasiveness is considered. In this study, we conducted detailed and intensive monitoring of the variation in yellow toadflax temporal ($\delta N/\delta t$) and spatial ($\delta n/\delta t$) dynamics in order to identify invasive populations. Analysis of the frequency distributions of $\delta N/\delta t$ and $\delta n/\delta t$ within yellow toadflax populations were used to measure invasiveness.

We monitored yellow toadflax population demographics to determine which life-history states were most responsible for the observed population dynamics and might thus be targeted to promote population decline. By studying transitions in the NIS life cycle, we hoped to expose potential vulnerabilities in this cycle that could then be effectively exploited for control (Harper 1958). A similar yet reciprocal method, population viability analysis, is used in the study of rare plant and animal populations. In population viability analysis, population biologists study the minimum number of individuals required to maintain a viable population of a particular species and the persistence of different populations (Allphin and Harper 1997; Crawley 1997). Cousens and Mortimer (1995) stated that little is known about the spatial and temporal dynamics of NIS populations in agricultural systems. Based upon the relative volume of work done in agricultural versus natural systems, much less is known about the dynamics and potential invasiveness of NIS in natural systems.

This study evolved from earlier studies that addressed the population dynamics of NIS in this region. Maxwell et al. (1988) used the population modeling approach to evaluate leafy spurge (*Euphorbia esula*) development and control and identified the transition parameters which influenced population growth. Trainor (2003) used a matrix

model to study the population dynamics of the NIS tansy ragwort (*Senecio jacobaea*) in a range of environments where it was found in Northwestern Montana. Hulting (2004) examined the spatial and temporal dynamics of NIS in diversified cropping systems. He found that crop diversity and crop management practices and the environments that they create could determine the relative success of NIS populations.

The study species, yellow toadflax, presents a challenge for land managers because it invades a variety of upland plant communities, including those that lack obvious human disturbance (Pauchard et al. 2003). This species was selected for monitoring because land managers in this region were concerned about its invasive potential. The clonal growth and short-distance dispersal of yellow toadflax cause it to form discrete patches with boundaries that facilitate its study (Nadeau and King 1991; Saner et al. 1995). It is very invasive in mountain grasslands (Saner et al. 1995). Prolific vegetative reproduction and potentially high seed production allow for rapid spread and high persistence (Saner et al. 1995). A patch in one Canadian study was observed to increase 418% in area in a single season and a second, one-acre patch was observed to expand to cover 85 acres in a five-year period (Zimmerman 1996).

Study Objectives

The specific objectives of this study were:

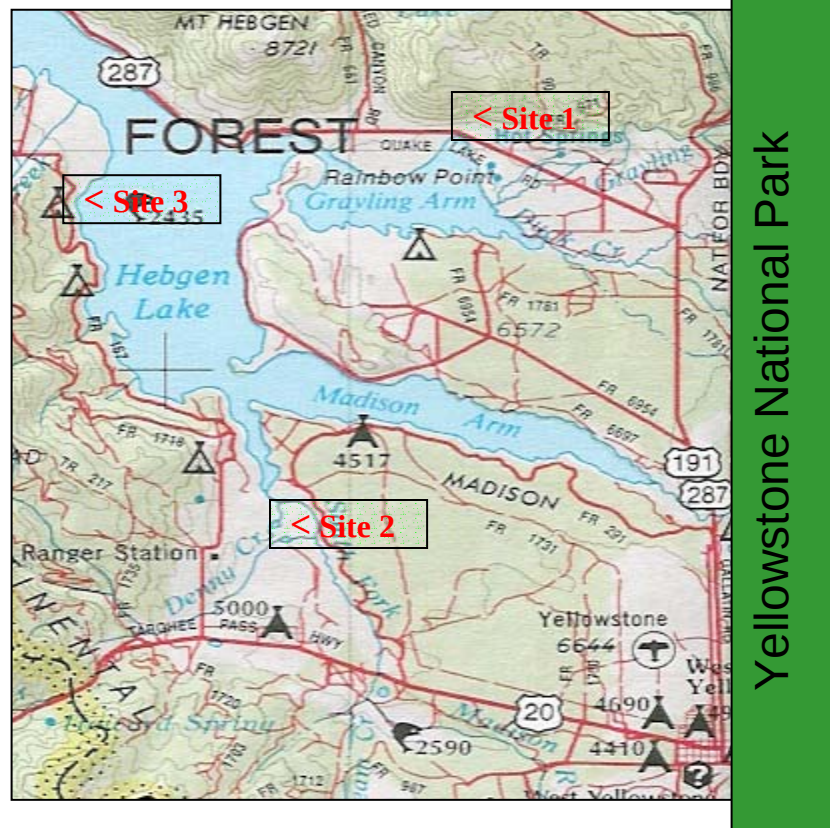
- I. To determine which life history transitions promote yellow toadflax invasiveness within study populations:
 - i. by monitoring life history states (non-flowering ramets, flowering ramets, fruiting ramets, and seed producing ramets) and transitions between states for populations in two different environments;
- II. To quantify yellow toadflax invasiveness:
 - i. by determining if study populations consistently increased and/or decreased in density ($\delta N/\delta t$) over time;
 - ii. to determine the spatial scale(s), at which yellow toadflax was invasive, i.e., metapopulation (the two sites), population (patch), or within patch (patch interiors and edges);
- III. To compare the relative invasiveness of yellow toadflax populations using an invasiveness index.

Materials and Methods

Study Area Descriptions

Yellow toadflax populations were monitored at two study sites located in the Gallatin National Forest of Montana, U.S.A., 6 km (site 1) and 10 km (site 2) west of Yellowstone National Park (Figure 2.1). Three populations (patches) were studied at each study site, patches 1-3 at site 2 and patches 4-6 at site 2. The patches were all within 100 m of each other at both sites. Field data collection took place during the summers of 2001, 2002 and 2003.

Figure 2.1. Study Site Locations near West Yellowstone, Montana



Site 1 was located at 44° 48'N, 111° 12'W. It lies at an elevation of 2220 m on a steep south-facing ridge with slopes of approximately 33°. It is approximately 600 m above the two-lane highway. Site 1 had no obvious human disturbance. Sources of natural disturbance included slope movement, elk grazing and trampling, and small animal burrowing. The frequency of fire in shrub and grasslands for the Northern Range of nearby Yellowstone National Park is 20-25 years (Houston 1973). It is not known when this site last burned.

The three site 1 study patches were located in a big sagebrush (*Artemesia tridentata*)/Idaho fescue (*Festuca idahoensis*) habitat type (Despain 1990). Dominant shrubs also included bitterbrush (*Purshia tridentata*) and creeping Oregon-grape (*Mahonia repens*); dominant grasses also included Sandberg's bluegrass (*Poa secunda*); and dominant herbs were silvery lupine (*Lupinus argenta*), sulfur buckwheat (*Erigeron umbellatum*) and prairie smoke (*Geum triflorum*). Scattered limber pine (*Pinus flexilis*) and Douglas fir (*Pseudotsuga menziesii*) grew nearby, and the habitat type changed to closed canopy forest just above Site 1. Soils were limestone-derived clays that are relatively high in nutrients (Rodman et al. 1996).

Site 2 was located at 44° 37'N, 111° 00'W, near the south shore of Hebgen Lake, where the South Fork of the Madison River enters the lake. The site lies at an elevation of 1851 meters and the topography is almost flat. Natural sources of disturbance included moose, elk and bison grazing, small animal burrowing and recurring fire. The site is crossed by and received human disturbance from several unimproved roads that provide fishing and other recreational access to the South Fork of the Madison River and

Hebgen Lake. The soils are rhyolite-obsidian sands that were formed on glacio-fluvial outwash plains (Rodman et al. 1996). These soils are well-drained and low in nutrients. Patches 4 and 5 were located in a big sagebrush (*Artemisia tridentata*)/ Idaho fescue (*Festuca idahoensis*) habitat type (Despain 1990). Dominant species also included Sandberg's bluegrass, silvery lupine, sulfur buckwheat, cushion phlox (*Phlox pulvinata*) and prairie smoke. Patch 6 differed from patches 4 and 5 in that it was located in a closed canopy lodgepole pine (*Pinus contorta*) forest with little understory cover.

Site 2 is subject to disturbance from periodic fires, but it is not known when this site last burned. In the lodgepole pine forests in nearby Yellowstone Ecosystem, fires occur with a frequency of 22-400 years, and are often stand replacing, (Arno 1980; Romme 1982; Romme and Despain 1989).

Field Data Collection

Three discrete yellow toadflax patches were monitored at each study site (Figure 2.1). The three patches at each of the two sites made up discrete metapopulations, and each individual patch was a discrete yellow toadflax population. Field observations were performed in the spring and fall from May of 2001 through September of 2003. Patches 4 and 5 at site 2 were added in September of 2001 and patch 6 at site 2 was added in June of 2002. A 1 m² grid was established over each yellow toadflax study patch at each of the 2 sites (Figure 2.2). Each grid extended at least 1 m beyond the border of each patch. A complete census was conducted of all yellow toadflax plants in each patch. One m² quadrats were randomly selected from the grid, stratified by edge versus interior portions

of each patch. Three edge and 3 interior quadrats were selected in each patch. Patches corners were located for future reference using a differentially corrected global positioning system (a Trimble GeoExplorer 3 GPS). The quadrats were permanently marked with road hairs (fringed plastic highway markers) so that they could be relocated for successive year census counts. A PVC frame divided into $1/16 \text{ m}^2$ sub-sample cells was used to identify subsample areas and facilitate mapping of individual stems (Figure 2.3). Counts were made within the $1/16 \text{ m}^2$ sample quadrats to maximize the accuracy of density counts and for estimating small changes in density and spatial occupation from year to year.

Patch interiors and edges were sampled separately because population growth within patch interiors and edges may be different. Patch interiors had higher plant densities in the initial full patch census, thus density dependent regulation may have an important influence on demographic processes. Edge 1 m^2 quadrats were selected for study with the stipulation that at least 3, $1/16\text{th m}^2$ cells within the edge quadrats extended beyond the patch boundary, i.e. had no yellow toadflax at the beginning of the study. Interior, 1 m^2 quadrats were selected for study from those within the remainder of the patch. Within each patch (i.e., each distinct population), individual 1 m^2 quadrats were treated as samples or experimental units, and the $1/16\text{th m}^2$ cells were treated as sub-samples.

Figure 2.2. Example of Interior and Edge 1 m^2 quadrat configuration

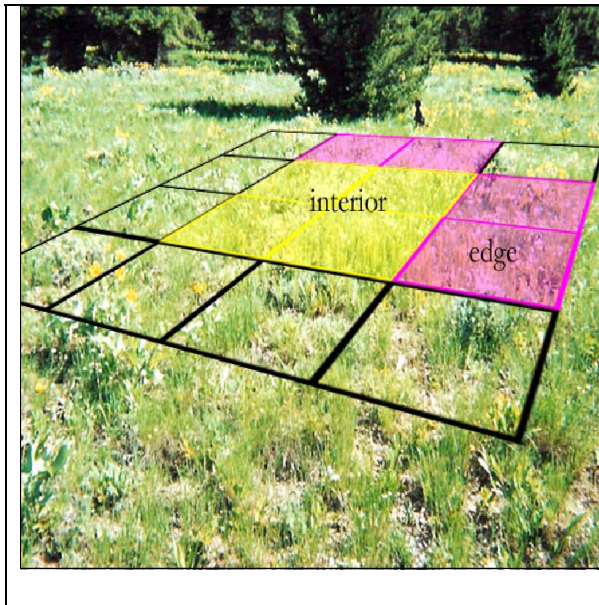


Figure 2.3. Sampling a $1/16\text{ m}^2$ quadrat



Changes in yellow toadflax ramet density and demography were monitored after emergence in June and after seed set in late August and early September of each year (2001, 2002, 2003). The location of each yellow toadflax stem within the $1/16\text{ m}^2$ cells in each 1 m^2 quadrat was mapped onto transparent field data sheets. In the spring, loops of differently colored wire were tied around each stem base to differentiate between seedlings and vegetative shoots and to aid in calculating mortality. In the fall, stem locations were again mapped onto field data sheets, and the locations of individual dead, non-flowering and flowering stems were recorded. Numbers of flowers, fruits and seed per flowering plant were also recorded.

Data Analysis

We studied yellow toadflax populations to answer the question of whether these populations were consistently increasing, decreasing or not changing in density and/or spatial extent. To do this, we monitored $\delta N/\delta t$, the change in population density over time; defining δN as the change in the density of yellow toadflax stems within individual $1/16 \text{ m}^2$ sub-samples. Sub-samples where the density was 0 at both t and $t + 1$ were not included in the calculation of $\delta N/\delta t$. This is because, especially in edge quadrats, these sub-samples would skew the distributions towards 0 and could potentially obfuscate trends in population $\delta N/\delta t$. A yellow toadflax population was considered invasive if it increased in density and/or spatial extent over time; in decline if it was decreasing in density and/or spatial extent; and stable if it was neither increasing nor decreasing in density and/or spatial extent. Statistical analysis was performed using S-Plus 2000 and Excel XP.

To assess the contribution of $\delta N/\delta t$ to invasiveness, charts were created to show the frequency distributions for each population in question (Figures 2.4-2.11). These populations included the cumulative populations for site 1 and site 2, time 1 (2001 to 2002) and time 2 (2002 to 2003), patch interiors and edges, and the six individual patches. The frequency distributions for the six individual patches were split into the two time transitions and also into patch interior and edge portions of each population. These frequency distributions show 6 cases for $\delta N/\delta t$:

1. $\delta N/\delta t = 0$ at both N_t and N_{t+1} ;
2. $\delta N/\delta t > 0$ at both N_t and N_{t+1} ;
3. Decrease, $\delta N/\delta t$ at $N_{t+1} < \delta N/\delta t$ at N_t ;

4. Decrease to 0, $\delta N/\delta t$ at $N_t < 0$, $\delta N/\delta t$ at $N_{t+1} = 0$;
5. Increase, $\delta N/\delta t$ at $N_{t+1} > \delta N/\delta t$ at N_t ;
6. Increase from 0, $\delta N/\delta t$ at $N_t = 0$, $\delta N/\delta t$ at $N_{t+1} > 0$.

Yellow toadflax population growth rate ($\delta N/\delta t$) frequency distributions were compared with theoretical (null) distributions using the one-sample Kolmogorov-Smirnov Test in S-plus 2000. Kolmogorov-Smirnov tests whether the observed distribution differs from the null distribution. The null distribution reflected a stable equilibrium population with mean of 0 and a standard deviation calculated from the empirical distribution. A balance of negative growth sample areas and positive growth sample areas within the population represents the null hypothesis or a stable equilibrium population. A population with a Kolmogorov-Smirnov P-value ≥ 0.05 meant that the population did not differ from a normal distribution centered at $\delta N/\delta t = 0$ and could therefore be considered stable. A population with a P-value ≤ 0.05 differed significantly from a theoretical distribution, and was either predominantly positive or declining.

If the observed distribution was found to be significantly different from the null distribution then the median and skew of the distributions were calculated and used in further calculation of a continuous index of invasiveness. The formula for our index is:

$$\text{Invasiveness} = \text{median} + \text{skew} + \text{proportional increase} - \text{proportional decrease} + \text{local colonization} - \text{local extinction}.$$

In calculating this index, the population growth rate median $\delta N/\delta t$ was entered if the populations were determined to be significantly different from the theoretical

distributions using the Kolmogorov-Smirnov Test. A value of “0” was entered in the median column if these populations were not significantly different. Skew was used to characterize the asymmetry of each population distribution around its mean. If the skew was greater than 0, the population was showing a trend towards positive growth; if the skew was less than 0, the population was showing a trend towards negative growth. Colonization was defined as the proportion of $\delta N/\delta t$ growth where this growth was from 0 at t and greater than 0 at $t + 1$. Extinction was defined as the proportion of $\delta N/\delta t$ decline where this decline was to 0 from t to $t + 1$. As stated previously, sub-samples with zero values for both N_{t+1} and N_t were removed from the analysis.

We monitored yellow toadflax demographic parameters in order to determine which life history state transitions were driving yellow toadflax invasion. Population demographics were recorded during the years 2002 and 2003 and for three different spatial scales, the metapopulation (site), population (patch), and within-patch scales. The demographic parameters that we studied included yellow toadflax live stem, non-flowering stem, flowering stem, dead stem and seed densities m^{-2} . We also recorded values for the number of flowers and fruits m^{-2} ; the ratio of non-flowering, flowering and dead stems to total live stems; and the number of flowers, and the number of fruits and seeds per flowering stem. Populations were considered to be significantly different when their standard deviations did not overlap.

Results

Yellow Toadflax Population Demographics

No seedling emergence was recorded at either site in 2002 and 2003. The stem, leaf and flower bud-eating weevil *Gymnaetron antirrhini* was present on toadflax plants at both site 1 and site 2. However, we did not measure their presence or any impact of their presence on yellow toadflax density or demographics.

Overall yellow toadflax fall live-stem density, averaged over both sites and two years (2002 and 2003), was 28 m^{-2} (Table 2.1). Fall non-flowering stem density was 23 stems m^{-2} and flowering stem density was 5 stems m^{-2} . Overall spring to fall mortality was 28%. Twelve percent of the stems counted in spring produced flowers in the fall, and average flower production was 8 flowers per flowering stem. Average fruit production was 0.9 m^{-2} , with 0.2 fruits produced per flowering stem. The average seed production was 6 m^{-2} with 1.1 seeds produced per flowering stem.

Table 2.1. Yellow toadflax population demographics averaged across each year, site, interior or edge, or patch. tls = total live stems, stdev = standard deviation, fls = flowering stems, fl = flowers, ds = dead stems, fr = fruits, sd = seeds.

	tls m ⁻²	nfs m ⁻²	fls m ⁻²	ds m ⁻²	fl m ⁻²	fr m ⁻²	sd m ⁻²	% nfs	% fls	% dead	fl/fls	fr/fls	sd/fls
Mean	28.25	23.57	4.69	10.80	38.18	0.93	5.19	60%	12%	28%	8.15	0.20	1.11
stdev	3.18	2.66	0.98	1.51	9.61	0.57	5.49	0.07	0.03	0.04	2.05	0.12	1.17
2002	26.75	21.14	5.61	10.60	31.71	1.73	5.75	57%	15%	28%	5.65	0.31	1.02
stdev	3.04	2.40	1.10	1.44	7.28	0.79	2.75	0.06	0.03	0.04	1.30	0.14	0.49
2003	29.75	26.01	3.76	11.00	44.66	0.14	4.63	64%	9%	27%	11.86	0.04	1.23
stdev	3.32	2.90	0.83	1.57	11.46	0.14	7.26	0.07	0.02	0.04	3.05	0.04	1.93
Patch Interior	38.40	30.87	7.54	15.21	60.38	1.29	8.25	58%	14%	28%	8.01	0.17	1.09
stdev	3.73	3.06	1.21	1.84	11.42	0.49	7.39	0.06	0.02	0.03	1.51	0.07	0.98
Patch Edge	17.68	15.98	1.72	6.22	15.12	0.56	2.00	90%	10%	26%	8.79	0.33	1.16
stdev	2.33	2.07	0.60	0.98	6.98	0.63	2.14	0.09	0.03	0.04	4.06	0.37	1.25
Site 1	38.65	31.68	7.00	13.30	56.60	1.38	4.44	61%	13%	26%	8.09	0.20	0.63
stdev	3.69	3.07	1.18	1.69	11.69	0.69	2.42	0.06	0.02	0.03	1.67	0.10	0.35
Patch 1	22.12	17.12	5.00	10.69	47.54	0.54	1.85	52%	15%	33%	9.51	0.11	0.37
stdev	2.59	2.07	0.94	1.62	11.47	0.27	1.03	0.06	0.03	0.05	2.29	0.05	0.21
Patch 2	47.54	41.19	6.46	20.50	37.33	0.50	1.71	61%	9%	30%	5.78	0.08	0.26
stdev	3.87	3.38	1.07	2.03	7.43	0.30	0.97	0.05	0.02	0.03	1.15	0.05	0.15
Patch 3	55.64	43.36	12.29	7.39	105.83	4.64	14.57	69%	19%	12%	8.61	0.38	1.19
stdev	4.55	3.62	1.66	0.97	16.04	1.40	4.86	0.06	0.03	0.02	1.31	0.11	0.40
Site 2	9.17	8.72	0.44	6.22	4.44	0.11	6.56	57%	3%	40%	10.00	0.25	14.75
stdev	1.25	1.22	0.21	1.03	2.02	0.13	8.67	0.08	0.01	0.07	4.55	0.30	19.50
Patch 4	5.79	4.71	1.07	4.36	19.07	0.07	2.21	46%	11%	43%	17.80	0.07	2.07
stdev	1.53	1.28	0.40	1.06	6.99	0.07	2.07	0.13	0.04	0.10	6.52	0.06	1.93
Patch 5	4.58	4.50	0.08	4.08	1.00	0.00	0.00	52%	1%	47%	12.00	0.00	0.00
stdev	1.07	1.07	0.07	0.76	0.87	0.00	0.00	0.12	0.01	0.09	10.39	0.00	0.00
Patch 6	20.83	20.42	0.42	9.83	0.50	0.25	17.08	67%	1%	32%	1.20	0.60	41.00
stdev	1.54	1.53	0.16	1.11	0.43	0.22	14.79	0.05	0.01	0.04	1.04	0.52	35.51

Table 2.2. Population P-values calculated using Anova. tls = total live stems, stdev = standard deviation, fls = flowering stems, fl = flowers, ds = dead stems, fr = fruits, sd = seeds.

	tls m ⁻²	nfs m ⁻²	fls m ⁻²	ds m ⁻²	fl m ⁻²	fr m ⁻²	sd m ⁻²
2002 v. 2003	0.65	0.37	0.36	0.88	0.46	0.15	0.80
Site 1 v. Site 2	0.000002	0.00005	0.002	0.02	0.005	0.06	0.71
Interior v. Edge	0.005	0.01	0.01	0.002	0.02	0.42	0.21
Patch	0.000007	0.0003	0.02	0.03	0.002	0.06	0.17

When yellow toadflax demographics were for the years 2002 and 2003 were compared, there were few significant differences (Table 2.2). The numbers of non-flowering, flowering and dead stems m⁻² were statistically similar, as were the numbers of flowers, fruits and seeds produced m⁻².

Most parameters and census values for the different life-history stages were significantly higher at site 1 than at site 2 (Table 2.1). These included non-flowering, flowering and dead stems m⁻²; flowers and fruits m⁻²; and flowers per flowering stem. Non-flowering stem density was 4.4 times higher, and flowering stem densities were 15.9 times higher at site 1 versus site 2. The number of flowerings stems m⁻² at site 1 did not result in a statistically higher number of seeds produced m⁻². The numbers of flowers and fruits per stem were also consistent across sites. The only demographic parameter that was higher at site 2 than site 1 was spring to fall stem mortality, which was 40% at site 2 versus 26% at site 1.

When the demographics for patch interiors were compared to patch edges, the total number of live, dead, non-flowering, and flowering stems, and also flowers m^{-2} and flowers per flowering stem were all significantly higher in patch interiors than patch edges (Table 2.1). However, there was no significant difference in the ratio of Fall dead stems to live stems between patch interiors and patch edges, indicating that there was no difference in stem mortality between patch interiors and edges. While the ratio of flowering stems to non-flowering stems was 2 times higher in patch interiors, the number of flowers, fruits and seeds per flowering stem did not differ between patch interiors and edges.

For individual patches, demographic parameters were generally higher at site 1 patches than site 2 patches (Table 2.1). Patches 2 and 3 at site 1 had the highest mean live stem densities, 56 and 48 m^{-2} respectively. The lowest stem mean densities occurred in patches 4 and 5 at site 2, 6 and 5 m^{-2} respectively. The highest densities of flowers, fruits and seeds occurred in patch 3 at site 1 (106, 5 and 15 m^{-2}). No seeds were counted in any of the patches at site 2 in 2002, or at site 1 in 2003. The number of seeds produced m^{-2} did not vary across individual patches.

Population $\delta N/\delta t$

The frequency distribution for patch 1 time 1 was not analyzed because of insufficient data and also because of problems with data recording. Patch 6 was established in 2002, so no data was collected at time 1.

Results from the Kolmogorov-Smirnov Test showed that each study population growth rate frequency distribution differed from the theoretical null growth rate distribution which had standard deviations calculated from the empirical distributions with the means and medians set to 0. Thus, all of the study populations were regarded as significantly increasing or decreasing.

The mode for each of the frequency distributions was for the case where $\delta N/\delta t = 0$ at both N_t and N_{t+1} ; i.e., where yellow toadflax was not present in the 1/16 m² sub-samples at either time. Within the individual patches, the proportion of sub-samples where there was no change in density, across all of the frequency distributions studied, averaged 0.57 (Table 2.2).

Median $\delta N/\delta t$ s for the population growth rate frequency distributions were positive at site 2, time 1 and patch edges, and negative at site 1, time 1 and patch interiors (Table 2.2). The median $\delta N/\delta t$ values ranged between 3 and -3. Within the individual patches, medians were positive for all cases at patches 1 and 3 at site 1 (times 1 and 2 and patch interiors and edges). Medians were also positive at patch 4 site 2, time 2 and for interiors of patch 4. Medians were negative in all other cases.

Skews were for the most part positive where population frequency distribution median $\delta N/\delta t$ s were positive and negative where these medians were negative (Table 2.2). The exceptions were at site 2, time 1 and interior, patch 3 time 1 and the edges of patches.

Figure 2.4. Site 1 and site 2 yellow toadflax fall density distributions ($\delta N/\delta t$).

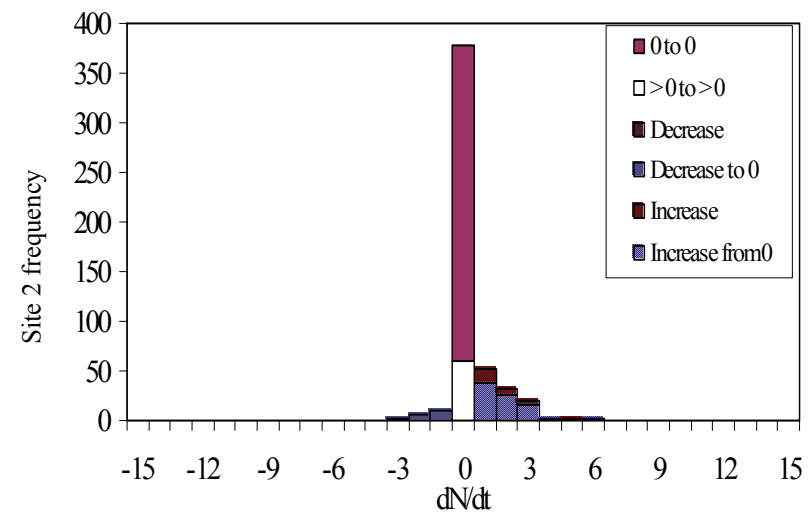
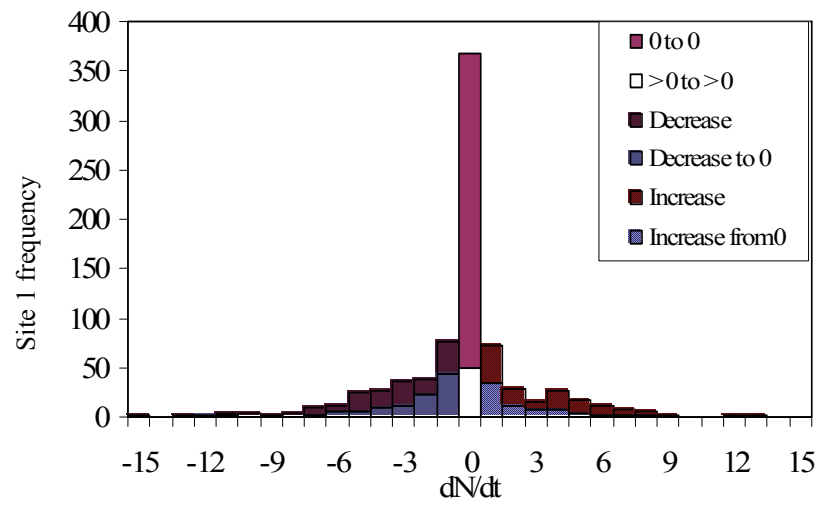


Figure 2.5. Time 1 and time 2 and patch interior and edge yellow toadflax fall density distributions ($\delta N/\delta t$).

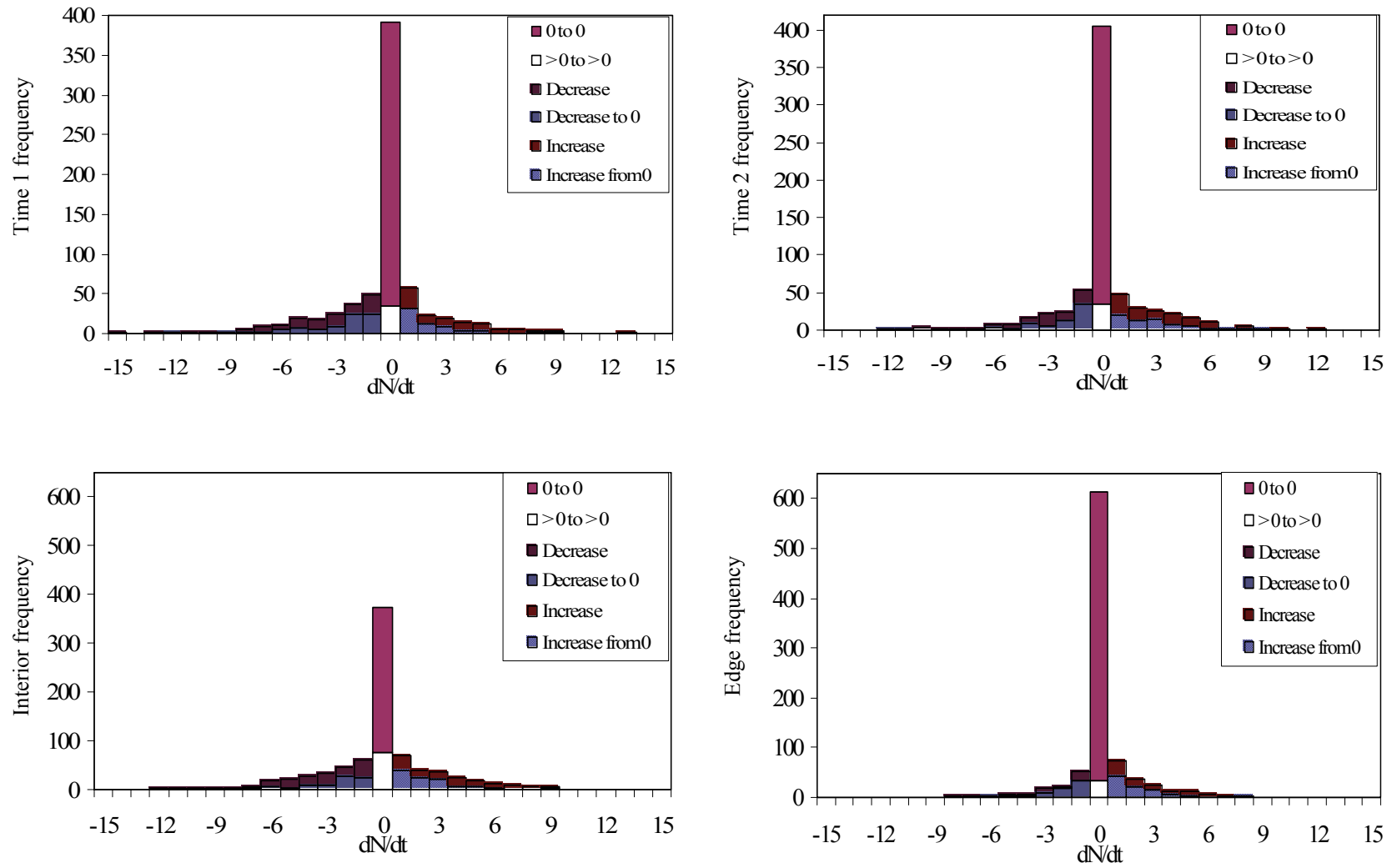


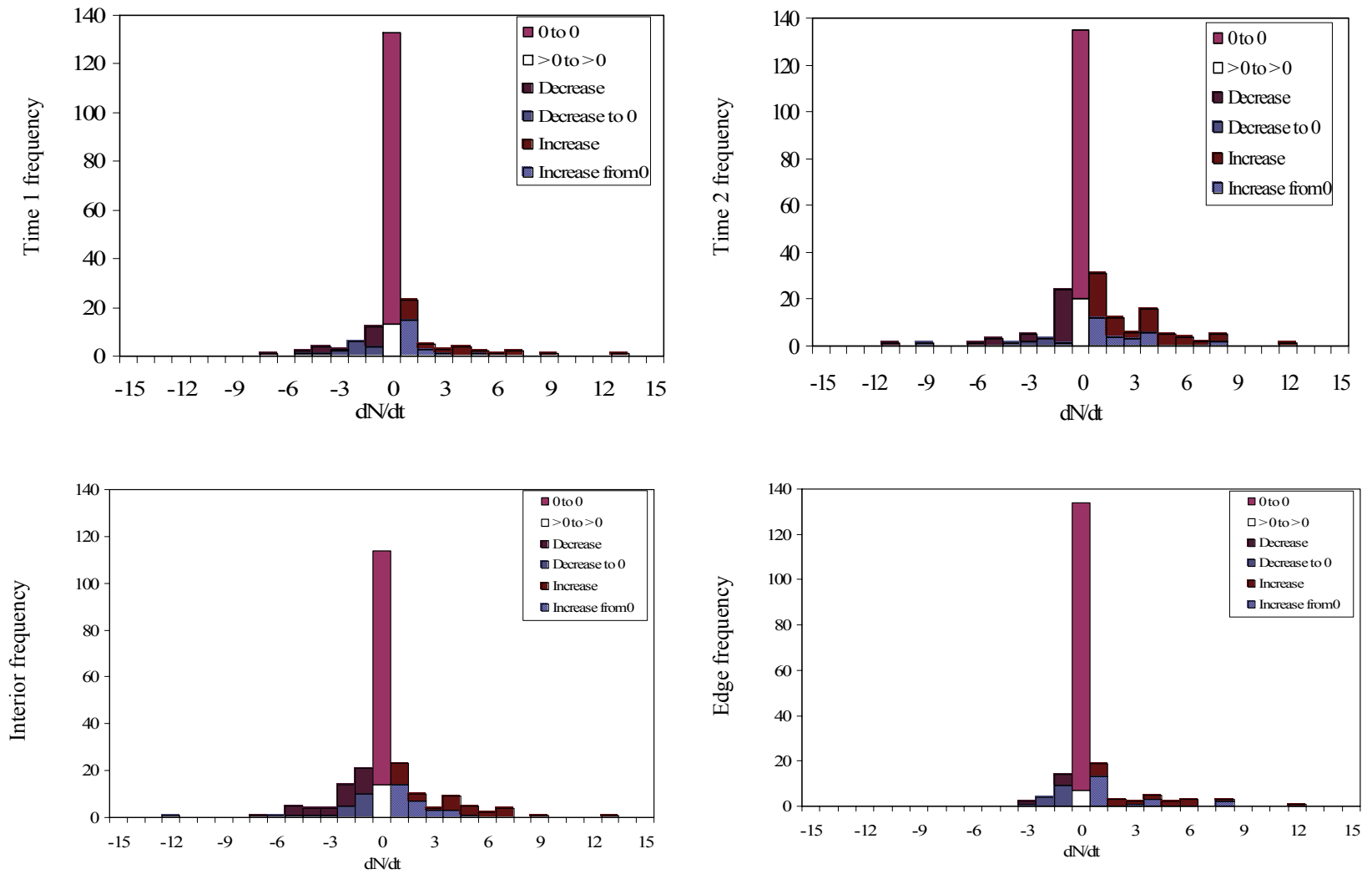
Figure 2.6. Patch 1, site 1 yellow toadflax fall density distributions ($\delta N/\delta t$).

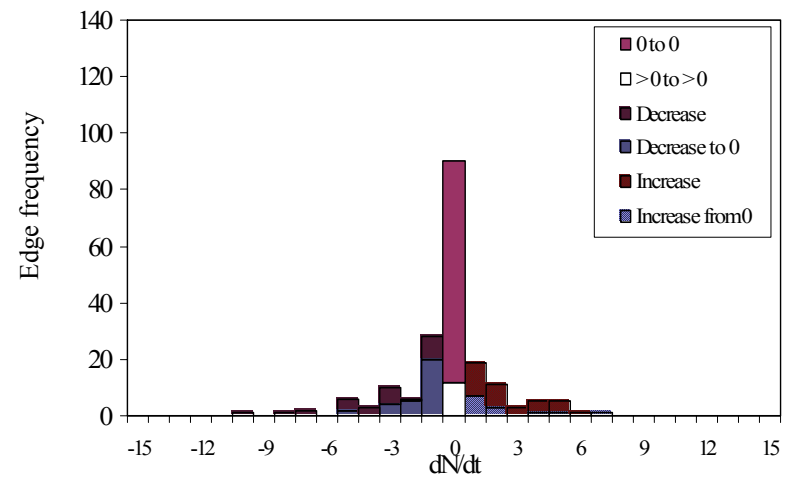
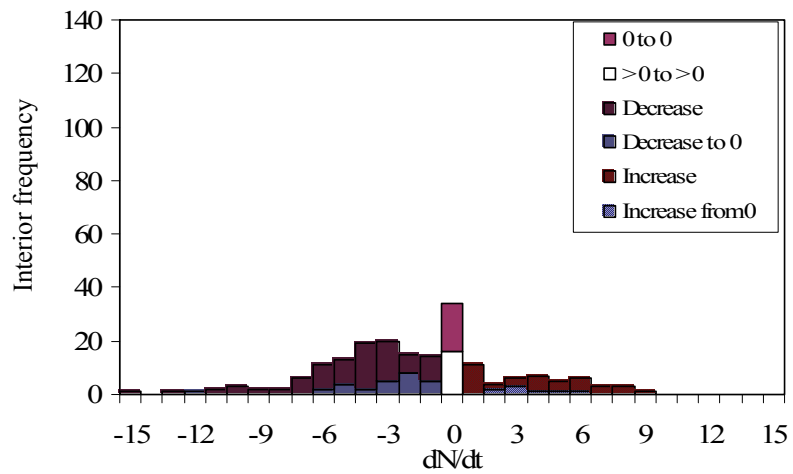
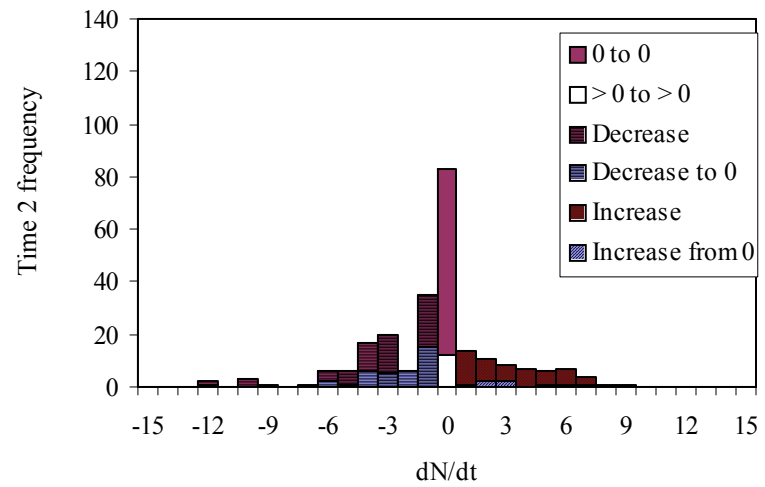
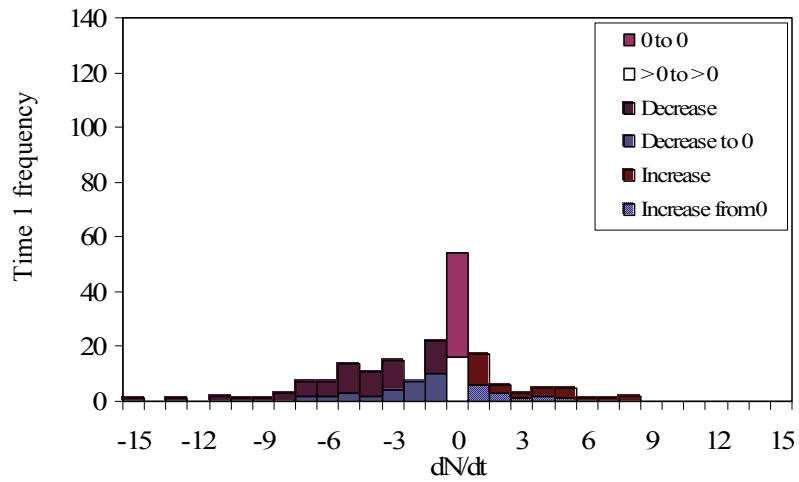
Figure 2.7. Patch 2, site 1 yellow toadflax fall density distributions ($\delta N/\delta t$).

Figure 2.8. Patch 3, site 1 yellow toadflax fall density distributions ($\delta N/\delta t$).

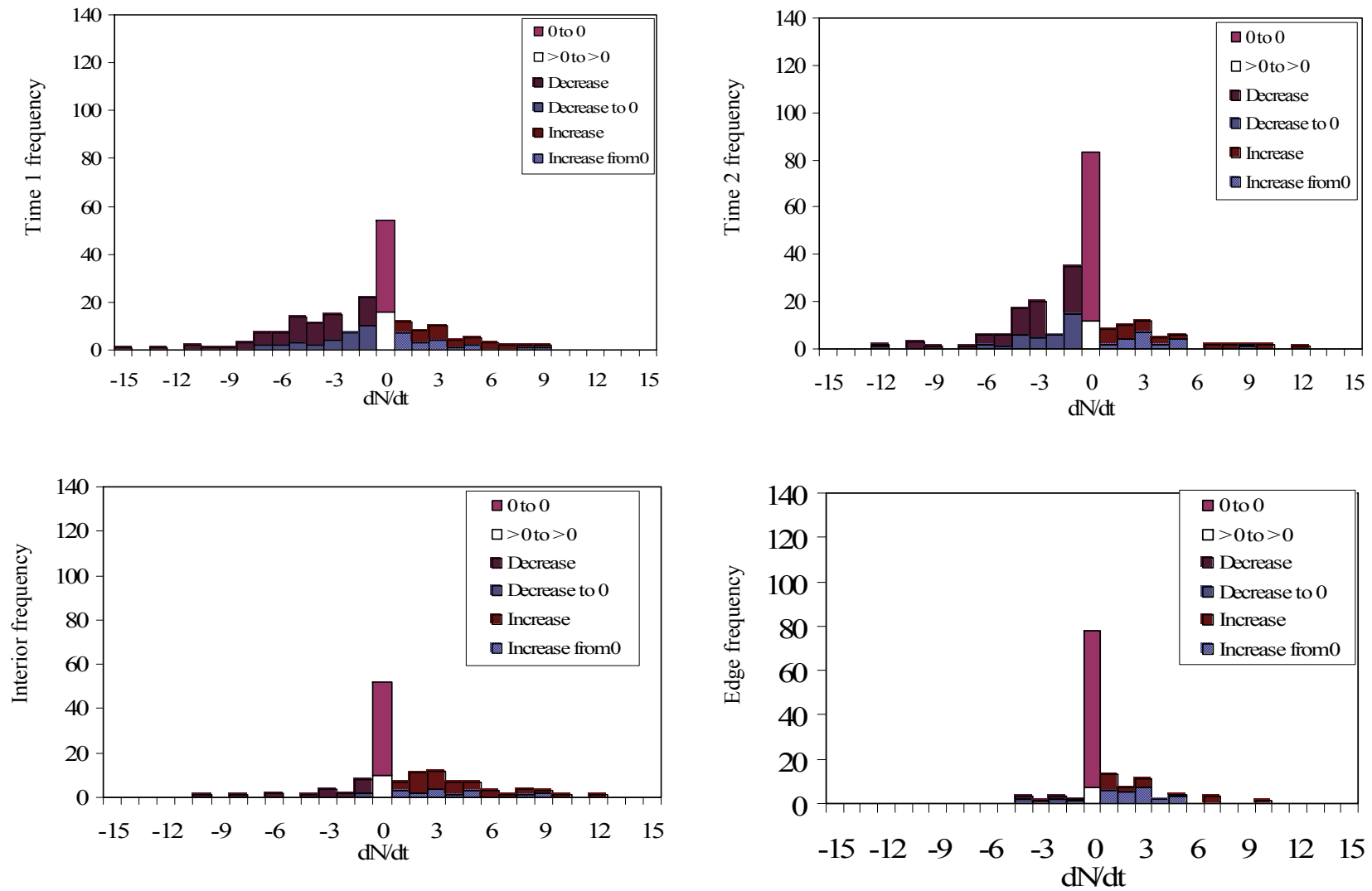


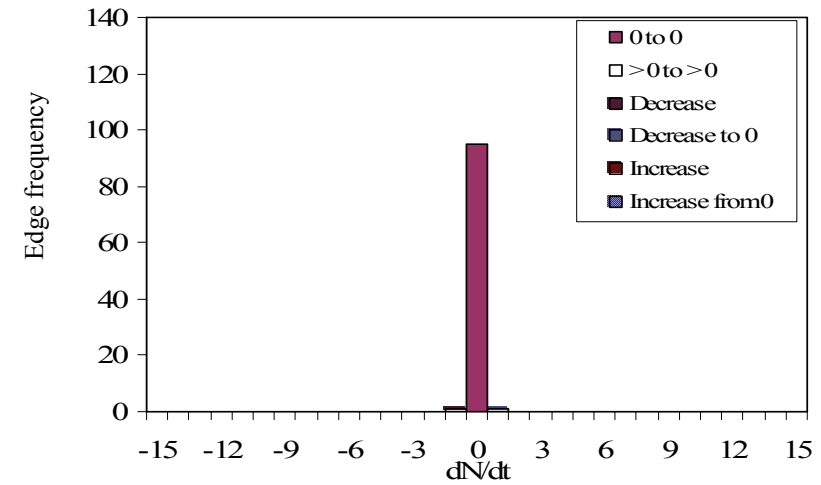
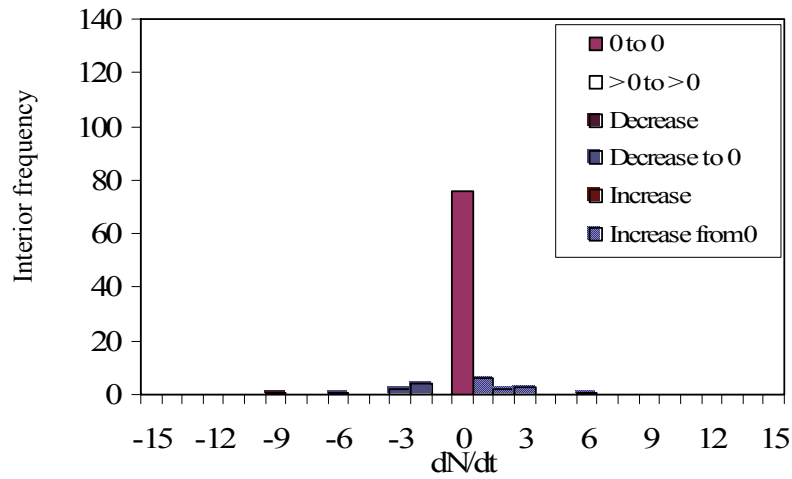
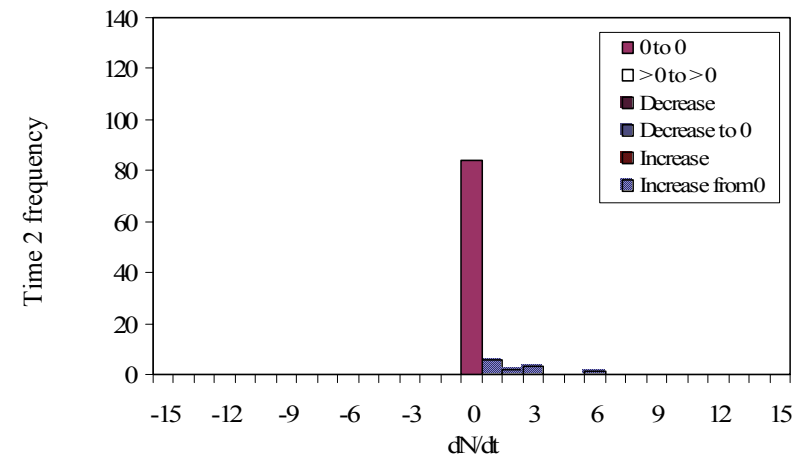
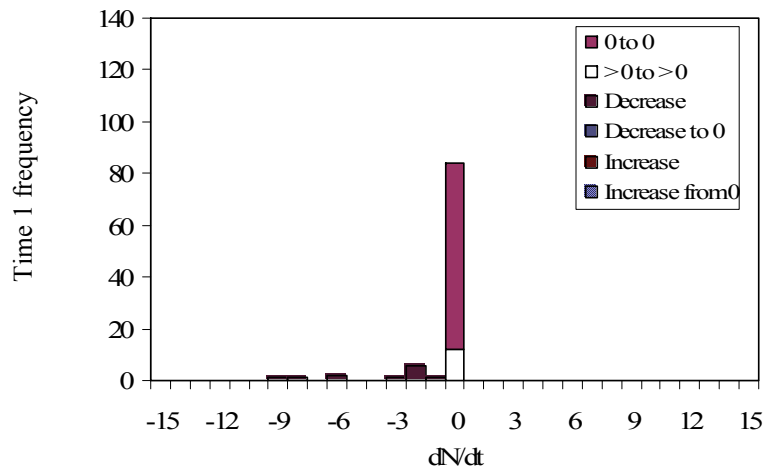
Figure 2.9. Patch 4, site 2 yellow toadflax fall density distributions ($\delta N/\delta t$).

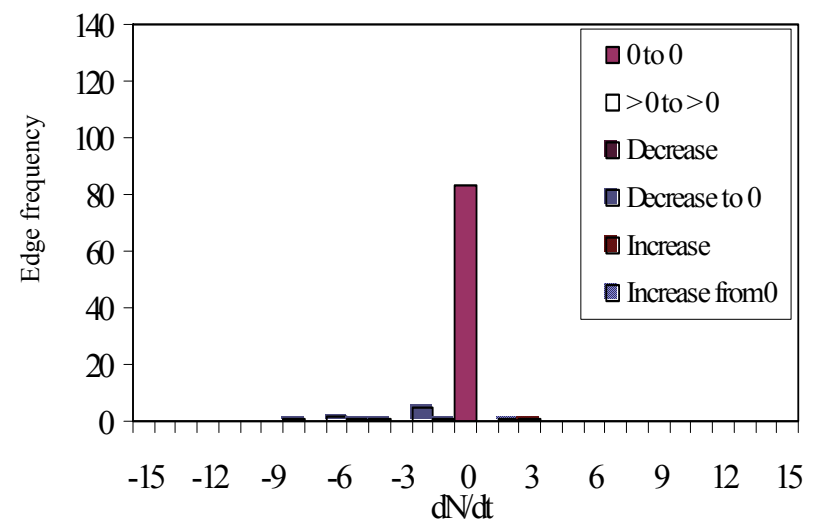
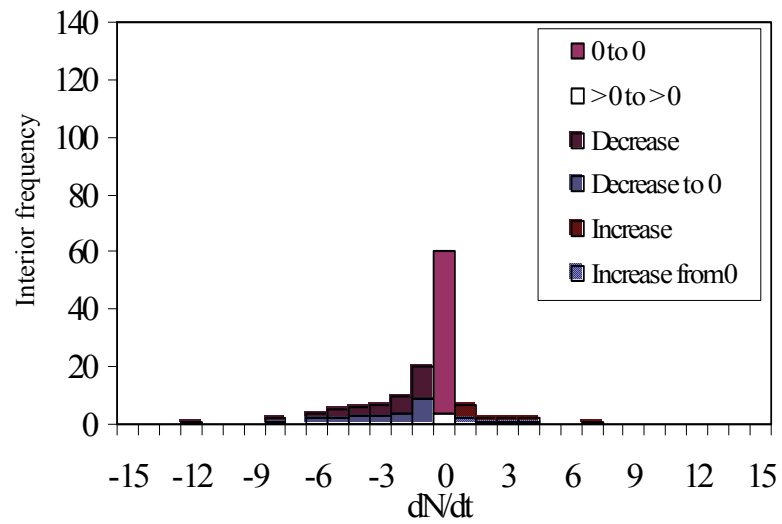
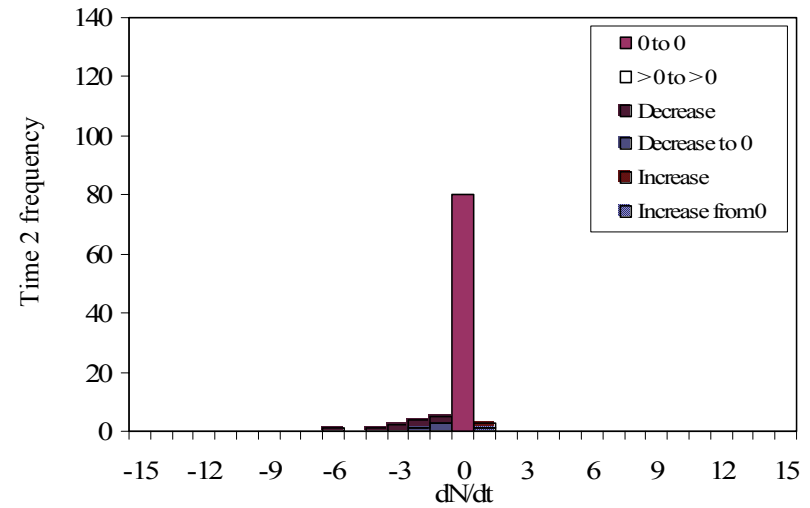
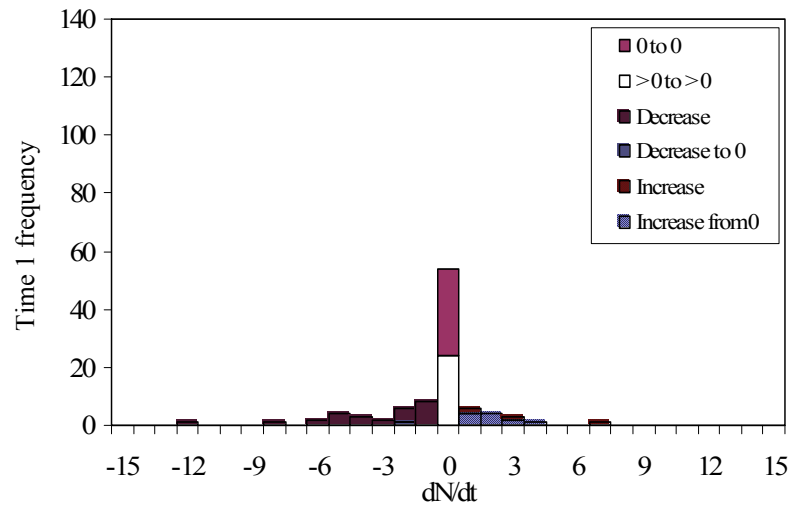
Figure 2.10. Patch 5, site 2 yellow toadflax fall density distributions ($\delta N/\delta t$).

Figure 2.11. Patch 6, site 2 yellow toadflax fall density distributions ($\delta N/\delta t$).

No data collected at Patch 6, Time 1

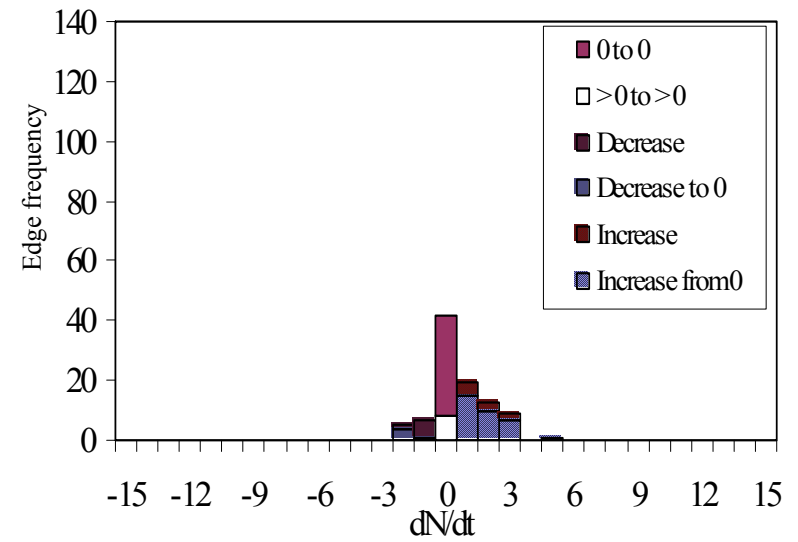
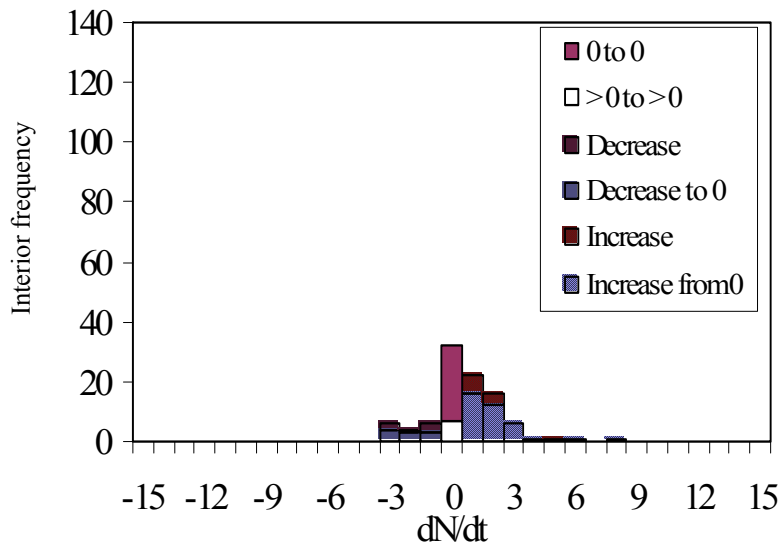
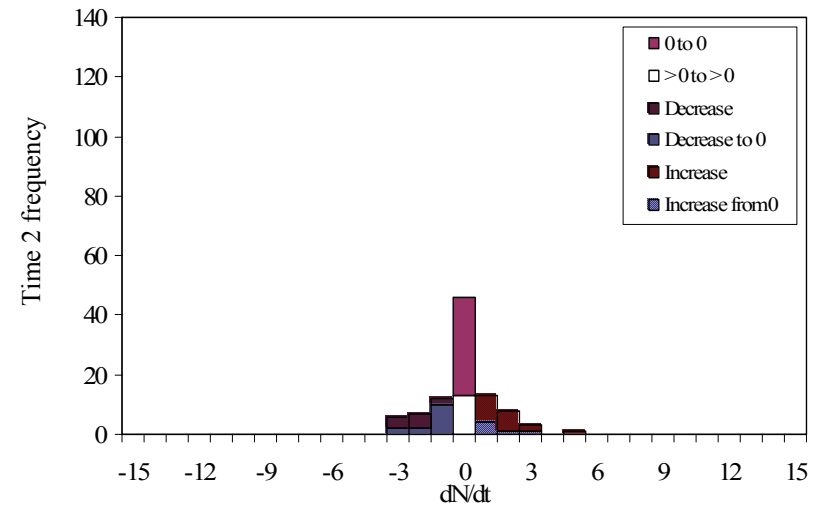


Table 2.3. Patch $\delta N/\delta t$ frequency distribution medians, mean skews, and Kolmogorov-Smirnov p-values; time 1 = 2001-2002 and time 2 = 2002-2003; na shows where not enough data for analysis; a significant P-value ($P \leq 0.05$) means that the particular frequency distribution differs significantly from a normal distribution (mean = 0, standard deviation = 1); invasive populations, in bold, have P-values ≤ 0.05 and a median $\delta N/\delta t < 0$.

		Median $\delta N/\delta t$	P-value	Mean Skew		Median $\delta N/\delta t$	P-value	Mean Skew
Site 1		-1	<0.0001	-0.206				
Site 2		1	<0.0001	-0.814				
Time 1		-1	0.0016	-0.143				
Time 2		1	0.0000	-0.355				
Interior		-1	0.0003	-0.271				
Edge		1	0.0000	0.046				
Patch 1	Time 1	1	0.016	0.922	Interior	1	0.02	0.252
	Time 2	1	0.0001	0.049	Edge	1	<0.0002	1.152
Patch 2	Time 1	-2	<0.0001	-0.096	Interior	-3	<0.0001	0.017
	Time 2	-1	0.0048	-0.452	Edge	-1	0.0013	-0.246
Patch 3	Time 1	2	<0.0001	0.216	Interior	3	<0.0001	0.410
	Time 2	2	<0.0001	-0.265	Edge	2	<0.0001	0.078
Patch 4	Time 1	-3	<0.0001	-1.018	Interior	1	<0.0001	-0.814
	Time 2	2	<0.0001	1.752	Edge	-1	na ¹	na ³
Patch 5	Time 1	-2	0.0072	-0.445	Interior	-2	<0.0001	-0.296
	Time 2	-2	0.0002	-0.560	Edge	-2	0.0003	0.135
Patch 6	Time 1	na ²	na ²	na²	Interior	-1	<0.0001	-0.413
	Time 2	-1	0.04	0.179	Edge	-1	<0.0001	0.126

Notes: 1. Patch 6 established in 2002

2. Median and skew were calculated from frequency distributions with zero values removed, note this when comparing these values to the frequency distributions in Figures 2.4 through 2.11

Table 2.4. Frequency distribution summaries showing proportion of increase to decrease in $\delta N/\delta t$, and proportion of no change in $\delta N/\delta t$; and also proportion of local colonization to extinction ($\delta n/\delta t$). Values below were calculated from frequency distributions with zeros removed.

	Site 1	Site 2	Interior	Edge	Time 1	Time 2						
Proportion Increase	0.24	0.59	0.27	0.19	0.20	0.23						
Proportion Decrease	0.30	0.07	0.28	0.13	0.25	0.20						
Proportion No Change	0.46	0.34	0.45	0.68	0.55	0.57						
Local Colonization	0.36	0.13	0.46	0.53	0.43	0.41						
Local Extinction	0.42	0.76	0.34	0.63	0.46	0.50						
No Change	0.13	0.05	0.20	0.05	0.09	0.08						
Interior V. Edge	P1I	P1E	P2I	P2E	P3I	P3E	P4I	P4E	P5I	P5E	P6I	P6E
Proportion Increase	0.26	0.20	0.24	0.23	0.45	0.32	0.13	0.00	0.11	0.02	0.44	0.50
Proportion Decrease	0.23	0.10	0.58	0.30	0.15	0.07	0.08	0.02	0.43	0.11	0.13	0.17
Proportion No Change	0.51	0.70	0.18	0.47	0.41	0.61	0.79	0.98	0.47	0.86	0.44	0.33
Local Colonization	0.47	0.50	0.17	0.29	0.28	0.56	1.00	0.00	0.36	0.50	0.79	0.77
Local Extinction	0.39	0.70	0.25	0.54	0.11	0.56	0.88	0.50	0.44	1.00	0.42	0.63
No Change	0.12	0.05	0.47	0.13	0.19	0.09	0.00	0.00	0.07	0.00	0.19	0.22
Time 1 v. Time 2	P1T1	P1T2	P2T1	P2T2	P3T1	P3T2	P4T1	P4T2	P5T1	P5T2	P6T1	P6T2
Proportion Increase	0.21	0.32	0.22	0.25	0.38	0.40	0.00	0.13	0.16	0.03	na ²	0.26
Proportion Decrease	0.14	0.15	0.49	0.41	0.07	0.13	0.13	0.00	0.28	0.14	na	0.26
Proportion No Change	0.66	0.53	0.29	0.35	0.55	0.47	0.88	0.88	0.56	0.83	na	0.48
Local Colonization	0.48	0.33	0.33	0.14	0.40	0.40	0.00	1.00	0.73	0.33	na	0.24
Local Extinction	0.50	0.21	0.33	0.37	0.33	0.25	0.00	0.00	0.04	0.31	na	0.56
No Change	0.10	0.15	0.30	0.14	0.07	0.17	0.14	0.00	0.44	0.00	na	0.28

Note: 1. Patch 6 established in 2002

Table 2.5. Continuous invasiveness index; P = patch, T = time, I = interior, E = edge, prop. = proportion.

	Median	Skew (+)	Prop. Increase ($\delta N/\delta t > 0$) (+)	Prop. Decrease ($\delta N/\delta t < 0$) (-)	Colonization $N_{t1} = 0$ $N_{t2} > 0$ (+)	Extinction $N_{t1} > 0$ $N_{t2} = 0$ (-)	Continuous Invasiveness Index (=)
Site 1	-0.25	-0.21	0.24	0.3	0.36	0.42	-0.58
Site 2	0.5	-0.81	0.59	0.07	0.13	0.76	-0.42
Time 1	-0.33	-0.14	0.27	0.28	0.46	0.34	-0.36
Time 2	0.33	-0.37	0.19	0.13	0.53	0.63	-0.08
Interior	-0.25	-0.27	0.2	0.25	0.43	0.46	-0.60
Edge	0.5	0.05	0.23	0.2	0.41	0.5	0.49
P1 T1	0.5	0.92	0.21	0.14	0.48	0.5	1.47
T2	0.5	0.05	0.32	0.15	0.33	0.21	0.84
I	0.33	0.25	0.26	0.23	0.47	0.39	0.69
E	1	1.15	0.2	0.1	0.5	0.7	2.05
P2 T1	-0.33	-0.10	0.22	0.49	0.33	0.33	-0.70
T2	-0.25	-0.45	0.25	0.41	0.14	0.37	-1.09
I	-1	0.02	0.24	0.58	0.17	0.25	-1.40
E	-0.33	-0.25	0.23	0.3	0.29	0.54	-0.90
P3 T1	0.5	0.22	0.38	0.07	0.4	0.33	1.10
T2	0.33	-0.27	0.4	0.13	0.4	0.25	0.49
I	0.5	-0.41	0.45	0.15	0.28	0.11	0.56
E	0.67	0.08	0.32	0.07	0.56	0.56	1.00
P4 T1	na ¹	na ¹	na ¹	na ¹	na ¹	na ¹	na ¹
T2	1.33	1.75	0.13	0	1	0	4.21
I	0.67	-0.81	0.13	0.08	1	0.88	0.03
E	na ¹	na ¹	na ¹	na ¹	na ¹	na ¹	na ¹
P5 T1	-1	-0.46	0.16	0.28	0.73	0.04	-0.89
T2	-1	-0.56	0.03	0.14	0.33	0.31	-1.65
I	-1	-0.30	0.11	0.43	0.36	0.44	-1.70
E	-0.5	0.14	0.02	0.11	0.5	1	-0.96
P6 T1	na ²	na ²	na ²	na ²	na ²	na ²	na ²
T2	-0.5	0.18	0.26	0.26	0.24	0.56	-0.64
I	-0.5	-0.41	0.44	0.13	0.79	0.42	-0.23
E	-0.5	0.13	0.5	0.17	0.77	0.63	0.10

Notes: 1. Excluded because of insufficient data

2. Patch 6 established in 2002, no data collected at time 1

The proportion of subsample frequency distributions that increased in density ($\delta N/\delta t > 0$) averaged 0.23 and ranged from 0 for the edges of patch 4 to 0.5 for the edges of patch 6, both at site 2. Site 2 had a higher proportional increase in density than site 1, although these results were skewed by much higher increases in density at patch 6, than patches 4 and 5, all at site 2. The proportion of sub-samples that decreased in density ($\delta N/\delta t < 0$) averaged 0.2 across all patch populations, and ranged from 0 for patch 4, site 2 time 1, to 0.58 for the interiors of patch 2 at site 1.

The proportion of local colonization over increase in $\delta N/\delta t$ averaged 0.46 across all patch populations, and ranged from a high of 1.00 for the interiors of patch 4, site 2 and also time 2 at patch 4, to 0.00 for the edges of patch 4 (Table 2.3). Overall, colonization was higher at site 1 versus site 2 and patch edges versus patch interiors, although within individual patches there was a great deal of variation.

The proportion of local extinction ($\delta N/\delta t < 0$) averaged 0.42 and ranged from a high of 1.00 for the edges of patch 5, site 2, to a low of 0.00 at time 1 and patch 4 (Table 2.3). Overall, extinction was higher at site 2 versus site 1 and patch edges versus patch interiors, although within individual patches there was a great deal of variability.

Invasiveness Index

I then evaluated the relative invasiveness of yellow toadflax populations using our invasiveness index (Table 2.4). With this equation, our determination of invasiveness was based not just upon an increase in density over time ($\delta N/\delta t$), but also skew, proportional increase and decrease in density, and local colonization and extinction.

Index values less than 0 indicated populations that were in decline. Positive or negative index values close to 0 indicated populations that were relatively stable. Using these criteria, most of the populations were only slightly positive or negative. The results are shown in an order of decreasing rank in Table 2.5. The most invasive populations in decreasing order (those in the top quartile) were patch 4 time 2, patch 1 time 1, patch 3 time 1, patch 3 edge, patch 1 time 2 and patch 1 interior.

Discussion

The results indicated that vegetative reproduction and growth drove yellow toadflax patch persistence and, for certain populations, expansion. These conclusions were consistent with other studies (Nadeau et al. 1992; Saner et al. 1995; Lajeunesse 1999). Observed evidence for the importance of vegetative reproduction included low seed production, distinct patch margins, and the lack of observed seedlings within established patches. It appears that low seed production and seedling emergence may be limiting the creation of new satellite patches, as no new satellite patches were observed near previously existing patches. None the less, there are widely distributed patches in the region that are difficult to explain unless there are rare events when germination and seedling survival rates are relatively high. Pauchard et al. (2003) concluded, in a study conducted within the same region as our study, that vegetative reproduction and growth drove yellow toadflax patch expansion, and that the creation of new satellite patches was the result of seed dispersal.

The population demographic factors that I observed had lower values than those found in other studies of yellow toadflax. This may be the result of our study having taken place in an area with a relatively high elevation and a harsh climate. Also, growing season precipitation was lower than the mean normal precipitation and temperatures were higher than mean normal temperatures (Figures 1.1 and 1.2).

Seed production at both study sites was very low when compared with other studies, with an average of only 1.1 seeds per flowering stem. In other studies, an average of 165 seeds per stem was produced in the presence of seed predators, and 824 to 5,584 seeds per stem were produced in the absence of seed predators (Zilke and Coupland 1954; Darwent et al. 1975; Saner et al. 1995). *Gymnaetron antirrhini*, a weevil that has been shown to reduce seed production, was present at site 2 study populations and may have been a factor in low seed production at that site. While environmental stress and the seed predator may have been limiting seed production, these factors were not quantified in our study.

Average yellow toadflax stem density varied from a low of 5 to a high of 56 m⁻² across the 6 study patches. These densities were lower than the 94 to 160 stems m⁻² found in Canadian grasslands (Bakshi and Coupland 1960), and the average density of 200 stems m⁻² found by Pauchard et al. (2003) in the same region. Similar to Pauchard et al. (2003), we also observed a great deal of variation in patch density across the landscape.

We began with several questions with regard to the invasiveness of yellow toadflax in the Northern Rocky Mountains. First, were the study populations invasive; that is, were they increasing in density over time? Second, could different determinations

be made about invasiveness depending upon the scale (metapopulation, patch and within patch) at which these populations were observed? Third, within invasive populations, was there enough variation in the level of this invasiveness to warrant that management precedence should be given to certain populations over others?

We quantified invasiveness by studying growth rate frequency distributions ($\delta N/\delta t$) for yellow toadflax populations, and then by creating an invasiveness index from statistics derived from these distributions. After three seasons of data collection and analysis we found that, using our invasiveness index, populations were invasive, both in terms of $\delta N/\delta t$ and our invasiveness index, at site 2, time 2, patch edges, patches 1 and 3 at site 1, and patch 4 at site 2. Yellow toadflax was invasive in 1 of the two sites, 3 of the six patches, 3 out of the 6 interior quadrats and 2 out of 6 edge quadrats.

We found, as did Stohlgren et al. (1999), that different conclusions could be reached about the invasiveness of a particular species, depending upon the scale at which this invasiveness was observed. The metapopulation at site 1 was determined to be invasive, although only two of the three individual populations within that metapopulation were invasive. Conversely, the metapopulation at site 2 was determined not to be invasive, although one of the three populations within that metapopulation was invasive. The determination of invasiveness did not vary between patches and the interiors and edges within these patches. Where patch populations were determined to be invasive (or not invasive), the interior and edge populations for those patches were also invasive (or not invasive). When the temporal scale of invasion was considered, yellow toadflax was declining over the time period of 2001 to 2002, but invasive for the time period of 2002 to 2003 at the metapopulation scale. While it is arguable, particularly

during a time of drought, whether this is too small of a time scale upon which to base any decisions, our effort was a good start.

Several studies have concluded that yellow toadflax was generally invasive in the Northern Rocky Mountains (Whipple 2001 in Yellowstone National Park; Pauchard et al. 2003 nearby in the Gallatin National Forest). These studies did not differentiate between invasive and non-invasive populations. Pauchard et al. (2003) also used a multi-scale method to study yellow toadflax patterns of invasion in the Gallatin National Forest and Yellowstone National Park. They found yellow toadflax to be invasive in both disturbed and undisturbed habitats, and also that ramet density within patches increased continuously over time.

The proportion of local colonization to increase in population $\delta N/\delta t$ was studied because local colonization events represented the probability of dispersal events. These events were potentially important to overall population dynamics and persistence of weed populations because new populations tend to have positive growth rates (Hulting 2004). The proportion of colonization was generally higher in invasive populations than non-invasive populations, indicating that these populations (patch interiors and patches 1 and 6) were increasing in spatial extent or filling in areas within established patches that had not previously been colonized. Local extinction as a proportion of total decrease in population $\delta N/\delta t$ also occurred at all of the populations studied, and was high at several populations, indicating that some of the populations (site 2, patch edges, patches 2 and 4) had decreased in spatial extent. That local colonization and extinction was occurring simultaneously within sub-samples in all of these populations as an indication of small-scale dynamics, even with populations that were increasing or decreasing in $\delta N/\delta t$.

New colonization was not correlated with an increase in overall density for every case. At site 2, patch edges, time 2, patch 1 time 1 and patch 1 edge, where population densities were increasing over time, the proportion of extinction relative to overall decline in $\delta N/\delta t$ was higher than the proportion of colonization relative to overall increase in $\delta N/\delta t$. These populations were declining in spatial extent but increasing in overall density.

Population $\delta N/\delta t$ decreased at site 1, time 1, patch interiors, and patches 2, 5 and 6. This suggests that these populations may not persist over time, although some sub-populations within these populations were increasing. Yellow toadflax populations persisted over the three summers of data collection for all of the populations studied. This persistence of yellow toadflax populations through drought and other hostile conditions has been attributed to its deep and extensive root system (Staniforth and Scott 1991), and this species may become invasive again when the hostile conditions end.

Because a determination of invasiveness for a particular species can vary, not only with the scale at which the species is observed within the landscape, but also for different habitats, land managers may be able to manage yellow toadflax with different levels of intensity depending upon where populations exist within the landscape. Sites 1 and 2 were also in different environments. While they had the same plant community, site 1 was over 300 m higher, was much steeper, had a different aspect, and had higher nutrient soils than site 2. Rew et al. (in press b) also found that NIS abundance varied between different environments.

Using our invasiveness index, we calculated a value for the invasiveness of each of the study populations, and then listed these populations in order of decreasing

invasiveness (Table 2.5). These populations were then ranked by quartile, with populations in the first quartile being the most invasive, although other scales could be applied. Our study also showed that the invasiveness of yellow toadflax populations varied depending upon the scale and environment in which invasiveness was considered. I believe that the monitoring of NIS populations at different scales and in different environments, combined with a consideration of the relative invasiveness of different NIS populations could have real value to land managers in prioritizing different populations for management. More work is needed to determine the utility of this index, and also the relevance of a particular index value or rank as a threshold for priority management.

There are several problems with making a conclusion about the invasiveness of yellow toadflax over time in this study area. The first problem is that, while it is thought that yellow toadflax was introduced into the study area just over 100 years ago, we do not know when toadflax became established at the two sites. Second, mean growing season precipitation over the three years of this study was only 81%, 73% and 80% of the 55-year mean (Figure 2.3). It is possible that yellow toadflax may become more invasive when and if moisture conditions improve, as shoot densities have been observed to increase with increased precipitation (Zilke 1954 in Saner et al. 1995). While I collected no data to support this at my study sites, I observed yellow toadflax flower and seed production to be more vigorous in riparian and lacustrine wetland environments where water may be less of a limiting factor than in adjacent uplands. Third, while the study lasted three years, the duration of the study was too short for making firm conclusions about population dynamics and the role of ecological processes during invasion (Hubbell 2001). Haber (1997) recommended a minimum of 5 years to account for seasonal

fluctuations in temperature, growing season and precipitation. Another graduate student will continue this study for at least three more seasons, and different conclusions may be drawn at that time. It was not feasible to visit each yellow toadflax population more than once during the spring census. Emergence of new shoots was spread out over the early growing season and. At a certain size new genet are impossible to differentiate from ramets, thus it was difficult to distinguish seedlings (see seedling cotyledons) from vegetative shoots.

NON-INDIGENOUS PLANT SPECIES OCCURRENCE AND ESTABLISHMENT WITH DISTANCE FROM A ROAD

Introduction

Roads and NIS Invasion

Roads provide immense benefits to humanity for travel, commerce, communication and recreation (Lugo and Gucinski 2000). However, in protected natural areas roads can have a variety of detrimental impacts (Cole and Landres 1996). Roads are important dispersal corridors for non-indigenous species (NIS) (Timmins and Williams 1990; Brothers and Springarn 1992; Tyser and Worley 1992; Spellerberg 1998; Gelbard and Belnap 2003), which often occur near roads (Spellerberg 1998; Weaver et al. 2001; Pauchard and Alaback 2004; Rew et al. b in press). These results implicate roads and trails as primary vectors of NIS dispersal into protected wildland areas (Pauchard and Alaback 2004).

Studies have addressed the many aspects of the problem of NIS and roads in different ways. Lugo and Gucinski (2000) described roads as human-created ecosystems because they occupy physical space, have structure, support a specialized biota, exchange matter and energy with other ecosystems, and experience temporal change. These researchers equated the establishment of a road upon a landscape to adding a new ecosystem to an existing one. Environmental conditions along roads can differ from previously existing environmental conditions in terms of altered light availability, soil

texture, compaction and chemistry, increased water runoff, and repeated disturbance from maintenance and off road driving (Rejmánek 1989; Hobbs 1991; D'Antonio and Vitousek 1992; Gelbard and Belnap 2003). Road runoff can increase water and nutrient availability for roadside plants (Holzaphel and Schmidt 1990; in Gelbard and Belnap 2003). This increased water from roads can promote NIS invasion in arid environments (White et al. 1997).

These “road ecosystems” can link otherwise spatially separated habitats in much the same way as riparian corridors, by providing a homogeneous environment throughout the length of the corridor (Lugo and Gucinski 2000), and thus providing a conduit along which populations can spread; which can lead to spread from roads into the interiors of protected natural areas (Landres et al. 1998). Gelbard and Belnap (2003) found that NIS richness and cover increased as roads improved from four-wheel drive tracks to paved roads. These researchers hypothesized that this was because improved roads made natural habitats more vulnerable to invasion by increasing repeated disturbance from clearing and roadfill, maintenance, herbicide treatment and compaction.

Non-indigenous species may respond better than indigenous species to the alien substrates and altered disturbance, water and nutrient regimes found on roadsides (Mack and Thompson 1982; Tyser and Worley 1992). Once established, roadside NIS patches can then serve as points of introduction and also reservoirs for the spread of NIS into the interiors of natural areas (Tyser and Worley 1992; Pauchard and Alaback 2004). This can result in changes in plant community composition through the displacement of indigenous species (Randall 1996), and ultimately, a reduction in native biodiversity in

protected natural areas (Mack et al. 2000). Once established, NIS patches may persist along road corridors as long as roads provide conditions that favor their growth and success over indigenous species (Greenberg et al. 1997).

Harrison et al. (2002) observed NIS invasion from roads in a California peninsular nature reserve. These researchers stated that roads act as linear disturbances that support invasion by NIS and also as infrequent sources of NIS propagules entering indigenous grasslands. They concluded that the arrival of successful propagules is a rare and sporadic event, and also that the subsequent NIS population growth may be so rapid that the ongoing movement of seeds along roads may have no detectable influence on local NIS abundance.

Propagule Pressure and Effects on Invasion

The loss of indigenous seed banks and seed sources can lead to a change in species composition from indigenous plant communities towards communities dominated by NIS (D'Antonio and Vitousek 1992). For example, dominance of disturbed prairie by introduced species has been found to be a function of seed availability (Wilson and Belcher 1989). Where NIS seed rain is high, prairie communities can be taken over by NIS; while in the absence of NIS propagules, indigenous species can revegetate even previously cultivated lands (Inouye et al. 1987).

For seed propagules which arrive by wind, seed dispersal is a function of adaptations to wind dispersal such as seed mass and shape, the presence of wings or a pappus, the height of the parent plant, and whether or not the presence of neighboring

plants acts to block wind (Howe and Smallwood 1982; Burrows 1986; Augspurger 1986, 1989). In the study described below, we studied Canada thistle (*Cirsium arvense* Scop.) and smooth brome (*Bromus inermis* L.). Canada thistle, unlike smooth brome, has an adaptation (a pappus) that allows its seeds to be transported by wind for several kilometers (Wood and Del Moral 2000). However, most seeds of both Canada thistle (Kramer 1975) and smooth brome (Bakker 1960) fall near the parent plant.

Secondary dispersal of seed following seed rain can critically alter the subsequent structure of plant communities (Cabin et al. 2000). Drivers of secondary dispersal include animals, gravity, wind, water and cultivation (Cousens and Mortimer 1995). Secondary dispersal is affected by barriers and soil surface characteristics such as surface roughness, vegetation structure and organic matter (Stamp 1989; Mack and Harper 1997).

Once seeds have reached the soil surface, vertical movement of seeds within the soil can then result from processes such as precipitation, freeze-thaw cycles, and mechanical soil disturbance (Chambers et al. 1991). Seed characteristics such as size, shape, appendages, adhesive coats and large hairs also affect seed incorporation into the soil because these characteristics can facilitate soil entrapment and burial. Vertical movement of seeds within the soil can be affected by soil structure, particle size and clay content (Chambers et al. 1991). In the absence of cracks in the soil, small seeds reach greater depths in soils of small particle size than larger seeds; and most species that form persistent seed banks tend to have small seeds (Chambers et al. 1991; Thompson et al. 1994). Large seeds are less likely to be incorporated deep into the soil because they are

less likely to fall into cracks or be buried by earthworms or other soil animals (Thompson et al. 1994).

After seeds enter the soil, the soil seed bank can serve as the genetic “memory” of the plant community, affecting plant population dynamics and community structure by supplying a pool of genetic material and enabling a range of responses to environmental variability and adverse conditions (Teo-Sherrell et al. 1996). Zhang *et al.* (1998) found that for annuals, the above-ground non-indigenous populations depended on the soil seed bank. Despite this, there is usually no correlation between the composition of the seed bank and the established vegetation community (Roberts 1981; Forcella 1992; Cardina and Sparrow 1996; Mack and Harper 1997). Moore (1980) explained that this was because late successional species generally do not have persistent seeds.

Upon reaching the soil surface, many seeds are lost to germination and death from predation (birds, small mammals, seed eating insects and earthworms) and other causes including fungal attack and physical damage (Harper 1977; Cousens and Mortimer 1995). In one study, the majority of seed losses in a sage-steppe ecosystem were caused by fungal pathogens and decomposition, with smaller seeds more likely to be lost (Crist and Friese 1993). Seed bank numbers decline most dramatically in the first year, after which the decline curve is much less steep (Cousens and Mortimer 1995). Buried viable seed density also declines with increasing disturbance due to seed germination (Thompson 1978).

Seed eaters may prefer seed from certain species over others. Ants avoid seeds with non-lethal fungal infections due to decreased palatability (Crist and Friese 1993).

For seed eating birds, choice was influenced by seed chemistry, and grass seeds were favored over the seeds of forbs because of lower levels of tannins and alkaloids (Diaz 1996). Size affects survival, as larger seeds are more likely to be consumed by granivores such as ants, rodents and birds. One study showed a 62% removal of *Lolium rigidum*, 49% removal of *Chondrilla juncea* over 24 hours (Kelrick et al. 1986; Reader 1993).

Germination and Emergence

Should a seed survive to germinate, it must still face processes that can select for the traits of certain species. For example, in invaded semi-arid grasslands with continuous living and dead plant cover, large *Bromus* seeds may have a germination advantage over smaller seeds (Belnap and Phillips 2000). Small seeds have smaller nutrient reserves than larger seeds, are more likely to have a light requirement for germination, and need to be closer to the surface to emerge (Venable and Brown 1988). In early successional species, germination is often inhibited by filtered (high red/far red) light, where as understory species do not generally require light for germination (Schenkeveld and Verkaar 2000). In the absence of soil disturbance, seedling recruitment is typically limited to the uppermost layers of the soil (2.5 cm) representing only a small fraction of the total soil seed bank (Thompson 1992). Initial seedling emergence of many species was higher on coarse textured sandy loams than on organic soils (Chambers et al. 1991). Thus, different soil textures created along roadsides may affect relative emergence values.

After germination, seedling survival is negatively affected by increasing plant density and competition for resources (Hartgerink and Bazzaz 1984). Surface litter can have either positive or negative feedbacks on seedling survival and establishment. The presence of plant litter can have positive feedbacks on seedling establishment because increased litter can result in higher soil water retention and a more favorable microclimate for germination (Harper and Benton 1966; Suding and Goldberg 1999). Conversely, litter and vegetation can have negative feedbacks because less light was available for seedlings, and because seed herbivory, pathogen loading, phytotoxin release and nutrient immobilization increased with increasing litter depth (Xiong and Nilsson 1999).

Not all sites are equally conducive to seedling emergence. Safe sites or “gaps” are microsites where all of the conditions required for a species’ germination are met (Harper 1961). Many NIS are pioneer species which are more suppressed by competition from existing vegetation than are later successional species adapted to closed habitats (Fenner 1978). Safe sites may be created in the vegetation by the death of large plants, by the natural spacing of plants resulting from limited water availability and competition, by animal burrowing and other natural disturbances, and by human disturbance (Hutchings 1997). In bunchgrass plant communities, it is thought that the high light intensity and frequent breaks in plant cover may facilitate NIS invasion (Forcella and Harvey 1983). Canada thistle offers an example of how safe sites may affect germination and persistence. During germination, abundance of Canada thistle depends on the density

of safe sites; a threshold safe site density exists below which populations went extinct and above which populations grew geometrically (Silvertown and Smith 1988).

Study Goals

The studies cited above have detailed that many factors contribute to the successful establishment of plants in natural areas after dispersal from their parent plants. The study presented below explores the contribution of NIS propagule pressure with distance from roads. The purpose of this study was to increase our understanding of how NIS colonize wildland areas adjacent to roads.

First, we hypothesized that, because of increased soil water from road runoff, soil water would be greatest near the road and decrease with increasing distance from the road. Second, we hypothesized that the number of available safe sites for invasive species establishment would increase with proximity to roads, due to increased soil water from road runoff, and decreasing competition from indigenous plants. Third, we hypothesized that seed rain and seed bank density would be greatest close to the road and smooth brome and Canada thistle patches. Fourth, we hypothesized that seed loss would increase with increasing distance from the road, as seed predators such as rodents and birds would be less active near the road because of human activity.

Materials and Methods

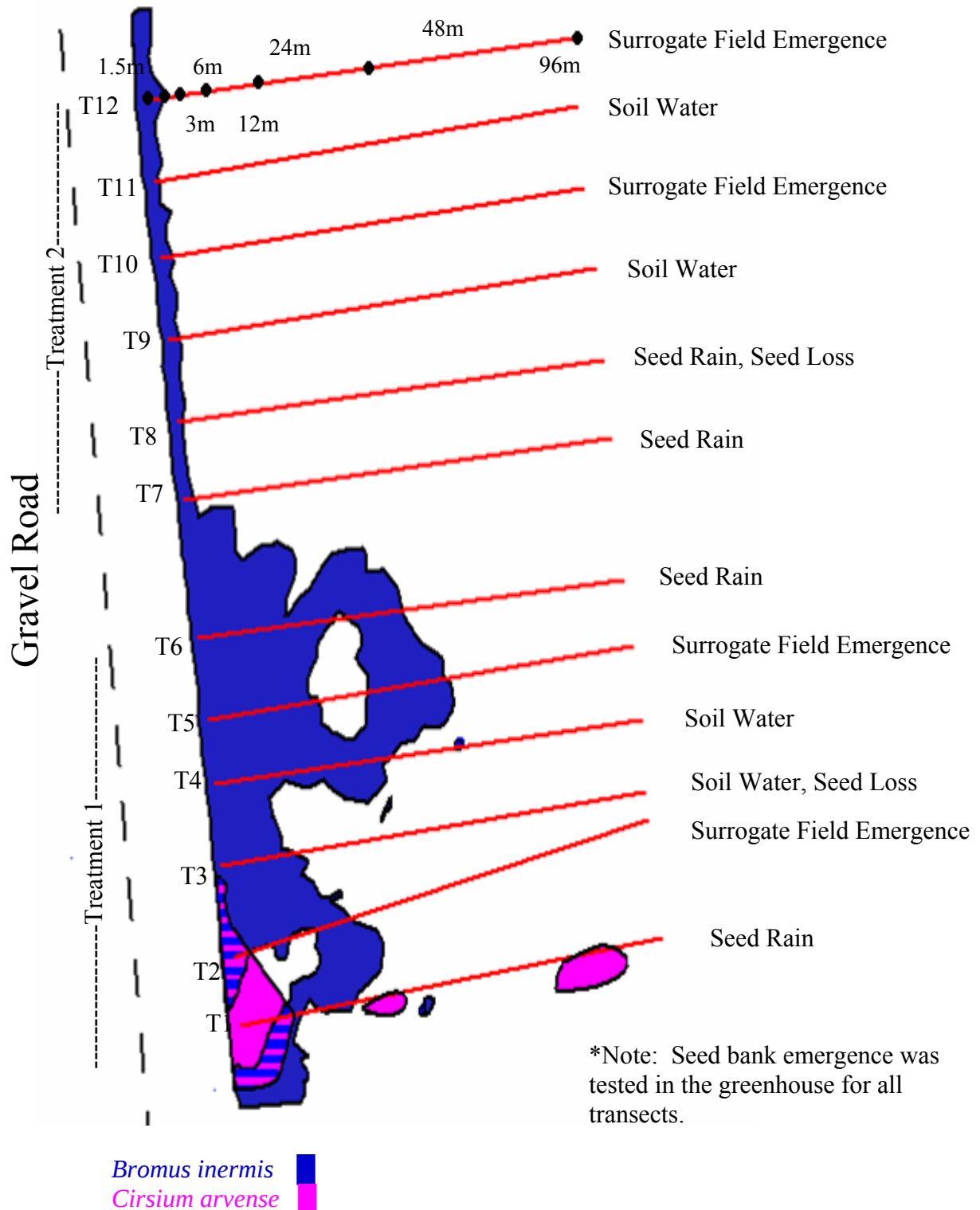
Site 3 Description

Site 3 is located in the Gallatin National Forest just west of Hebgen Lake at 44° 47' 30' N, 111° 16' 40' W, and at an elevation of 1980 m. The site lies on a wide bench in a large montane meadow. Site slopes are gentle, from 2 to 4%, except for the first 1 to 2 meters along the road shoulder where slopes are from 60 to 70%, measured with a clinometer. Soils are loams and sandy loams. This study took place within an Idaho fescue (*Festuca idahoensis*) / bluebunch wheatgrass (*Pseudoroegneria spicata*) habitat type (Despain 1990). Dominant species also included Sandberg's bluegrass (*Poa sandbergii*), sticky geranium (*Geranium viscosissimum*), silvery lupine (*Lupinus argenteus*) and the NIS smooth brome (*Bromus inermis*). Observed disturbance at this site came from off-road vehicles, elk, deer and cattle grazing and small animal burrowing.

Data Collection

Twelve transects were established at the site (Figure 3.1). Six transects were established where smooth brome had spread well into the grassland from the road and where Canada thistle was also present (Figure 3.1; transects 1-6 in treatment 1). Another 6 transects were established where smooth brome was only present immediately adjacent to the road and where no Canada thistle was present (transects 7-12; treatment 2). We had originally intended to establish the latter six transects where smooth brome and

Figure 3.1. Diagram of transect locations and experimental treatments at site 3. Treatment 1 includes transects 1-6, treatment 2 includes transects 7-12.



Canada thistle were not present, however smooth brome was widely planted in this region along roadsides and no suitable sites were found.

Seven sampling stations were installed along each transect at distances of 1.5 m, 3 m, 6 m, 12 m, 24 m, 48 m and 96 m from the road (Figure 3.1). The sampling stations were marked with white-painted rebar. Transects were randomly divided so that soil water, emergence and seed rain were studied along two transects each in both treatment areas with 2 replicates per treatment (Figure 3.1). Site monitoring took place weekly from May through October of 2003.

Soil Water

To describe variation in soil water with distance from the road and over the season, we recorded soil water at the 7 sampling distances; along transects 3 and 4 in treatment 1, and transects 9 and 11 in treatment 2. Buried gypsum blocks were used to measure changes in soil water. Electrical conductivity between electrodes in the gypsum blocks, measured in bars using a Delmhorst KS-D1 meter, increases with increasing water (Delmhorst Instrument Co.). As soil water tension approaches 0 bars, the soil nears field capacity and plants have adequate available water. As soil water tension increases towards 15 bars, virtually all plant available soil water has been used and plants experience water stress.

The gypsum blocks were installed per manufacturer instructions (Delmhorst Instrument Co.). Prior to installation, the blocks were soaked in water for 24 hours, then taken out of the water to partially dry for one hour, prior to burial. Next, the gypsum

blocks were then buried at a depth of 15 cm at the each of the 7 sampling distances along each of the 4 soil water transects (Figure 3.1). Electrical conductivity of the blocks was recorded weekly during the first week after burial to allow the blocks to come to equilibrium within the soils, as per manufacturer's instructions.

At the end of the field season, the gypsum blocks were collected and then calibrated as follows (Cooperative State Research, Education and Extension Service 2000): individual gypsum blocks were collected with the surrounding 0.61 l of soil and placed in pots. The pots and soil were oven dried at 105 °C and then weighed dry. The pots were then thoroughly wetted and placed back in the oven. Every two hours, the pots were taken out, weighed and gypsum block electrical conductivity was measured. This was done until there was no weight change. This data was used to create a calibration curve for the gypsum blocks, and for subsequent data collection.

Surrogate NIS Field Emergence

Two surrogate NIS, radish (*Raphanus sativa*) and spring wheat (*Triticum aestivum*), were used to test the distribution of safe sites for emergence with distance from the road and also whether the distribution of these safe sites differed between the two treatments. This was done at transects 2 and 5 in treatment 1 and transects 10 and 12 in treatment 2 in the spring and fall of 2003. Surrogate species were used because we did not wish to introduce NIS seeds to areas of this meadow where they had not already established. Radish and wheat were chosen as the surrogate NIS as these seeds were

commonly available, dormancy problems were not expected, and these species were unlikely to be invasive.

Prior to sowing, seed germination was tested in a Conviron 125 L growth chamber. Two lots of fifty seeds each for each surrogate species were placed in individual petri dishes on paper moistened with 2 ml of water. After 3 days, 98% of the radish and 100% of the wheat had germinated. One radish seed succumbed to a fungus.

For the spring emergence study, two 0.1 m² wire rings for each of the two species were set at each sampling distance along the two transects in each treatment. The rings were placed at 0.5 m and 1 m on either side of each transect. On May 26, 2003, fifty seeds were sown in each ring. Two rings were sown with radish and two rings were sown with wheat. The seeds were scattered on the soil surface and the species placements were randomized. Surrogate NIS emergence in the rings was monitored during the weekly site visits. This procedure was repeated for the fall emergence study in new rings placed beside the existing rings so that late emergence from spring-sown seeds would not be counted. Seeds for the fall emergence study were sown on September 4, 2003.

Percentage cover by species, bare ground and litter cover were estimated by eye in each of the rings. This was performed in late June for the spring emergence study and September for fall emergence.

Seed Rain

To determine whether seed rain of the target NIS, smooth brome and Canada thistle, varied with distance from the road and between the two treatments, seed rain was evaluated along transects 1 and 6 in treatment 1, and transects 7 and 8 in treatment 2. Seed traps were made by sliding plastic 0.07 m² page protectors over thin plywood boards cut to the same size. The traps were placed horizontally but flush to the ground, secured with long spikes and painted with Tanglefoot[®] (The Tanglefoot Company), a sticky adhesive. One seed trap was placed at 1.5 m, 3 m, 6 m, and 12 m and two traps at 24 m, 48 m and 96 m. Additional traps were placed at the greater distances to increase the likelihood of catching seeds farther away from their sources. The seed traps were placed in the field prior to smooth brome and Canada thistle seed set and removed on October 20, 2003. Smooth brome and Canada thistle seeds which stuck to the seed traps were identified and counted. The traps were checked weekly and changed if disturbed.

Seed Bank Greenhouse Emergence

Soil cores were collected to a depth of 10 cm using a 10 cm diameter soil corer on May 22, 2003. This was performed at each of the 12 transects to determine whether seed bank emergence varied with distance from the road and between the two treatments. Ten cores were taken at 1.5 m, 3 m, 6 m and 12 m and bulked into one sample for each distance; twenty cores were taken at 24 m, 48 m and 96 m and bulked into two samples for each distance. Cores

were taken within a 1 m radius of each sample distance. The bulked samples were placed in separate 0.6 l pots at the MSU Plant Growth Center. The soil was stirred, wetted, and then kept moist for the duration of the experiment. The pots were checked for smooth brome and Canada thistle seedling emergence every two weeks for two months. After each sample period, the soil was stirred. This was repeated four times.

Seed Loss

Seed loss was evaluated along transects 3 and 8 using wheat, radish, Canada thistle and smooth brome seeds. The seeds were placed in 10 cm diameter seed dishes. Fifty seeds of each species were placed in each dish. The dishes were lined with paper filters to prevent the seeds from floating out during heavy rain events. The seed dishes were placed flush with the ground, with dishes on either side of both transects at each sampling distance. They were placed in the field the first week of September. After 3 weeks, the dishes were collected and the remaining seeds counted.

Data Analysis

Soil water tension (bars), emergence, seed rain, seed bank, seed loss and indigenous species richness and cover were compared against distance (and soil water tension for field emergence) using correlation analysis. We considered this correlation worthy further analysis when the correlation coefficient (r) was ≥ 0.4 . Where the correlation was ≥ 0.4 , we then used simple linear regression to describe the relationship between distance from the road and the response variables. The two treatments were then compared using analysis of variance. Differences in the means were assessed based upon

Fisher's protected LSD test at $P = 0.05$ (Fischer 1926). Statistical analyses were performed using S-Plus 2000 (Mathsoft, Inc.) and Excel XP (Microsoft, Inc.).

Results

Soil Water

As expected, soil water decreased significantly over the growing season (Figure 3.2; $P < 0.00001$, $r = 0.719$), calculated using linear regression. At the start of the growing season in late May and early June, average soil water was near field capacity. Soil water declined until it approached the permanent wilting point in August and remained near the permanent wilting point through the end of the growing season (Figure 3.2).

Soil water varied significantly between the two treatments (Figure 3.3; $P = < 0.00001$, $r = -0.24$), calculated using Anova. Average soil water tension was higher at treatment 1 (10.39 bars) than treatment 2 (9.55 bars). However, the low correlation coefficient ($r < 0.04$) showed that treatment explained little of the variation in soil moisture.

Figure 3.2. Box plots of soil water tension by date. Field capacity is neared as soil water tension approaches 0. Permanent wilting point is neared as soil water tension approaches 15. Solid line is median, shaded areas represent 50% of data, bars represent remaining 45% of data, bars with circles represent outliers.

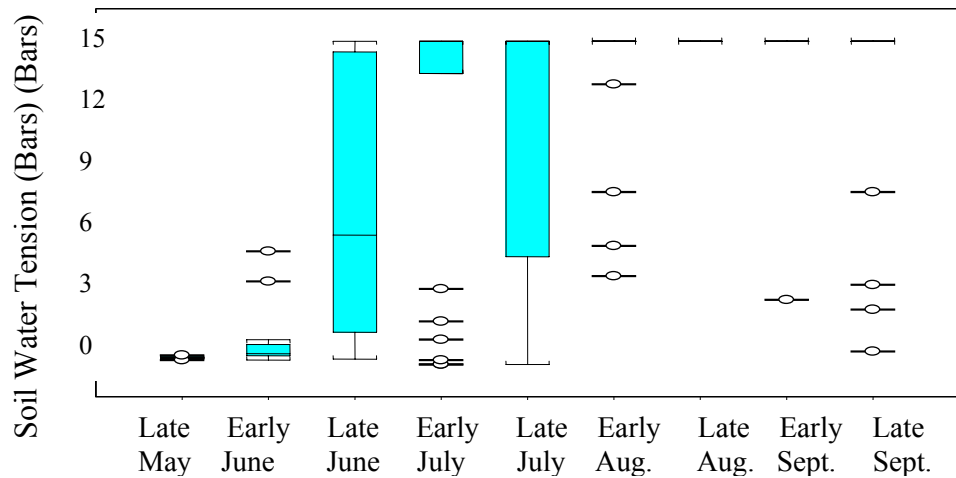
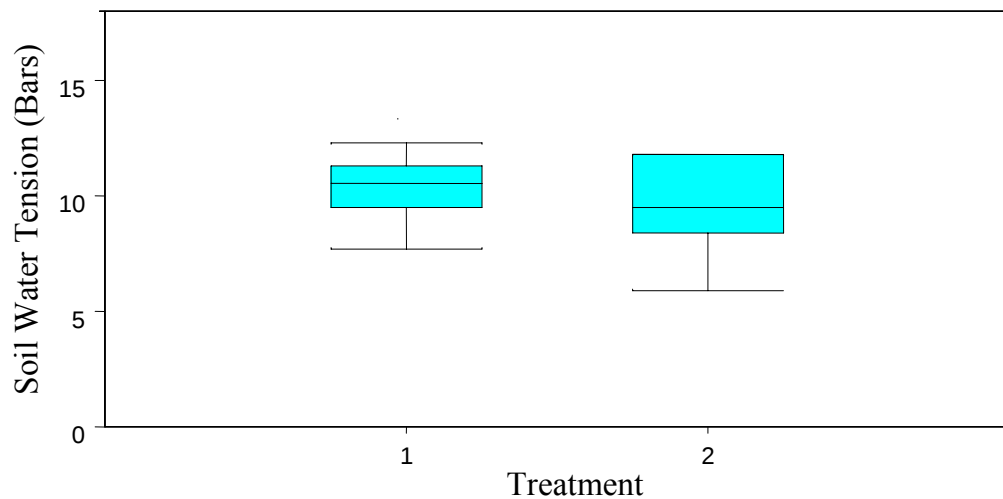
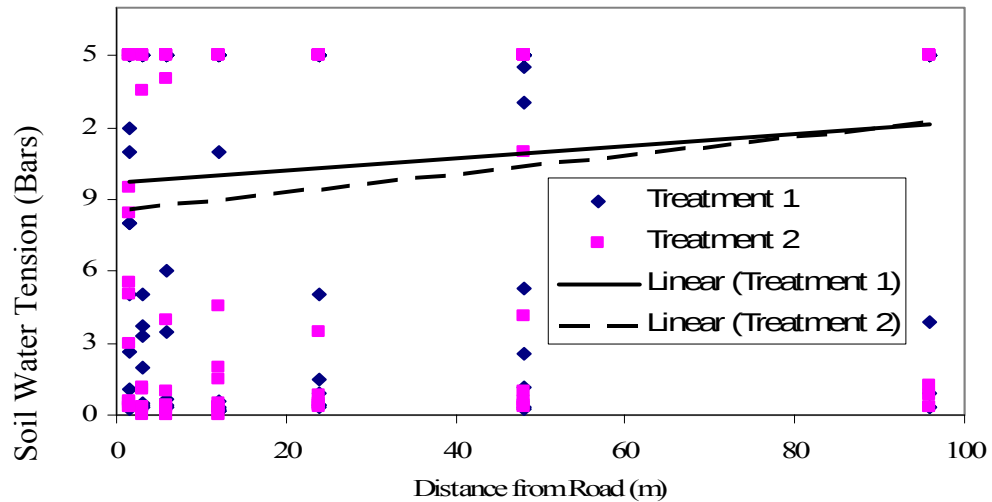


Figure 3.3. Box plots of soil water tension by treatment. Field capacity is neared as soil water tension approaches 0. Permanent wilting point is neared as soil water tension approaches 15. Solid line is median, shaded areas represent 45% of data, bars represent remaining 50% of data.



$P = 0.00001$, $r = -0.24$

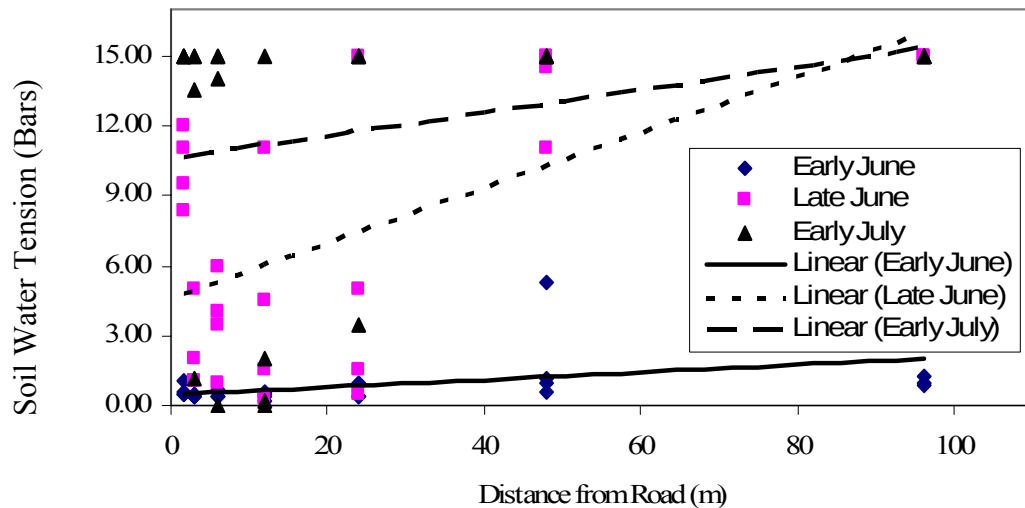
Figure 3.4. Soil water tension by distance from the road for treatments 1 and 2 with all data combined across the entire season for site 3. Field capacity is neared as soil water tension approaches 0; permanent wilting point is neared as soil water tension approaches 15.



Treatment 1 Soil water tension = $0.026 (\text{distance}) + 9.67$; $P = 0.1473$, $r = 0.13$

Treatment 2 Soil water tension = $0.039 (\text{distance}) + 8.48$; $P = 0.0395$, $r = 0.184$

Figure 3.5. June soil water tension with distance from road. Field capacity is neared as soil water tension approaches 0; permanent wilting point is neared as soil water tension approaches 15



Early June Soil water tension = $0.016 (\text{distance}) + 0.454$; $P = 0.009$, $r = 0.485$

Late June Soil water tension = $0.119 (\text{distance}) + 4.61$; $P = 0.0001$, $r = 0.673$

June $P = 0.009$, $r = 0.485$; late June $P = 0.0001$, $r = 0.673$). The proportional change in soil water over time (data not shown) did not vary significantly with distance from the road ($P = 0.303$, $r = 0.202$).

Surrogate NIS Field Emergence

We found no significant relationships between distance from the road and radish spring ($P = 0.607$; $r = -0.102$) or fall ($P = 0.092$; $r = -0.324$) emergence (Figures 3.6 and 3.7). Nor did we find significant relationships between soil water and radish spring ($P = 0.099$; $r = -0.559$) or fall ($P = 0.151$; $r = -0.279$) emergence (Figures 3.8 and 3.9).

However, soil water was measured at a depth of 10 cm and the seeds were sown at the soil surface. We also tested for correlation between radish emergence and the cover for bare ground, litter, non-indigenous grasses and forbs, and grasses and forbs. We found little correlation ($r < 0.04$) between radish emergence and these parameters. In both the spring and the fall, wheat emergence numbers were too low for statistical analysis.

Unlike what we had originally hypothesized, average soil water (averaged across the growing season) did not vary significantly with distance from the road for either treatment (Figures 3.4; treatment 1 $P = 0.147$, $r = 0.130$; treatment 2 $P = 0.040$, $r = 0.184$) for the whole season combined. When looked at bimonthly, soil water decreased significantly with distance from the road only in the month of June (Figure 3.5).

Figure 3.6. Radish field emergence with distance from the road in spring 2003.

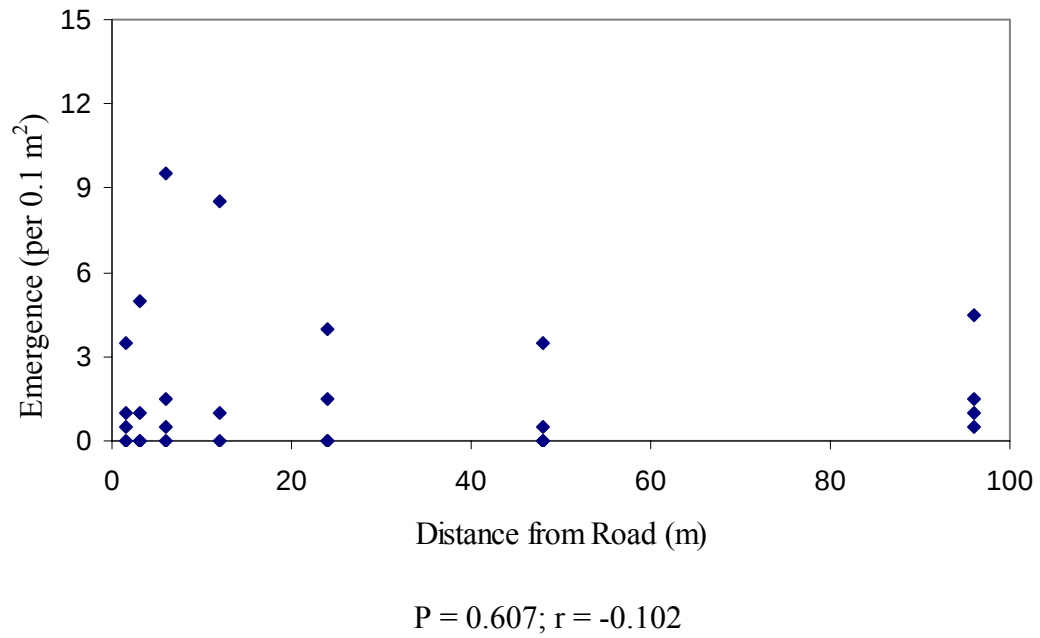


Figure 3.7. Radish field emergence with distance from the road in fall 2003

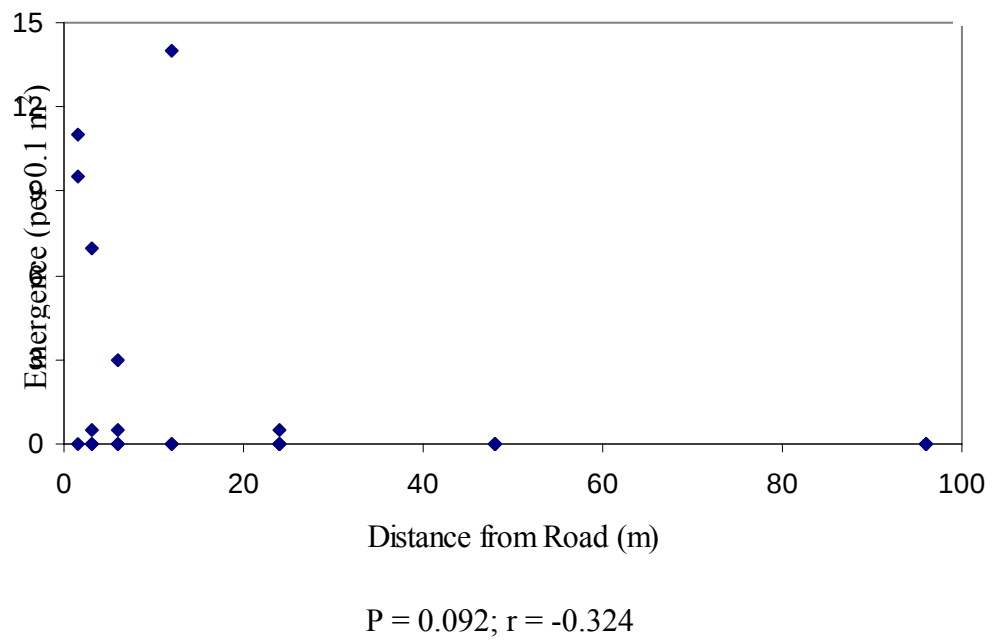
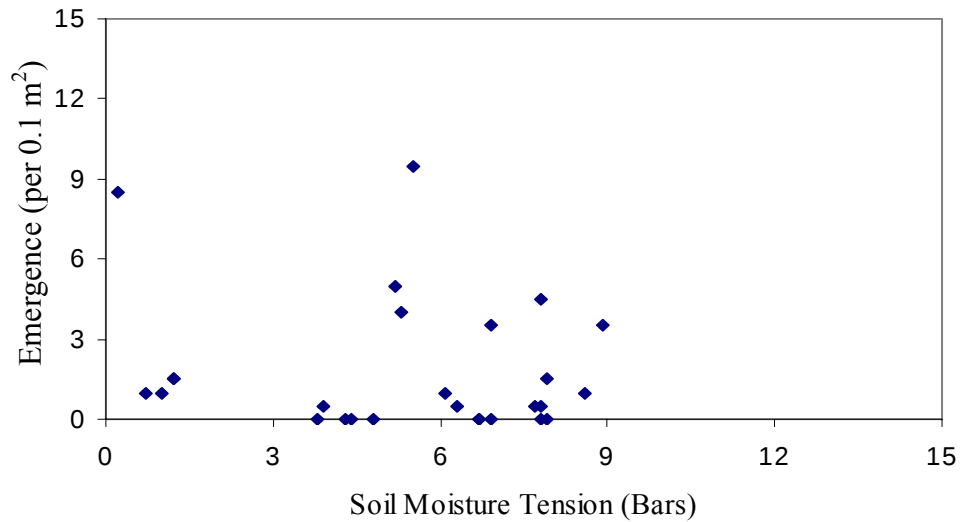
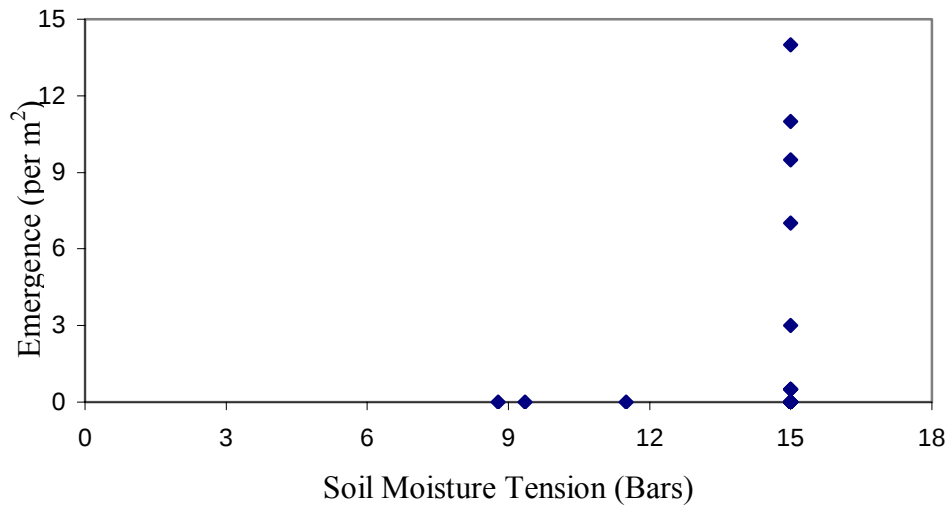


Figure 3.8. Radish field emergence with soil water in spring. Soils near field capacity as soil water tension nears 0 bars. Plants near the permanent wilting point as soil water tension nears 15 bars.



$P = 0.099$; $r = -0.559$

Figure 3.9. Radish field emergence with soil water tension in Fall; Soils near field capacity as soil water tension nears 0 bars; plants near the permanent wilting point as soil water tension nears 15 bars.



$P = 0.151$; $r = -0.279$

Seed Rain

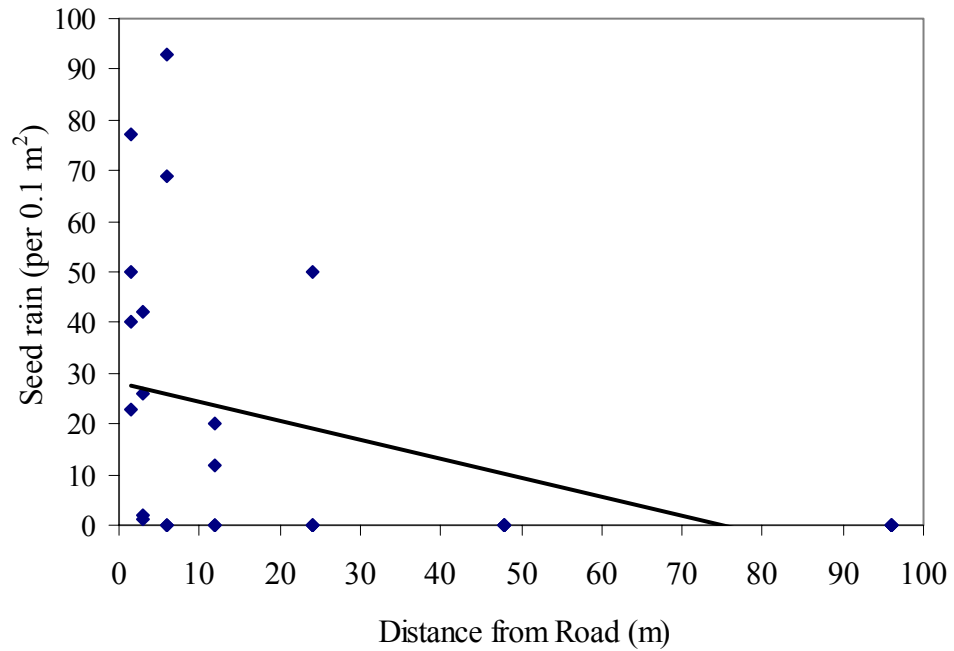
Smooth brome seed rain per m^2 ($P = 0.037$, $r = -0.396$) was lower at treatment 2 than treatment 1 but the low correlation coefficient shows a low correlation between seed rain and treatment. Canada thistle seed rain ($P = 0.080$, $r = -0.336$) did not differ significantly between the two treatments.

Smooth brome seed rain decreased significantly with increasing distance from the road (Figure 3.10; $P = 0.003$, $r = -0.546$). Canada thistle seed rain did not decrease with increasing distance from road ($P = 0.638$, $r = -0.093$). However, the three Canada thistle patches were distributed along transect 1 and the seed rain for this species decreased with distance from transect 1 (Figure 3.11; $P = 0.007$, $r = -0.426$).

Twenty-five Canada thistle seeds and 409 smooth brome seed were caught by the seed traps. Average smooth brome seed rain was 263 seed m^2 ($\pm 146 \text{ seed m}^2$), while average Canada thistle seed rain was much lower at 15 seeds m^2 ($\pm 9 \text{ seeds m}^2$). Smooth brome seeds were not found on seed traps located outside of the smooth brome patches. Twenty eight percent of the Canada thistle seeds trapped were found on traps located over a meter from Canada thistle patches.

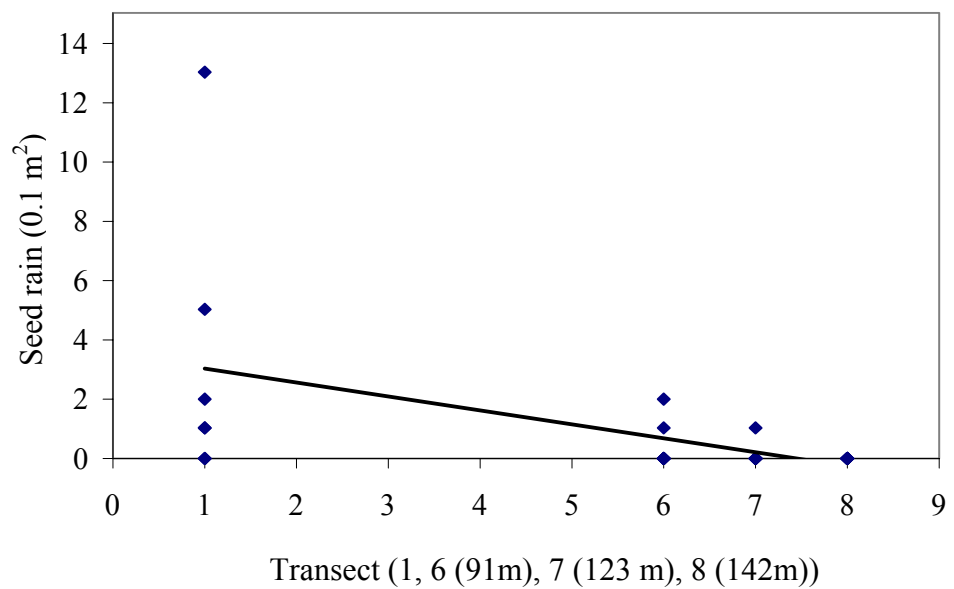
Where present, smooth brome had an average density of 157 stems m^2 and Canada thistle had an average density of 5.7 stems m^{-2} . Average smooth brome seed production was 56 seeds per stem. Seed heads were grazed from 17% of smooth brome

Figure 3.10. Smooth brome seed rain with distance from the road.



Smooth brome seed rain = $-10.61 \ln(\text{distance}) + 44.41$; $P = 0.018$; $r = -0.445$

Figure 3.11. Canada thistle seed rain with distance from transect 1.



Canada thistle seed rain = $-0.729(\text{transect}) + 3.53$; $P = 0.007$; $r = -0.426$

stems by the end of the season. Average Canada thistle seed production was 312 seeds stem and 1778 seeds m².

Seed Bank Emergence

Ninety-eight smooth brome seedlings emerged during the greenhouse seed bank study. Smooth brome seed bank emergence varied between the two treatments, with more seedlings emerging from treatment 1 (Figure 3.12; $P = 2.47 \times 10^{-007}$, $r = -0.528$).

Smooth brome seed bank emergence decreased significantly with increasing distance from the road (Figure 3.13; $P = 2.06 \times 10^{-007}$, $r = -0.531$). Only 4 Canada thistle seedlings emerged during the greenhouse seed bank study, too few to perform data analysis.

Figure 3.12. Smooth brome seed bank emergence for the two treatments. (emergence per 0.6 l for 1.5-12 m; per 1.2 l for 24-96 m). Solid line is median, shaded areas represent 50% of data, bars represent remaining 45% of data.

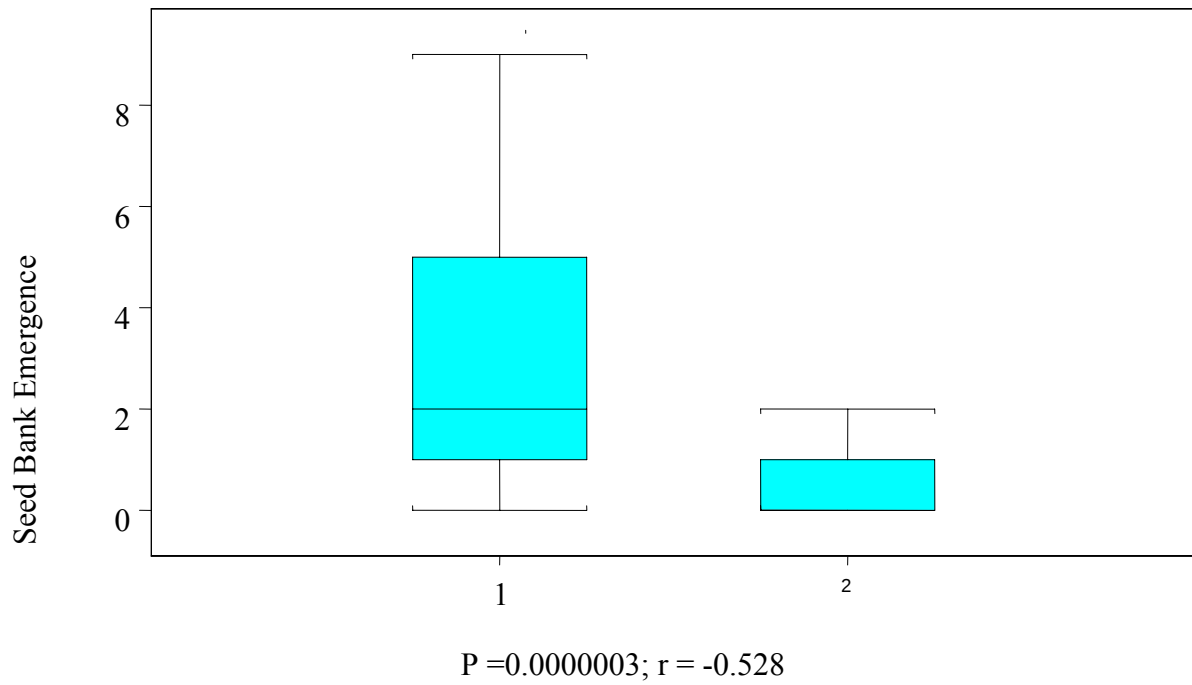
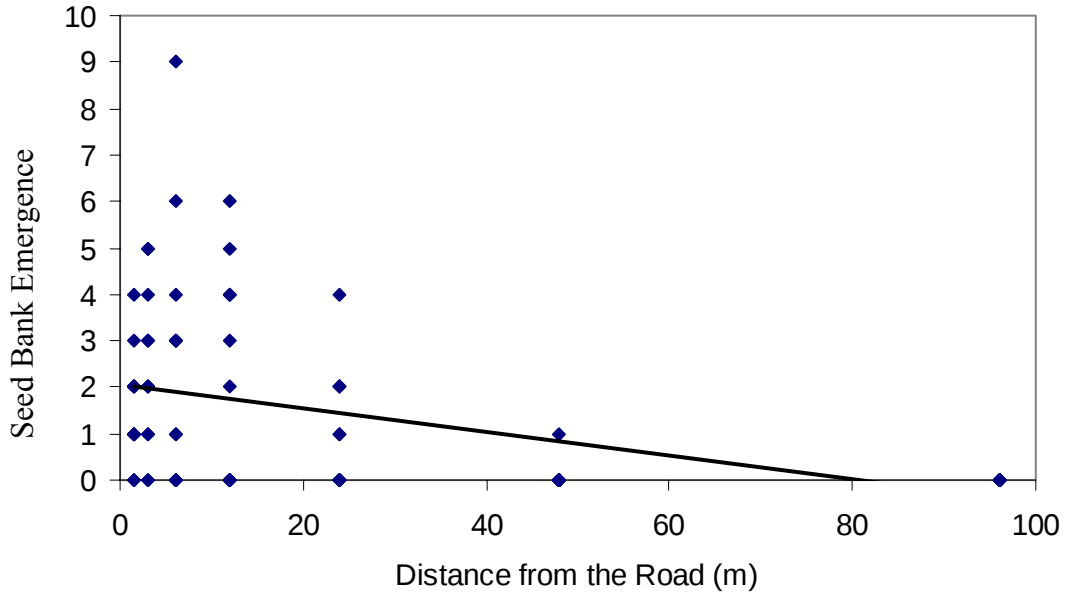


Figure 3.13. Smooth brome seed bank emergence with distance from road.

(emergence per 0.6 l for 1.5-12 m; per 1.2 l for 24-96 m).

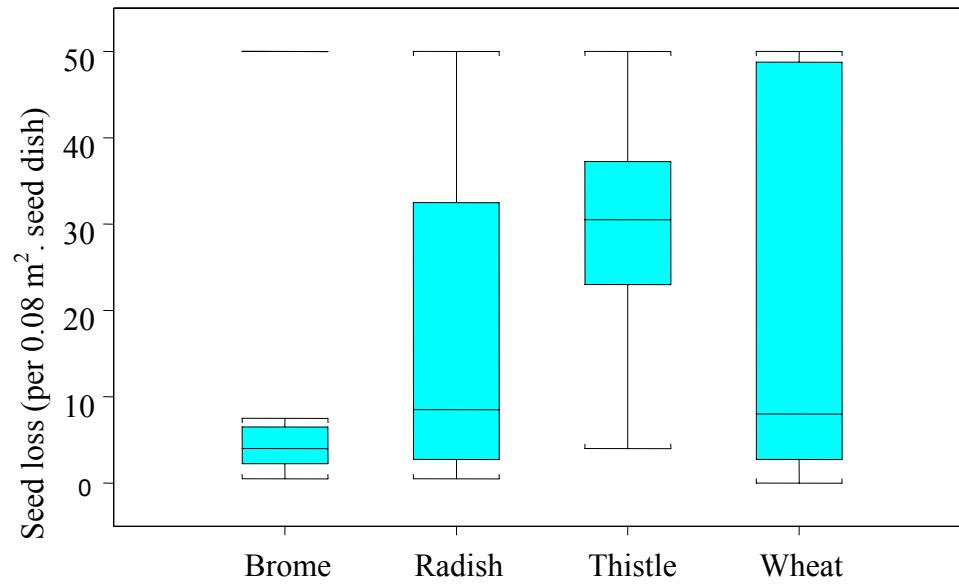


Smooth brome seed bank = $-0.026 (\text{distance}) + 2.055$; $P = 0.0000002$, $r = -0.531$

Seed Loss

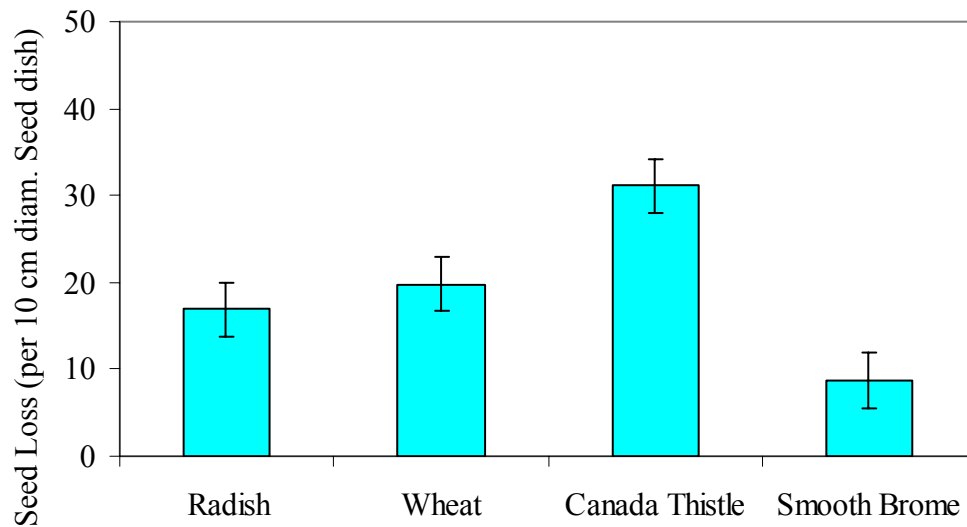
Seed loss did not vary significantly correlation by treatment ($P = 0.110$, $r = 0.152$). However, there was an increase in seed loss with distance from the road for smooth brome ($P = 0.05$, $r = 0.28$) and Canada thistle ($P = 0.04$, $r = 0.36$) (Figures 3.16 and 3.17), although the correlations between seed loss and distance were not very strong. Seed loss for wheat ($P = 0.98$, $r = 0.007$) and radish ($P = 0.24$, $r = 0.17$) did not decline with distance from the road (Figures 3.18 and 3.19). Over the three weeks that the seeds were in the field, 8.3% of seed dishes were pulled up and chewed by a large animal, so these data were excluded from further analysis.

Figure 3.14. Relative seed loss by species from original 50 seeds per dish. Solid line is median, shaded areas represent 50% of data, bars represent remaining 45% of data, bars with circles represent outliers.



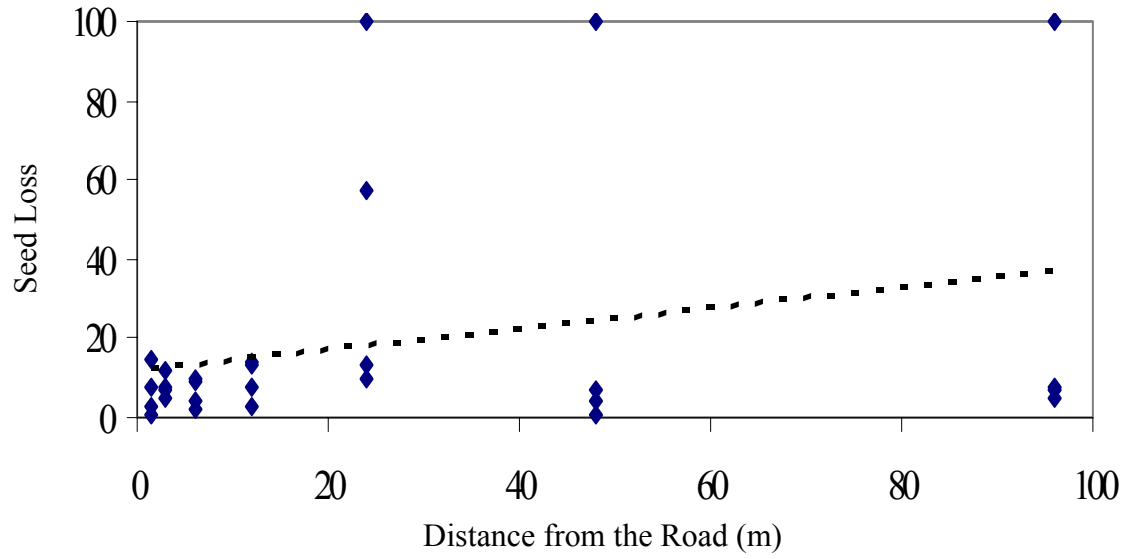
$P = 0.00004$, $r = 0.573$

Figure 3.15. Mean and standard error of seed loss for the 4 study species.



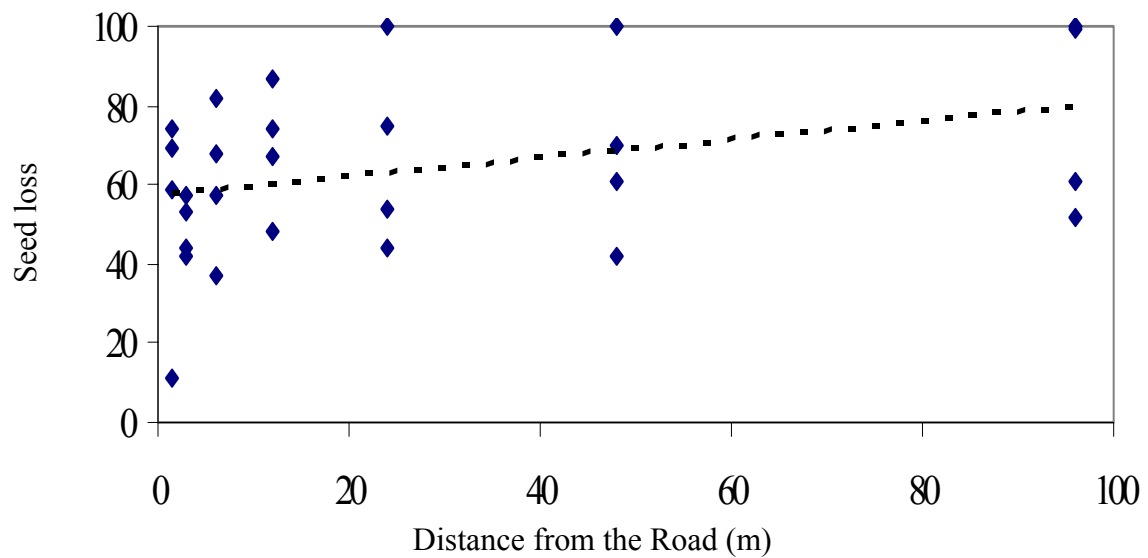
$P = 0.0004$, $r = 0.330$

Figure 3.16. Smooth brome seed loss with distance from the road.



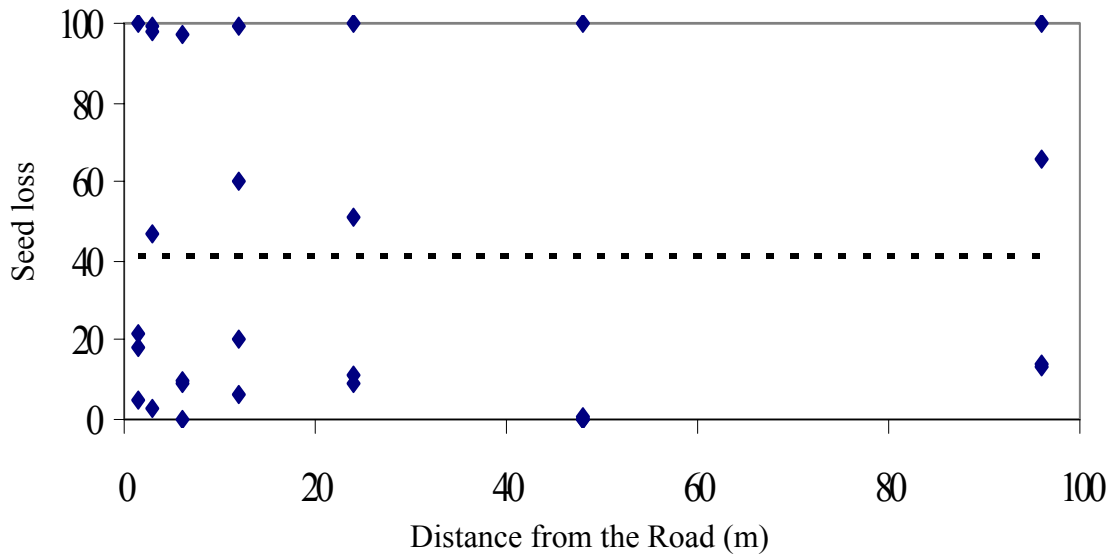
$P = 0.05, r = 0.28$

Figure 3.17. Canada thistle seed loss with distance from the road.



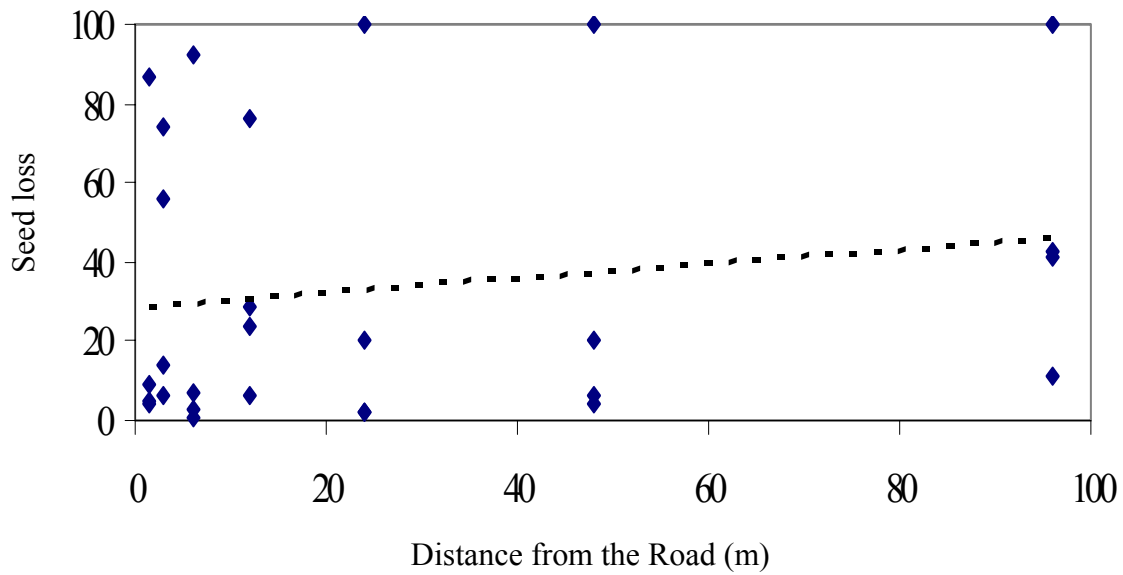
$P = 0.04, r = 0.36$

Figure 3.18. Wheat seed loss with distance from the road.



$P = 0.98, r = 0.007$

Figure 3.19. Radish seed loss with distance from the road.



$P = 0.24, r = 0.17$

Correlations between individual species seed loss were strong, and analysis of variance showed that there were significant differences between the population means (Figure 3.14; $P = 0.00004$, $r = 0.573$). Figure 3.15 shows the mean seed loss and standard error for each species. Canada thistle had the highest mean seed loss, and smooth brome had the lowest mean seed loss. Radish seed loss was not significantly different from wheat seed loss.

Plant Community Composition

We characterized the composition of the study area plant community to provide a context for the interpretation of our results. The bunchgrass plant community was diverse, with 53 indigenous forbs in 17 families, and 9 indigenous grasses and 2 indigenous sedges identified at the site. Nine non-indigenous forbs in 4 families, and 2 non-indigenous grasses were also present. Average indigenous species cover at site 3 was 47%, non-indigenous species cover was 16%, and bare ground cover was 37%. Overall litter cover was 12%.

Percent cover for individual species was generally low and only 5 indigenous species had over 2% cover. The dominant indigenous herbs in order of decreasing cover were sticky geranium 8%, silvery lupine 3%, and yarrow (*Achilla millefolium*) 2%. Dominant indigenous graminoids in order of decreasing cover were Sandberg's bluegrass 9%, Hood's sedge (*Carex hoodii*) 3%, mountain brome (*Bromus carinatus*) 2%, Idaho fescue 2%, and blue-bunch wheatgrass 2%.

Four smooth brome patches were present, one main patch and three small satellite patches located within a few meters of the main patch (Figure 3.1). Along transects 1 through 6 (treatment 1), smooth brome extended 15 m to over 60 m from the road. Smooth brome was only present within 3 meters of the road along transects 7 through 12 (treatment 2). Smooth brome had the highest overall cover of any plant at the site. Its cover averaged over the entire site was 14%, and it had an average cover of 29% in rings where it was recorded. This species made up 91% of total NIS cover at site 3. Canada thistle was present in three patches with the largest patch along the road at transects 1 and 2 (Figure 3.1). Two smaller patches were found just south of transect 1 at 30 m and 90 m. Canada thistle cover, averaged over the entire site, was 0.1%. It had an average cover of 4% in the rings where it was recorded.

Besides smooth brome and Canada thistle, other NIS included quackgrass (*Agropyron repens*), bull thistle (*Cirsium vulgare*), hound's tongue (*Cynoglossum officinale*), black medic (*Medicago lupulina*), dandelion (*Taraxacum officinale*), yellow salsify (*Tragopogon dubius*), shepherd's purse (*Capsella bursa-pastoris*), penny cress (*Thlapsi arvense*) and white clover (*Trifolium repens*). Cover for all NIS averaged over the entire site was 16%. No NIS other than smooth brome had over 1% cover. Litter and bare ground cover did not vary significantly ($P \geq 0.05$) with smooth brome presence or absence.

Indigenous species cover ($P = 0.0001$, $r = 0.210$) increased significantly with distance from the road, while NIS cover ($P = < 0.0001$, $r = -0.474$) decreased significantly with distance from the road (Figure 3.20). Indigenous species cover

increased from a low of 17% at 3 m to a high of 64% at 48 m and 96 m. Non-indigenous species cover decreased from a high of 47% at 3 m to a low of 0.5% at 96 m. The correlation coefficient for NIS cover with distance did meet our criteria for significance ($r < 0.40$), however, the low correlation coefficient showed that little of the variance in indigenous species ($r = 0.210$) cover was explained by distance.

Indigenous species richness ($P < 0.0001$, $r = 0.399$) increased significantly with distance from the road, while NIS richness ($P < 0.0001$, $r = -0.496$) decreased significantly with distance from the road (Figure 3.21). Indigenous species richness increased from a low of 1.8 species per 0.1 m² at 1.5 m to a high of 6.2 species per 0.1 m² at 24 m and 48 m. Richness for NIS decreased from a high of 1.1 species per 0.1 m² at 1.5 m to a low of 0.1 species per 0.1 m² at 96 m. The correlation for indigenous species richness was only slightly below our criteria for significance ($r < 0.40$), while the correlation for NIS was higher than this criteria.

Indigenous species cover ($P = 3.67 \times 10^{-10}$, $r = 0.333$) and richness ($P = 0.001$, $r = 0.254$) differed between the two treatments (Figures 3.22 and 3.23). Both cover and richness for indigenous species were higher at treatment 2, where brome was only present along the road, than treatment 1, where brome extended well into the study area. Neither of the correlation coefficients for indigenous species cover and richness met our criteria for significance ($r < 0.40$), showing that little of the variance in either indigenous species cover or richness was explained by differences between the two treatments.

Non-indigenous species cover ($P = 3.47 \times 10^{-7}$, $r = -0.474$) and richness ($P = 2.38 \times 10^{-6}$,

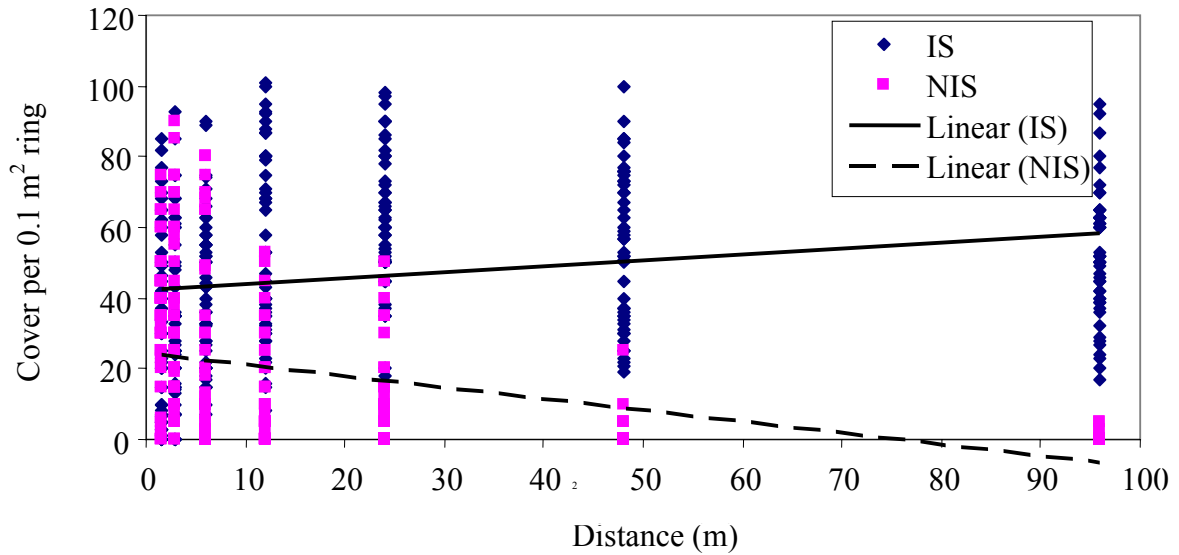
$r = -0.254$) also differed significantly between the two treatments (Figures 3.24 and 3.25).

Richness and cover for NIS were both significantly higher at treatment 1 than treatment 2. Interestingly, while the correlation between NIS cover and treatment was significant, the low correlation coefficient for NIS richness ($r < 0.40$) showed that little of the variance in NIS richness was explained by differences between the two treatments.

In Figures 3.20 through 3.25, I showed that indigenous species richness and cover decreased significantly with distance from the road, and was also higher at treatment 2, where smooth brome was only present along the road, than treatment 1, where smooth brome extended well into the study area. However, the low correlation coefficients ($r < 0.04$) showed that neither distance nor treatment sufficiently accounted for variation in indigenous species cover and richness. The results were different when indigenous species cover and richness were plotted against smooth brome cover. Indigenous species cover ($P < 0.0001$, $r = -0.450$) and richness ($P < 0.0001$, $r = -0.559$) decreased significantly with increasing smooth brome cover (Figures 3.26 and 3.27). Where smooth brome was present, indigenous species cover averaged 26% and indigenous species richness averaged 3 species per 0.1 m^2 . Where smooth brome was not present, indigenous species cover, 62% and richness, 5 species per 0.1 m^2 , were both higher than where smooth brome was absent.

Smooth brome was the only NIS to have any negative correlation with indigenous species cover and richness. Even when the cover for all NIS other than smooth brome was considered, there was no significant relationship between this combined NIS cover and indigenous species cover ($P = 0.79$, $r = 0.12$) or richness ($P = 0.62$, $r = 0.07$).

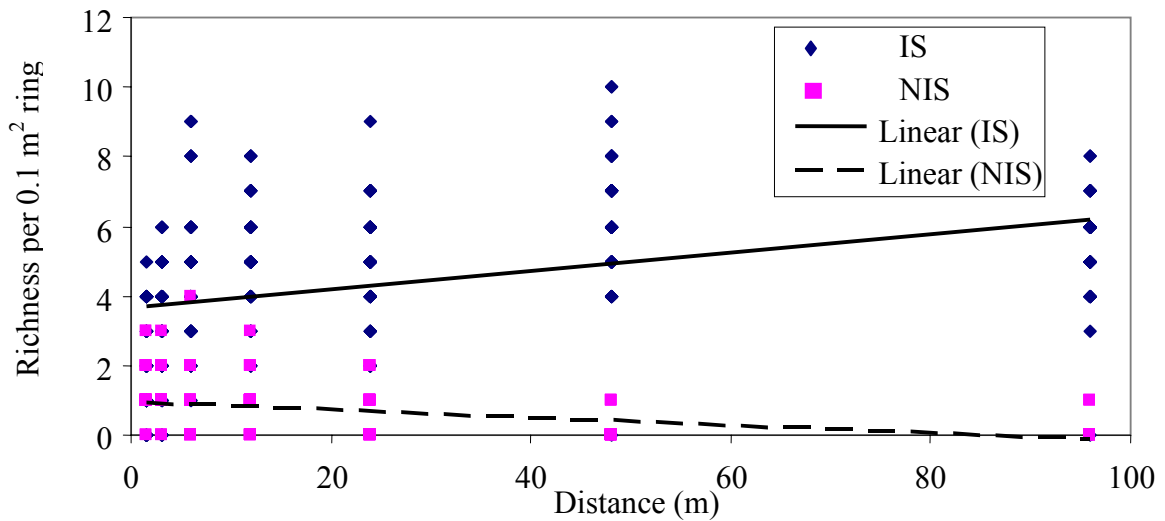
Figure 3.20. Indigenous and non-indigenous cover with distance from road; IS = indigenous species, NIS = non-indigenous species.



$$\text{IS cover} = 0.1661 (\text{distance}) + 42.459; P = 0.0001, r = 0.210$$

$$\text{NIS cover} = -0.3198 (\text{distance}) + 24.361; P < 0.0001, r = -0.474$$

Figure 3.21. Indigenous and non-indigenous species richness with distance from road; IS = indigenous species, NIS = non-indigenous species.



$$\text{IS richness} = 0.0264 (\text{distance}) + 3.6827; P < 0.0001, r = 0.399$$

$$\text{NIS richness} = -0.0112 (\text{distance}) + 0.9653; P < 0.0001, r = -0.496$$

Figure 3.22. Indigenous species cover by treatment, lines with solid circles show medians. Solid boxes represent 50% of data and bars represent the remaining 45% of the data.

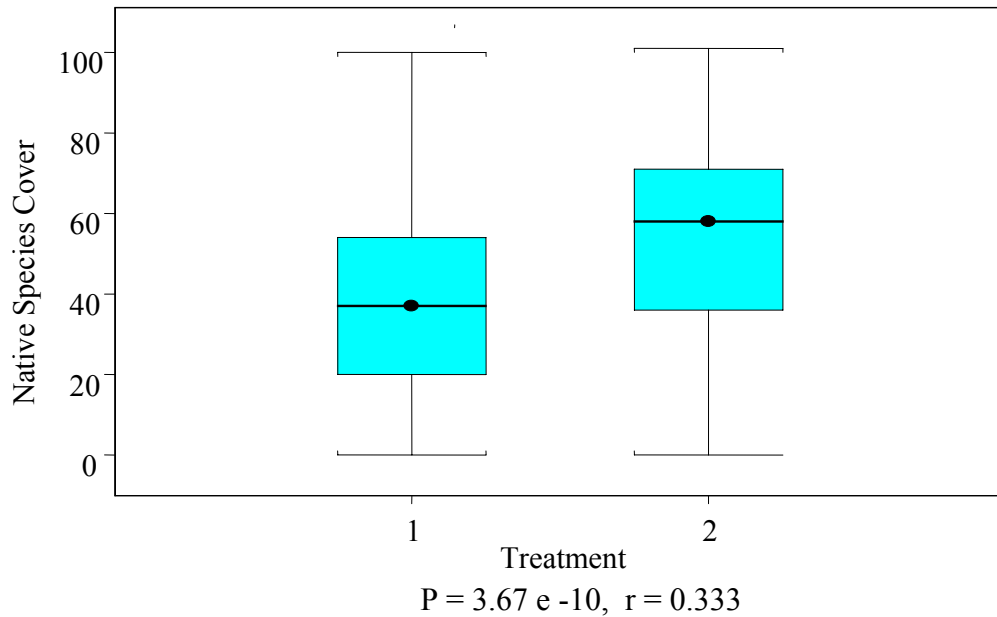


Figure 3.23. Non-indigenous species richness by treatment, bars with solid circles show medians, bars with empty circles show outliers. Solid boxes represent 50% of data and bars represent the remaining 45% of the data.

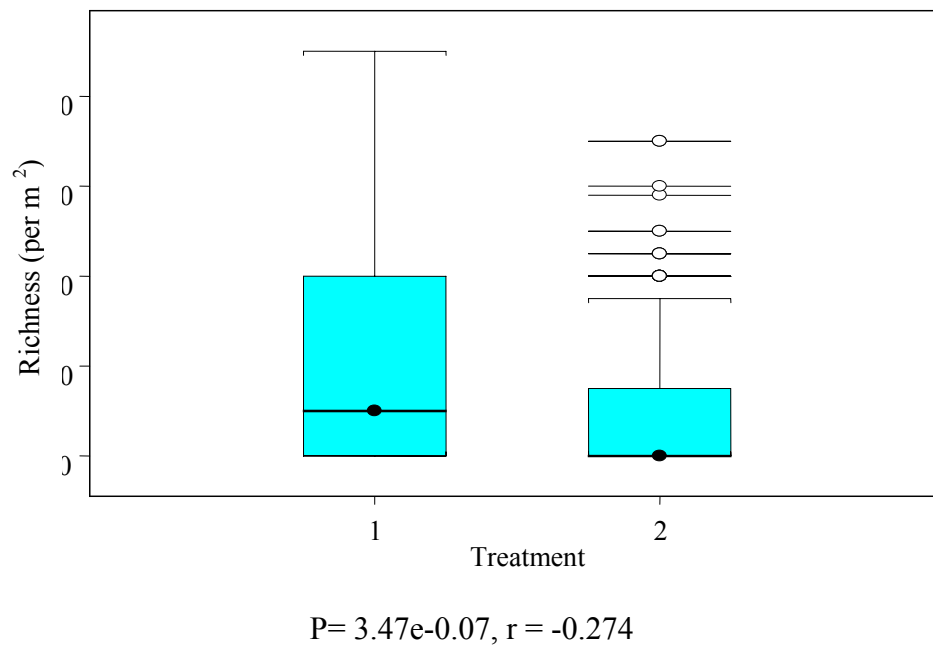


Figure 3.24. Indigenous species richness by treatment, bars with solid circles show medians, bars with empty circles show outliers. Solid boxes represent 50% of data and bars represent the remaining 45% of the data.

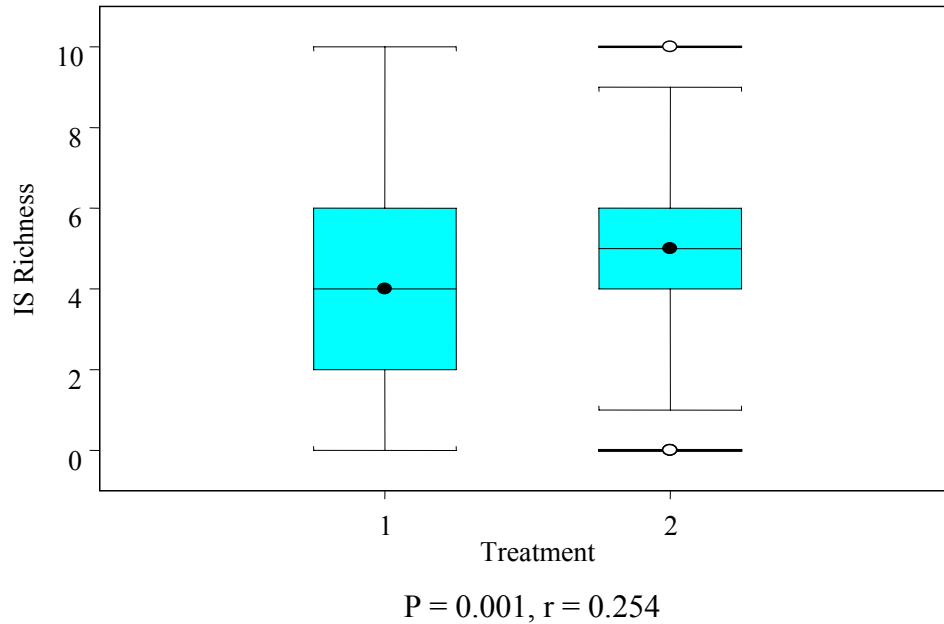


Figure 3.25. Non-indigenous species richness by treatment, bars with solid circles show medians, bars with empty circles show outliers. Solid boxes represent 50% of data and bars represent the remaining 45% of the data.

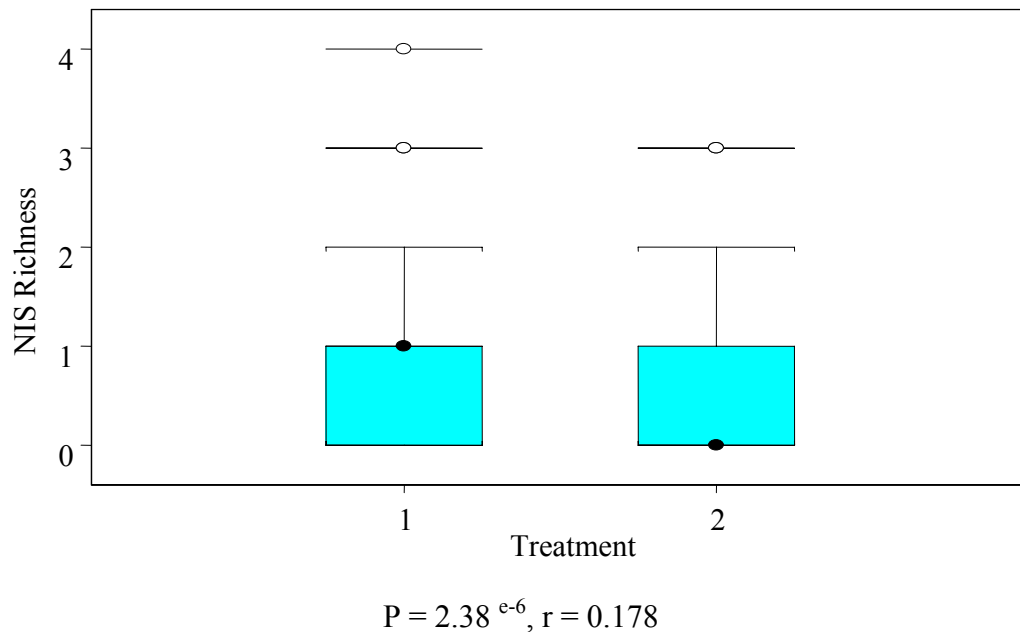
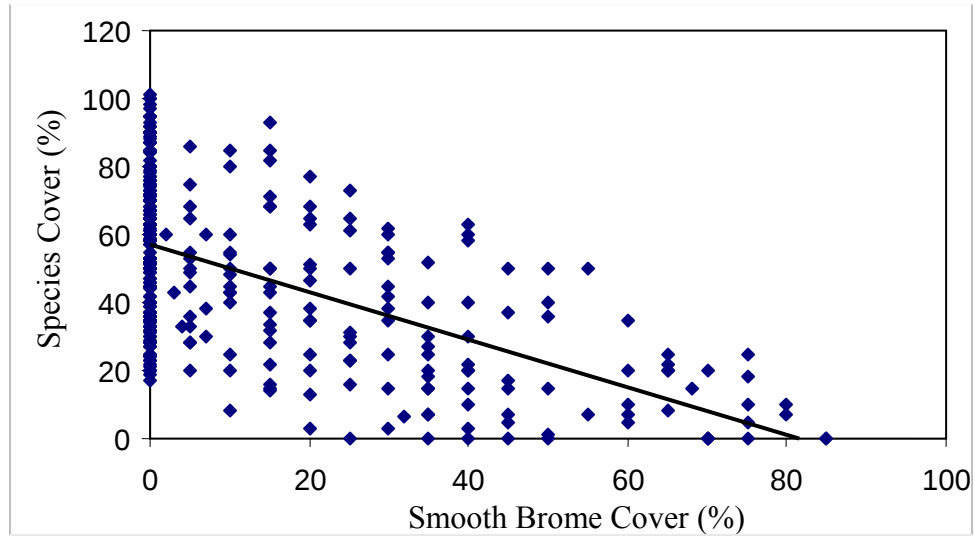
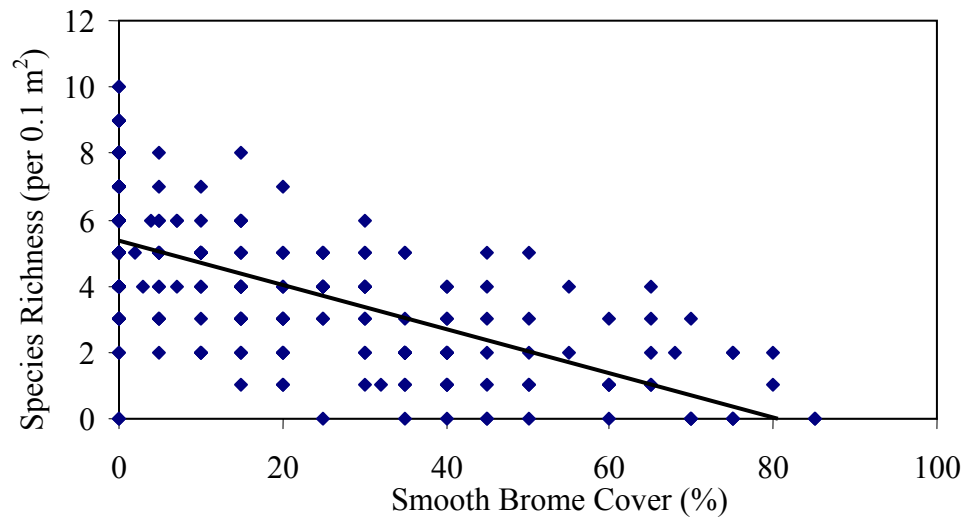


Figure 3.26. Indigenous species cover versus smooth brome cover



Indigenous species richness = $-0.699 (\text{brome cover}) + 56.874$; $P < 0.0001$; $r = -.450$

Figure 3.27. Indigenous species richness versus smooth brome cover



Indigenous species richness = $-0.279 (\text{brome cover}) + 41.901$; $P < 0.0001$; $r = -0.559$

Discussion

Soil Water and Surrogate NIS Field Emergence

Roadside runoff can result in higher plant available water for plants growing near roads (Rejmánek 1989; Harvey 1990; Stohlgren et al. 1998), and White et al. (1997) hypothesized that this may allow for increased NIS invasion in arid environments. During the course of our study, soil water decreased with distance from the road only during the month of June. At the start of the growing season (May) soils were uniformly moist, while in August and September soils were uniformly dry.

No significant relationship was found between surrogate NIS emergence and either distance from the road or variation in soil water. I have two hypotheses as to why these relationships were not significant. First, this study took place during a drought year and results may differ during years of normal precipitation. Second, soil water was measured at 10 cm, while seeds were sown at the soil surface. I also hypothesize that the creation of safe-sites near roads for the emergence of the surrogate NIS may have been negated by competition from smooth brome and by a lack of disturbance from the road.

Seed Rain and Seed Bank Emergence

Roadside NIS patches have been found to provide propagules for NIS colonization into indigenous plant communities, especially after disturbance events (Parendes and Jones 2000). However, Harrison et al. (2002) found that once roadside patches become established, seed dispersal from the individual NIS patches is more

important to the local spread of NIS than longer distance seed movement along roads. Based upon the differences in seed rain and seed bank emergence between the two treatments, it appears that the former is the case for our study area. Smooth brome, Canada thistle and other NIS were established within the indigenous bunchgrass community well beyond roadsides that were obviously impacted by road disturbance and runoff. Canada thistle seed rain was not correlated with distance from the road, but rather with distance from the three Canada thistle patches located along transect 1, however the seed rain number was low. Smooth brome seed rain and seed bank emergence decreased rapidly with distance from the road and roadside brome patches. However, smooth brome seed rain and seed bank emergence were higher at treatment 1 where smooth brome extended well into the study area, than treatment 2 where smooth brome was only present along the roadside.

The different seed dispersal characteristics of these species appear to be reflected in the spatial distribution of the individual patches. Smooth brome was present along the road for the entire length of the study area and its satellite patches were located near the main roadside patch (Figure 3.1). The three Canada thistle patches were oriented along transect 1 perpendicular to the road. Canada thistle patches were more dispersed than the smooth brome patches, probably because of the greater dispersal ability for this species.

The small size and low number of Canada thistle patches and also the low density of these patches presented a problem for both trapping seeds and finding seeds in the seed bank. Also, winter comes early to this area and we were forced to pull the seed traps in

the third week of October. Some seeds were still attached to brome and thistle stems at the time the seed traps were pulled.

Seed Loss

Seed loss varied with distance from the road for smooth brome and Canada thistle, although the correlation coefficients were small. I had originally hypothesized that seed loss would increase away from roads, as seed predators would spend less time foraging near roads because of vehicle traffic and noise. This idea was supported by the work of Van der Zande et al. (1980) who found that birds avoided foraging near roads because of vehicular noise. The gravel road in our study area received little traffic and correlation coefficients may have been higher if we had performed this seed predation experiment along a busier road.

Seed loss did vary by species, a result probably explained by variable seed predation between species. Canada thistle had the highest seed predation, and smooth brome had the lowest seed predation. There was no significant difference in seed predation between radish and wheat. A search on the Yahoo! search engine (www.yahoo.com) showed that thistle seeds (no individual species were listed) are commonly sold as food for songbirds, suggesting that these seeds are known to be palatable. Conversely, Everett et al. (1978) found that deer mice avoided smooth brome seeds.

Other researchers have found that NIS invasion (Levin 2000) and plant community dominance (Wilson and Belcher 1989) were mostly a function of propagule

availability. Reader and Beisner (1991) found that seed predation had the potential to limit seedling emergence by reducing seed supply. Thus, differential seed predation may give a competitive advantage to certain NIS species such as smooth brome, the seeds of which are avoided by granivores relative to other species.

NIS and the Indigenous Plant Community

The original goals of this study were to investigate the relationship between propagule pressure, soil water, NIS surrogate emergence, seed loss and distance from roads. In doing this, I first characterized the plant community, including cover and richness, for both indigenous species and NIS. I did not intend to look at the impacts of NIS on the indigenous plant community at the site. However, trends were found within the data that warranted further investigation.

NIS cover and richness decreased with increasing distance from the road, a finding supported by many other studies (Spellerberg 1998; Weaver et al. 2001; Pauchard and Alaback 2004, Rew et al. in press b). Indigenous species richness and cover were both lower where smooth brome was present than where it was absent. The variation in indigenous species richness and cover was better correlated with the presence or absence of smooth brome than with distance from the road. Indigenous species cover dropped from 61.8% where smooth brome was absent to 26.2% where smooth brome was present; and richness dropped from 5.4 indigenous species per 0.1 m² where smooth brome was absent to 3.1 species per 0.1 m² where smooth brome was present. Because we did not introduce NIS into this plant community, we cannot infer cause and effect, only that

indigenous species cover and richness were negatively correlated with the presence of smooth brome.

Other studies performed in this region have found that indigenous plant cover and richness decreased with increasing NIS cover in bunchgrass plant communities. For example, Kedzie-Webb et al. (2001) found that the presence of spotted knapweed (*Centaurea maculosa*) resulted in reduced indigenous species cover and richness in an Idaho fescue/bluebunch wheatgrass community. Mack (1989) found that a closely related species, downy brome (*Bromus inermis*), had displaced indigenous species and reduced indigenous species diversity in the bunchgrass communities of the Great Basin.

Of the 11 NIS found at the site, only smooth brome was negatively correlated with indigenous plant cover and richness, even when the cover for all other NIS was combined. This finding is interesting, as land managers often take the “shoot first and ask questions later” approach to managing NIS on their lands. Managing NIS is expensive and time consuming. It is possible that some of the NIS other than smooth brome had only recently become established and were still increasing in cover at the site. However, it is also possible that smooth brome is the only NIS at the site that displacing indigenous species at this site. The other NIS may just add to the species diversity at the site without adversely impacting indigenous species richness or cover. If this is the case, then it justifies the differential management of NIS in wildlands by species and also by habitat, although more work is needed to confirm this idea.

Most of the techniques currently used to manage NIS in wildlands were adapted with little change from our efforts to control these species in intensively managed and

comparatively much less complex cropland systems. Thus, NIS management is often undertaken with little understanding of the what actually works to successfully control NIS in natural systems without harming indigenous species, much less the potential ecological impacts of these actions. A consequence is that, to date, there have been very few successes in the control of NIS in natural areas, in spite of the money and time spent on the problem (Hulme 2003). With this study, we have added ever so slightly to our understanding of the ecology of NIS in natural areas. Yet, we have only begun to understand the ecology of pristine natural systems, much less invaded systems. It is stating the obvious to say that more work needs to be done.

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