THE IMPACT OF INVASIVE SWEETCLOVER (*MELILOTUS ALBA*) IN EARLY-SUCCESSIONAL FLOODPLAIN HABITATS OF ALASKA

A

THESIS

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By

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Abstract

Sweetclover, *Melilotus alba*, is an invasive legume that has formed dense and extensive patches along several rivers in Alaska. The objective of my research was to determine if sweetclover can impact native seedling recruitment in floodplain habitats. To determine if sweetclover affects recruitment, I conducted a removal experiment along two rivers in Alaska. When compared to areas where sweetclover was removed, areas with sweetclover had 50% greater mortality of native seedlings. To determine if sweetclover shading was a mechanism through which this impact occurred, I grew eight floodplain plant species under a range of lighting conditions that were representative of shading under sweetclover. Increases in shading stressed each species but did not lead to mortality during the growing season. Competition for several resources, including light, likely led to the increased mortality of seedlings in the removal experiment. To determine if sweetclover is competitively superior to two native legumes, I conducted two additive series competition experiments. Despite using high densities of seedlings, there were few interactions between sweetclover and either native legume. The lack of interactions may indicate that sweetclover and native legumes occupied separate niche space. Together, these results provide a foundation for future research regarding the impacts of invasive plants in Alaska.

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Preface

I dedicate this thesis to my sister, Dacia, whose strength inspires me to live life to the fullest. I thank all my family and friends for volunteering their time to my research and keeping me sane. I thank Mark Winterstein, Gretchen Garcia, Andrea Chin, and Morgan Skidmore for their long-hours of assistance in the field and greenhouse. I thank Jeff Conn, John Fox, and Dana Thomas, who served on my committee, for their comments on my thesis. I especially thank my major advisor, Tricia Wurtz, for providing guidance throughout the course of my research and for her comments on my thesis. Finally, I thank Katie Villano for her constant support and encouragement over the last two years.

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This thesis is in manuscript format and has been divided into four chapters. Chapter 1 is a general introduction regarding the ecological effects of non-native plants and details the potential impacts of non-native sweetclover in floodplain habitats of Alaska. Chapters 2 and 3 have been formatted for submission to *The Journal of Ecology*, an international peer-reviewed journal. Both Chapters 2 and 3 contain specific methods, results, and conclusions drawn from those studies. Chapter 4 synthesizes major points from chapters 2 and 3 and discusses potential questions for future research in Alaska.

Chapter 1: General Introduction

Introduction

Non-native Plants in Alaska

Non-native plant species have invaded natural habitats in Alaska (Wurtz *et al*. 2005; Villano 2007; Conn *et al. in press*) and may be impacting the state's ecosystems. Eclipsed only by habitat destruction, invasive species are the second leading cause of declines in world-wide biodiversity (Wilcove *et al.* 1998). Two major mechanisms through which invasive species impact native habitats and reduce biodiversity are competitive displacement and the alteration of ecosystem processes (Mack *et al.* 2000; Levine et al. 2003). Species can compete for any limited resource, including light, water, soil nutrients, and pollinators (Harper 1977; Parker & Reichard 1998). Alterations of ecosystem processes include shifts in resource dynamics, changes to landscape form, and an increased disturbance regime (Vitousek & Walker 1989; D'antonio & Vitousek 1992; Wiedemann & Pickart 1996). Both competitive displacement and alterations of ecosystem processes can result in reduced species richness, changes in abundances of species, facilitation of other invasive species, alterations to the physical structure of communities, or shifts in native plant phenology (Woods 1993; Pyšek & Pyšek 1995; Woods 1997; Martin 1999; Levine *et al.* 2003). Since invasive plants can affect ecosystems and the structure of plant communities, land managers and researchers are concerned that invasive plant species are impacting natural habitats in Alaska.

A *weed* can be defined as a native or non-native plant that grows in a place where it is unwanted by humans. *Non-native species* originate from foreign habitats and their introduction is usually facilitated through human action. *Invasive plants* are a subset of non-native species that have self-sustained populations and can potentially spread over large areas of natural habitats (Richardson *et al.* 2000). Under this definition, different invasive species can have varying degrees of impacts in ecosystems. For instance, both common dandelion (*Taraxacum officinale)* and sweetclover (*Melilotus alba*) are invasive plants in Alaska (Alaska Natural Heritage Program (ANHP) 2005). However, when comparing each species' potential to impact habitats, *T. officinale* is considered to have a modest impact, while *M. alba* is considered to have the potential to transform ecosystem processes and alter the structure of plant communities (ANHP 2005).

Currently, 283 non-native plant species have been found in Alaska (Carlson & Shephard 2007), many of which are considered marginally invasive and are of little concern (ANHP 2005). Only 13% of Alaska's flora is non-native, which is low compared to other regions of North America (Carlson & Shephard 2007). For instance, 30% of Oregon's flora is composed of non-native species (Carlson & Shephard 2007). The low number of non-native plants in Alaska is likely due to the state's cold winter climate and short growing season, which may act as barriers against the establishment of non-native plant species. Furthermore, the vast majority of the state is sparsely populated and undeveloped, which reduces the potential for humans to spread non-native plant seed into ecosystems.

Yet, in recent years, warmer winters (Chapman & Walsh 1993), longer growing seasons (Myneni *et al*. 1997), and greater propagule pressure through increased human disturbances and commerce (Carlson & Shephard 2007) have likely increased the potential for non-native plant establishment in Alaska. For instance, between 1941 and 2006, the number of non-native plants recorded in Alaska has increased by 46% (Carlson & Shephard 2007). While this trend may be a result of greater awareness and monitoring efforts, the increase in non-native plants in Alaska has caused concern among land managers whose goal is to preserve natural habitats (Alaska Committee for Noxious and Invasive Plant Management 2005 and 2006). To address the concern of land managers, I conducted the first study of the ecological impacts of an invasive plant in floodplain habitats of Alaska.

Focal Species - Sweetclover

Melilotus alba, hereafter referred to as sweetclover, is a biennial legume with white flowers that can produce upwards of 350,000 seeds per plant (Klebesadel 1992; Turkington *et al.* 1978). First-year plants allocate a majority of resources to development of belowground structures, while second-year plants switch to aboveground reproductive growth (Turkington *et al*. 1978). In its second year of growth, sweetclover can reach upwards of 200 cm in height (Turkington *et al.* 1978). Sweetclover can grow in a wide range of climates and is tolerant of extremely cold temperatures (Ouellet 1976; Klebesadel 1992). Sweetclover is considered a ruderal species due to its close association with disturbance, shade-intolerance, rapid growth, short life span, large seed output, and ability to grow in a wide range of soils with low levels of soil moisture and nutrients (Turkington *et al.* 1978; Parker *et al*. 1993).

Sweetclover is native to Eurasia and was introduced to North America in the 17th century (Turkington *et al.* 1978). Sweetclover was likely brought to North America as an agricultural crop. Due to its association with soil *Rhizobia* sp. that fix atmospheric nitrogen, sweetclover is valued as a nitrogen-rich forage crop and soil amender (Turkington *et al.* 1978). In addition, sweetclover is considered a valuable source of pollen for honey production (Turkington *et al.* 1978). Since its introduction, sweetclover has escaped from agricultural settings and is now common along roadsides and waste places in all 50 U.S. states (Alaska Exotic Plant Information Clearinghouse 2005).

Sweetclover is common along roads and is now present along several rivers in Alaska (Wurtz *et al.* 2005). While the specific time of introduction in Alaska is unknown, sweetclover was reported as a component of roadside vegetation in 1929 (Klebesadel 1992). The presence of sweetclover along roadsides may result from its use as a vegetative cover to stabilize road-side soils after construction. It likely spread from roadsides, which often cross and parallel waterways in Alaska, to riparian habitats. Since the seed of sweetclover floats (Turkington *et al.* 1978), it has the potential to spread to new floodplain habitats far removed from human disturbances (Wurtz and Macander 2007). Currently, sweetclover is common along portions of the Stikine, Matanuska, and Nenana Rivers of Alaska (Conn *et al.* in press).

The species' traits and the characteristics of early-successional glacial floodplain habitats work in concert to allow sweetclover to succeed in some riparian habitats. Early-successional habitats along glacial rivers are highly disturbed, sparsely vegetated, and nitrogen deficient (Van Cleve & Viereck 1981; Walker & Chapin 1986; Chapin *et al.*

2006). Certain floodplains in Alaska appear to be ideal habitat for sweetclover because of its preference for disturbed sites and its ability to thrive on nutrient-poor soils (Smith & Gorz 1965; Parker *et al.* 1993). In addition, the ability of sweetclover to produce copious amounts of seed that are readily dispersed by water, likely allows sweetclover to colonize a variety of floodplain habitats.

Potential Impacts of Sweetclover in Alaskan Floodplain Habitats

In 2005, a consortium of land managers developed a ranking system of all the non-native species recorded in Alaska (ANHP 2005). As no data existed regarding ecological impacts of invasive plants in Alaska, this ranking was conducted to identify specific species with the greatest potential to affect ecosystems in the state. The ranking was based on potential ecological impacts, dispersal ability, potential distribution, and feasibility of control. Sweetclover was ranked among the top 10 invasive plant species in Alaska. Sweetclover is considered a serious threat to natural habitats for two main reasons. First, dense patches of sweetclover occur along some rivers in the interior, south-central, and south-east portions of Alaska. Since sweetclover patches were observed overtopping native vegetation, there was concern that sweetclover might compete with and affect the structure of native plant communities. Second, the ability of sweetclover to add nitrogen to habitats may facilitate the establishment of other invasive species and cause changes in to the structure of native plant communities (Tilman 1987; Maron & Conners 1996).

In my research, I focused on competitive interactions between sweetclover and seedlings of native vegetation. My hypothesis was that sweetclover limits recruitment (i.e. colonization and establishment) of native species through competition. Recruitment is a fundamental determinant of the long-term structure of plant communities (Tilman 1997; Clark *et al.* 1998; Hubbell *et al.* 1999; Turnbull *et al.* 2000; Foster & Tilman 2003; Yurkonis *et al.* 2005). My research questions were:

1) Does sweetclover limit recruitment of native species along floodplains in Alaska?

2) Is shading a mechanism through which sweetclover may limit recruitment of native species in early-successional floodplain habitats of Alaska?

3) Can sweetclover competitively displace native legumes that are common in early-successional floodplain habitats of Alaska?

To address question one, I conducted a removal experiment along the Healy and Nenana Rivers of interior Alaska. I determined the survival of native seedlings in plots where sweetclover was removed and plots where sweetclover was not removed. To address question two, I conducted a greenhouse shade experiment. I grew eight common floodplain plant species under a range of lighting conditions, which was representative of light levels under sweetclover, and determined if sweetclover shading impacted the growth and survival of each species. To address question three, I conducted seedling competition experiments between sweetclover and two common floodplain legumes, *Hedysarum alpinum* and *Oxytropis campestris*. I used final height and biomass of native legumes to determine if sweetclover was competitively dominant in mixture. Research regarding questions one and two are described in chapter two, while question three is detailed in chapter three.

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Chapter 2. Invasive sweetclover (*Melilotus alba*) impacts seedling recruitment along floodplains in Alaska[1]

Introduction

The rapid increase in non-native plants found in boreal forests of North America (Rose & Hermanutz 2004; Sumners & Archibold 2007; Carlson & Shephard 2007) has outpaced research regarding their impacts to boreal ecosystems. In the past, a cold climate and small human population were likely strong barriers against non-native plants establishing within boreal ecosystems. Recent warmer winters (Chapman & Walsh 1993), longer growing seasons (Myneni *et al.* 1997), and the potential of greater propagule pressure through increased human disturbances and commerce (Carlson & Shephard 2007) have likely altered these barriers and increased the potential of non-native plant invasion. For instance, between 1941 and 2006, the number of non-native plants recorded in Alaska has increased by 46% (Carlson & Shephard 2007). In select cases, non-native plants have invaded and begun to form extensive populations in natural habitats of Alaska (e.g. Conn *et al. in press*). Since invasive plants can dramatically alter ecosystem processes and the structure of plant communities (Wilcove *et al.* 1998; Mack *et al.* 2000; Levine *et al.* 2003), land managers and researchers are concerned that invasive plant species might be affecting natural habitats in the state. To address this concern, I conducted the first study of the ecological impacts of an invasive plant in floodplain habitats of Alaska.

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In other boreal ecosystems, riparian plant communities are highly vulnerable to invasion (Rose & Hermanutz 2004), and several floodplains in Alaska now support non-native plant species (e.g. seven non-native plant species were found along the Healy River of interior Alaska, Table 1). *Melilotus alba* Medik. (Fabaceae) is an invasive plant that has formed dense and extensive patches along several rivers in Alaska (Conn *et al. in press*). *M. alba*, hereafter referred to as sweetclover, is a biennial legume that grows 90-200 cm in height and can produce up to 350,000 seeds per plant (Turkington *et al.* 1978). Sweetclover is widely distributed along roadsides in Alaska (Wurtz *et al.* 2005), where it may have been sown as a vegetative cover to stabilize road-side soils after construction. Sweetclover growing along roadsides, which often parallel and cross waterways in Alaska, likely provided the propagules sweetclover required to invade riparian habitats. Because the seed of sweetclover floats (Turkington *et al.* 1978), it has the ability to spread to new floodplain habitats far removed from human disturbances (Wurtz & Macander 2007). Sweetclover is now common along extensive portions of the Healy, Stikine, Matanuska, and Nenana Rivers of Alaska (Table 2.1; Conn *et al. in press*). Sweetclover has become one of the most widespread invasive species along roadsides and along several rivers of Alaska (Wurtz *et al.* 2005; Conn *et al. in press*), yet nothing was known about the potential for it to impact riparian plant communities.

The objective of this study was to address the potential impacts of sweetclover on these floodplain plant communities. While invasive species can affect plant communities through numerous mechanisms (Levine *et al.* 2003), I focused on the potential for sweetclover to impact natural habitats through limiting the recruitment of native species.

Recruitment will be defined as the act of a seed colonizing and then establishing in a habitat. Alterations in recruitment can change the structure of plant communities (Clark *et al.* 1998; Hubbell *et al.* 1999; Foster & Tilman 2003) by affecting species richness and abundance (Tilman 1997; Turnbull *et al.* 2000; Yurkonis *et al.* 2005). To become a recruit, a plant must overcome environmental and biotic pressures such as flood events, soil conditions, dispersal limitations and interactions with other plants (Harper 1977). Invasive species present a particularly strong biotic pressure that may limit recruitment directly through competition for resources such as space (Brown & Fridley 2003), light (Huenneke & Thomson 1995; Reinhart *et al*. 2006), and water (Gordon & Rice 2000). Invasive species can also affect recruitment indirectly through mechanisms such as litter accumulation (Walker & Vitousek 1991), reduced soil disturbance (Thomas 2005), and altered soil microbial communities (Stinson *et al.* 2006). Although sweetclover may limit recruitment through numerous mechanisms, competition for light is a major factor that alters community composition throughout floodplain succession in Alaska (Walker & Chapin 1986; Chapin *et al.* 1994; Chapin *et al.* 2006). Therefore, I focused on shading as a mechanism by which sweetclover might impact floodplain habitats of Alaska.

Early-successional habitats along glacial rivers in Alaska are naturally disturbed, sparsely vegetated and open to light (Chapin *et al*. 2006). Native vegetation within disturbed riparian areas are primarily small herbaceous plants and saplings of shrub and tree species (Van Cleve & Viereck 1981). As floodplain succession progresses, light availability is reduced as shrubs and trees mature and eventually overtop and eliminate shade-intolerant species from the community (Van Cleve & Viereck 1981). Currently, along several floodplains in Alaska, dense stands of sweetclover overtop early-successional plant communities. I believe that sweetclover has introduced shade in habitats where native plants are adapted to high light availability. I hypothesized that the novel shade environment created by sweetclover on floodplains is a mechanism by which this invasive could limit the recruitment of native species.

To address my hypothesis, I used a two-part approach: a field study to determine if sweetclover was impacting native recruitment and a greenhouse study to determine the effect of shade on common early-successional floodplain species. To determine if sweetclover impacts native recruitment, I conducted a removal experiment along two Alaskan river floodplains. I addressed three questions: (1) Does sweetclover limit native recruitment? I hypothesized that competition from sweetclover limits the recruitment of native species. (2) Does the age of sweetclover determine the degree of impact it has on native recruitment? Second-year sweetclover is substantially taller than first-year sweetclover (i.e. 90-200 cm vs. 25 cm). Therefore, I predicted that shading would be greater in areas with second-year sweetclover, and if light is a limiting resource, I hypothesized that second-year sweetclover would have a greater impact on recruitment than first-year sweetclover. (3) Does sweetclover limit recruitment of native legumes more than other functional groups? Research in other ecosystems has suggested that invasive species impact functionally similar species more than functionally dissimilar species (Prieur-Richard *et al.* 2000; Fargione *et al.* 2003; Turnbull *et al.* 2005); I hypothesized that sweetclover would have a disproportionate impact on the recruitment of native legumes.

While the removal experiment would be capable of detecting the competitive impacts of sweetclover, it would be unable to isolate any particular mechanism through which sweetclover might limit recruitment. To isolate shading as a potential mechanism underlying the impact of sweetclover, I grew common floodplain species in a greenhouse shade experiment. In the greenhouse, I used lighting conditions that were representative of shading under sweetclover patches in the field. I addressed the following question: (1) Does shade stress or kill common floodplain species? Because most early-successional floodplain species are considered shade-intolerant, I hypothesized that increased shading would stress and kill native plants.

I conducted these two complimentary experiments to offer researchers and land managers insight into the impacts sweetclover can have on native vegetation and to provide a potential mechanism through which sweetclover can alter Alaskan floodplain communities. The questions I addressed here present the first step toward understanding the impacts of an invasive plant in Alaska.

Methods

Study Sites

I conducted the removal experiment along the Healy and Nenana Rivers of interior Alaska. Both rivers are part of the Yukon River drainage. The Healy River study site (63˚51’N, 148˚53’W) is located 30 km north of Denali National Park and Preserve; the Healy River is a tributary of the Nenana River. The Nenana River study site (64˚13’N, 149˚16’W) is located approximately 50 km north and downstream of the Healy

River study site; the Nenana River is a tributary of the Tanana River. Early-successional soils along the Nenana River have low soil nitrogen (1 ppm nitrogen, J. Conn *unpubl. data*) and are sandy with a neutral pH (90.4% sand, 8.2% silt, 1.4% clay and a pH of 7.4, T. Wurtz *unpubl. data*). The Healy and Nenana Rivers freeze during October and remain frozen until late April or early May. Vegetation emerges along each river during late May, while senescence occurs during mid September (*pers. obs*.).

Early-successional plant communities were surveyed along the Healy River study site during 2006 (Table 2.1). I created three floodplain transects that started at the Healy River and terminated 15 m within closed forest canopies. Floodplain transects were 160 to 290 m in length. Each transect was ≥ 500 m apart and positioned perpendicular to the river. Every 5 m along each floodplain transect, I placed an 8 m x 1 m belt transect. Each belt transect was perpendicular to its associated floodplain transect. I visually estimated the percent cover of all species within each belt transect. I used the methods of J. Conn (*unpubl. data*) who conducted a similar survey at my study site along the Nenana River in 2005. Subsequently, data from the Healy and Nenana River floodplain study sites were combined. The 15 species with the greatest combined cover within my study sites were (starting with the most abundant species): *Populus balsamifera* L., sweetclover, *Hedysarum alpinum* L., *Elaeagnus commutata* Bernh., *Alnus incana* spp. *tenuifolia* Nutt., *Oxytropis campestris* L., *Salix alaxensis* Andersson, *Chamerion latifolium* L., *Hedysarum boreale* spp. *mackenzii* Richardson, *Shephardia canadensis* L., *Picea glauca* Moench, *Salix niphoclada* Rydb., *Elymus trachycaulus* Link, *Festuca rubra* L., and *Rosa acicularis* Lindl. Currently, sweetclover is the most abundant species in early-successional habitats along the Healy River (Table 2.1) and third most abundant along the Nenana River (J. Conn *unpubl. data*).

Sweetclover Removal Experiment

To determine whether sweetclover was impacting native recruitment, I conducted a removal experiment along both the Healy and Nenana Rivers during 2006 and 2007. For each year and site combination, I selected twelve sweetclover patches that were ≥ 5 m x 5 m in area. Each patch had 50-90% sweetclover cover and was at least 50 m apart from any other selected sweetclover patch. During June 2006, I placed a block of three 2 m x 1 m plots within each sweetclover patch and randomly assigned one of four treatments:

(1) all vegetation removed (AVR)
(2) all sweetclover removed (ASR)
(3) all first-year sweetclover removed (1YSR)
(4) all second-year sweetclover removed (2YSR).

In each block, one plot had all vegetation removed (AVR). This treatment was created to determine native recruitment in the absence of plant competition. In each block, one plot had all first- and second-year sweetclover removed (ASR), leaving only native vegetation. This treatment was created to determine the competitive effect of native vegetation on native recruitment. In each block, both native vegetation and sweetclover were present in one plot (1YSR or 2YSR). However, to investigate if taller second-year sweetclover influenced native recruitment differently than first-year sweetclover, I placed half these plots in uniform patches of second-year sweetclover (1YSR) and the other half in uniform patches of first-year sweetclover (2YSR). I removed any sweetclover individuals of the non-targeted age class that were present in these plots. Both the 1YSR and 2YSR treatments were created to determine the competitive effect of sweetclover on native recruitment.

Each treatment was created by clipping either sweetclover, native vegetation, or both at the floodplain surface, taking care to minimize soil disturbance. The initial removal of vegetation did not result in complete mortality of targeted plants; therefore, I re-implemented treatments in July. To assure each plot had the same number of native seedlings at the beginning of the experiment, I removed all first-year non-sweetclover seedlings from each plot. To control for sweetclover potentially influencing recruitment from outside each plot, I created a 0.5 m buffer along the perimeter of each plot by removing all sweetclover. During June 2007, I replicated this design but added one additional treatment to each block, which was a 2 m x 1 m plot where I removed no vegetation (control).

To track and count the number of native seedlings in each plot, I marked every emerging native seedling during June, July, and August. In September, I determined whether marked seedlings survived the growing season. A seedling that survived the growing season was defined as a recruit. Data used in analyses were the percentage of native seedlings that survived and the number of recruits at the end of the growing season. To address whether sweetclover had a disproportionate impact on the recruitment of native legumes, in September 2007, I identified each recruit to genus or species and categorized them by the following functional groupings: trees and shrubs, graminoids, forbs, and legumes. To determine potential differences in the quantity of light available to native seedlings, in late August 2007, I measured photosynthetically active radiation (PAR) in each plot. Information on the quantity of PAR could offer insights into potential differences in recruitment among treatments. In the summer of 2007, eight blocks were washed away in a flood along the Healy River, and data from those blocks were removed from all analyses.

Sweetclover Shade Determination

As no information previously existed regarding the ability of sweetclover to shade floodplain surfaces, I measured PAR to determine the relationship between the amount of shade and percent cover of sweetclover. In early and late July 2006, I determined the amount of shade beneath 36 patches of unmanipulated sweetclover. I defined shade as the amount of PAR obstructed by the canopy of sweetclover. To determine sweetclover shading, I visually estimated sweetclover cover within a 1 m x 1 m quadrat and then used a Li-190 quantum sensor and Li-250a light meter to measure the quantity of PAR (Li-Cor, NE, Nebraska). I placed the quantum sensor parallel to the ground at the center of the quadrat and recorded a 15-second-averaged PAR value (*u*mol m^{-2} s^{-1}) at the floodplain surface and above the sweetclover canopy. I determined sweetclover shade values with the following equation: [1- (PAR below sweetclover/PAR above sweetclover)]*100.

Greenhouse Shade Experiment

To determine if shading can stress or kill early-successional floodplain plant species, I conducted a shade experiment in a University of Alaska Fairbanks Institute of Arctic Biology greenhouse during 2006 and 2007. Seven of the eight species I used were among the 15 most abundant species at my study sites. During the growing season of 2006, I grew native legumes (*H. alpinum* and *H. mackenzii*), a native forb (*C. latifolium*), and native shrubs (*S. alaxensis* and *A. tenuifolia*). During the growing season of 2007, I grew native legumes (*H. alpinum* and *O. campestris*), a native prostrate shrub (*Dryas drummondii* Richardson), and a native tree (*P. balsamifera*). I grew *H. alpinum* both years to determine if shade had a consistent effect on species across years.

In the greenhouse, I used five shade treatments to simulate light conditions that occur under different sweetclover densities in the field. I created the five shade treatments using 1 m x 0.5 m x 0.75 m structures covered in different densities of green shade-cloth: high shade (84.3 ± 0.3 percent obstruction of ambient PAR), medium-high shade (75.3 ± 0.3 percent obstruction of ambient PAR), medium shade (62.0 ± 0.3 percent obstruction of ambient PAR), medium-low shade (40.3 ± 0.3 percent obstruction of ambient PAR), and a control structure with no shade-cloth. I determined shade treatment values with the following equation: [1- (PAR below shade structure/PAR above shade structure)]*100. Each shade treatment was significantly different from one another ($F_{4,45} = 15{,}969$, $P < 0.001$, Tukey Test $P < 0.0001$ for each pairwise comparison). It is important to note that the quantity of ambient PAR is reduced when light enters a greenhouse. While I likely captured a range of lighting conditions under sweetclover, the shading treatments are not directly comparable to light values under sweetclover in the field.

At the beginning of the growing season (i.e. late May or June), I placed seed of each species in the top of a container (3 cm diameter x 17.5 cm deep, shaped like a cone) filled with Nenana River sediment. I presumed that this substrate had *Frankia* and *Rhizobia* sp., which are required to inoculate the roots of n-fixing *A. tenuifolia* and native legumes. To enable germination of legumes, I scarified legume seed with sand paper. After germination, all seedlings were allowed to grow unshaded for 2 weeks before the shading treatment were applied. Each shade treatment had three structures that I randomly placed in the greenhouse. I placed five seedlings of each species under each structure. All seedlings received ambient light and were watered when the soil in the containers appeared dry. I applied water and fertilizer through the use of an overhead boom to ensure that similar water volume was delivered to each seedling. Every third watering, I applied fertilizer dissolved at a ratio of 1:13:50 ppm of N:P:K, which is representative of early-successional floodplains soils (J. Conn *unpubl. data*).

I harvested all surviving seedlings after three months of growth (i.e. late August or September) to reflect the short growing season along the Healy and Nenana River study sites. While harvesting plants, I observed that the roots of *A. tenuifolia* and each native legume had nodules. I harvested shoots and roots of all seedlings and dried them at 70^{o} C for two weeks. Measured parameters were shoot height, biomass (root, shoot, and total), root to shoot biomass ratio, and growing season survival.

To determine the relationship between shade during the growing season and over-wintering mortality, I grew 15 additional seedlings of *A. tenuifolia*, *S. alaxensis*, *C. latifolium*, and *H. alpinum* under each shade treatment during 2006. In late September, I placed these seedlings outdoors in a planter box that was filled with Nenana River sediment. However, when a vehicle struck this planter box, the sample size of some species and treatments was reduced. After snow had melted in May of 2007, I determined survival of uncovered seedlings that were over-wintered outside.

Statistical Analyses

All statistical analyses were conducted with SAS 9.1 (SAS institute, North Carolina, USA). To address the first and second questions of the sweetclover removal experiment, I conducted analyses to determine differences in recruitment among treatments. I used four-factor analysis of variance (ANOVA) models (Proc Glimmex), where factors were block, year, site, and treatment. To meet model assumptions of normality and homogeneity of variance, data regarding the percentage of native seedlings that survived the growing season were logit transformed and fit to a binomial distribution. Similarly, data regarding the number of recruits that survived the growing season were natural log transformed and fit to a negative binomial distribution. Variability among plots within blocks was used as error. With similar distributions and transformations, I used two-factor ANOVA (i.e. block and treatment) models to determine if recruitment differed among the control, 1YSR, and 2YSR treatments. This was done to determine if a mixed age class of sweetclover affected recruitment differently than a uniform age class of sweetclover. Finally, I used a one-way ANOVA (Proc GLM) to determine if treatments caused differences in the quantity of available PAR. For all analyses, when significant differences existed among factors ($\alpha = 0.05$), I used pair-wise Tukey tests to determine differences among factor levels. To address the third question from the sweetclover removal experiment, I used Kruskal-Wallis tests to determine if treatment caused differences ($\alpha = 0.05$) in the abundance of seedlings within functional groups. If significant differences were found, I used a two-sided all-treatments multiple comparisons test to determine differences among treatment levels (Hollander & Wolfe 1999).

I used multiple linear regression to determine the relationship between date of sampling, sweetclover cover, and sweetclover shading along the Healy River floodplain. I conducted a general linear test to determine if date, which was included as an indicator variable, could be dropped from the regression model by comparing the full model (i.e. with date) to the reduced model (i.e. without date) (Kutner *et al.* 2005). If sweetclover shading was similar for both dates, then data was combined.

To address if shade stressed native floodplain species, I conducted analyses to determine the relationship between shading and the growth of native seedlings. I used one-way ANOVA models (Proc GLM) to determine if shade treatment caused differences in the growth parameters of tested species. When necessary, I log- or rank-transformed data to meet model assumptions of normality and homogeneity of variance. When significant differences existed ($\alpha = 0.05$), I used pair-wise Tukey tests to determine differences among levels of shade treatments. To determine if shade killed native floodplain species, I conducted analyses to examine the relationship between shading and survival of native seedlings. I used Fisher's Exact Test to determine if differences existed ($\alpha = 0.05$) among shade treatments and the proportion of seedlings that survived during the growing season and throughout the winter. When significant differences were found, I used pairwise z-tests to determine differences among levels of shade treatments.

Results

Sweetclover Removal Experiment

Native seedling recruitment did not differ between plots with mixed and uniform ages of sweetclover. When comparing the control, 1YSR, and 2YSR treatments, the percentage of native seedlings that survived ($F_{2,14} = 2.41$, $P = 0.13$) and number of native recruits ($F_{2,14} = 0.56$, $P = 0.56$) did not differ significantly. These findings suggest that plots with first- and second-year sweetclover were representative of the control in the sweetclover removal experiment. Since the control data was redundant and only exist for 2007, I dropped control from all analyses.

Native seedling recruitment was significantly limited in plots with sweetclover. Across study years and floodplain study sites, treatment had significant effects on the percent survival of native seedlings and number of native recruits (Table 2.2). When compared to the AVR and ASR treatments, approximately half as many native seedlings survived in the 1YSR and 2YSR treatments (Fig. 2.1a). As a result, when compared to the ASR treatment, there were half as many recruits in the 1YSR and 2YSR treatments (Fig. 2.1b). These findings suggest competition from sweetclover significantly reduced the survival of native seedlings and limited the number of native recruits. Percent survival of native seedlings and number of native recruits in the AVR and ASR treatments did not differ (Fig. 2.1a and 2.1b), suggesting native vegetation did not competitively affect native seedling recruitment. Similarly, percent survival of native seedlings and number of native recruits in the 1YSR and 2YSR treatments did not differ (Fig. 2.1a and 2.1b), suggesting age class did not determine the degree of impact sweetclover had on recruitment.

Removal treatments caused differences in the quantity of PAR available to native seedlings in August ($F_{3,44} = 35.11$, $P < 0.0001$). The quantity of PAR available in the 1YSR and 2YSR treatments was significantly less than the AVR and ASR treatments ($P < 0.0001$). Thus, sweetclover significantly limited the light available to native seedlings. The quantity of PAR in the AVR and ASR treatments did not differ (means of 1053 vs. 1000 umol m^{-2} s^{-1}, $P = 0.78$), suggesting native vegetation did not limit light to native seedlings. The quantity of PAR in the 1YSR and 2YSR treatments did not differ (means of 571 vs. 474 umol m^{-2} s^{-1}, $P = 0.63$), suggesting that the light available to native seedlings did not differ in plots with first- and second-year sweetclover.

While decreasing overall recruitment of native plants, sweetclover did not affect specific functional groups. The presence or absence of sweetclover did not affect seedling recruitment for trees and shrubs ($X^2 = 1.88$, df = 3, $P = 0.60$), graminoids ($X^2 = 5.61$, df = 3, $P = 0.13$), forbs ($X^2 = 1.07$, df = 3, $P = 0.78$), or legumes ($X^2 = 0.78$, df = 3, $P = 0.85$). While analyses did not detect differences in functional group recruitment among treatments, there was a consistent trend that the 1YSR and 2YSR treatments had fewer recruits in each functional group than the ASR treatment (Table 2.3). When looking at recruitment at the species level, a total of 16 species of recruiting seedlings were found across all ASR treatment plots, 14 species were found across all AVR treatment plots, and only 12 species were found across all 1YSR and 2YSR treatment plots (Table 2.4). In the ASR treatment, recruitment of *Festuca rubra* increased more than any other native species (six-fold increase compared to the 1YSR and 2YSR treatments, Table 2.4).

Sweetclover Shade in Field Sites

Sweetclover shade data collected on both dates in July did not differ ($F_{1,69} = 2.35$, $P = 0.13$). Sweetclover cover had a positive relationship with sweetclover shading ($R^2 = 0.84$, $P < 0.001$). Depending on its cover, sweetclover can shade 1 to 94% of available PAR along the Healy River floodplain (Fig. 2.2). PAR values collected above the sweetclover canopy ranged between 474.7 to 1341.3 *u*mol m^{-2} s^{-1}, while values below the canopy ranged between 53.3 to 742.5 *u*mol m^{-2} s^{-1}.

Greenhouse Shading Experiment

Shade treatments in the greenhouse experiment obstructed 9 to 85% of ambient PAR, which was representative of sweetclover shading along the Healy River floodplain (Fig. 2.2). *H. alpinum* had similar growth and survival responses during both years of the shade experiment. These findings suggest that greenhouse conditions were similar each year and, subsequently, that data for all species are comparable between years.

Increased shading had an inconsistent effect on height but reduced biomass of each species. With the exception of *H. alpinum*, there were differences among shade treatments and final seedling height of each species (Table 2.5). Increased shading decreased the mean height of *H. mackenzii*, increased the mean heights of *C. latifolium* and *D. drummondii*, and minimally altered the heights of *O. campestris*, *S. alaxensis*, *A. tenuifolia* and *P. balsamifera* (Fig. 2.3). Some species appeared to have a higher tolerance of shading. Both *A. tenuifolia* and *P. balsamifera* had a robust appearance when grown under the medium-high and high shade treatments, while each other species looked etiolated. Etiolation was likely the result of limited biomass production and elongated seedling internodes and petioles. Increased shading led to lower biomass of each species (Table 2.5, Fig. 2.4). For instance, *H. mackenzii* grown under high shading had 89% less biomass than when it was grown under the control. With the exception of *A. tenuifolia*, differences existed among shade level and root-to-shoot ratio (Table 2.5). For affected species, increased shading led to biomass allocation that was skewed towards shoot production (Fig. 2.4).

The level of shading that caused physiological stress differed among native species. Both *A. tenuifolia* and *P. balsamifera* had no differences in biomass between the control and medium-high shade treatments (Fig. 2.5), suggesting both species were tolerant of moderate to high shading. In contrast, when compared to the control, each other test species had significantly less biomass when grown under the medium-high shade treatment (Fig. 2.5); the reduction in total biomass exceeded 60% for *H. alpinum*, *H. mackenzii*, *S. alaxensis*, and *O. campestris*. These findings suggest both *A. tenuifolia* and *P. balsamifera* had a higher tolerance to shade than any other test species.

Shade had minimal effects on survival of species during the growing season but decreased survival of species that were over-wintered. For all species excluding *H. mackenzii*, there was no relationship between shade level and seedling survival during the growing season (Fisher's Exact Test, $P > 0.15$). For *H. mackenzii*, shade treatment affected survival during the growing season (Fisher's Exact Test, $P = 0.0009$). However, when comparing all shade treatments, only control seedlings died (33% mortality). The majority of *H. mackenzii* seedlings in the control treatment survived and achieved optimum biomass and height (Fig. 2.3 and 2.4), suggesting mortality in the treatment was due to water stress in individual containers. When seedlings were over-wintered, increased shading led to higher mortality of *S. alaxensis* and *A. tenuifolia* (Fig. 2.6). No relationship existed between shade treatments and over-wintering survival of *H. alpinum* or *C. latifolium* (Fig. 2.6). Yet *C. latifolium* seedlings only survived when grown under low shade levels, suggesting the over-wintering survival of *C. latifolium* may also be affected by high shading (0 of 12 combined survivors grown under medium-high and high shade treatments).

Discussion

Sweetclover Impacts on Native Plant Recruitment

This study demonstrates that sweetclover limits recruitment of native species within Alaskan floodplain habitats. At the beginning of the removal experiment, each plot was devoid of native seedlings. Throughout the growing season, the seed bank or seed rain supplied each plot with native colonizers. Presumably, differences in recruitment between plots with and without sweetclover were the result of interspecific competition between sweetclover and native seedlings. In the end, competition between sweetclover and native vegetation led to there being half as many native recruits in plots with sweetclover compared to plots where sweetclover was removed.

The age of the sweetclover remaining in the plots did not affect the degree of impact it had on native recruitment. There were no differences in recruitment between plots with first-year sweetclover and plots with second-year sweetclover. I had originally assumed areas with second-year sweetclover would experience the greatest shading and subsequently have the lowest recruitment. However, nearing the end of the growing season in August, the quantity of PAR did not differ between plots dominated by either age class of sweetclover. Regardless of age, sweetclover substantially reduced both the quantity of PAR and the number of native seedlings that survived.

While other studies have shown stronger competitive interactions among species that share functional groupings (Prieur-Richard *et al.* 2000; Fargione *et al.* 2003; Turnbull *et al.* 2005), in my experiment sweetclover did not disproportionately affect legumes. In fact, sweetclover did not selectively affect the number of recruits for any functional group. Though no significant selective reduction in recruits occurred, there was a trend that plots with sweetclover had fewer recruits within each functional group and had 25% less species than plots that solely had native vegetation. The aggregate reduction of recruitment within each functional group resulted in the overall reduction of recruits in plots with sweetclover. My results suggest that the traditional functional groupings I used may have been insufficient to describe the actual functional responses of floodplain seedlings. Sweetclover may impact species with a specific suite of traits that the functional groupings failed to isolate. For example, *F. rubra* clearly had reduced recruitment in the presence of sweetclover and may share traits with the invasive that caused strong competitive interactions. Perhaps results would indicate stronger interactions if I grouped species by other functional groupings, such as disturbance specialists or slow-growing perennials. Further, given the setting of my study sites, the methods used in the removal experiment might be inadequate to address the impacts sweetclover has on specific functional groups or species.

A lack of propagules may partially explain why I was unable to detect differences in the responses of specific functional groups to sweetclover. Both of the sites used in this study are highly disturbed and have sparse and patchy native vegetation. As a result, there were a limited number of recruits in each functional group across all experimental plots. For instance, the number of legume recruits that survived a growing season was 1.1 seedlings in plots with second-year sweetclover but only 2.8 seedlings in plots where sweetclover was removed. It is possible that the results that indicated sweetclover limits recruitment through competition are confounded with a potential lack of native propagules. Limitation of seed was an important factor in determining community composition in other ecosystems (Jackson 1985; Tilman 1997; Seabloom *et al.* 2003; Siemann & Rogers 2006) and might also be important along floodplain plant communities in Alaska. In a competition experiment I conducted, sweetclover seedlings grown at high densities did not competitively suppress seedlings of either *H. alpinum* or *O. campestris* (Chapter 3). This suggests some species in my removal experiment were not competitively displaced by sweetclover but were seed limited due to the sparse and patchy nature of these floodplain plant communities. In the future, the addition of native seed via seed addition experiments (Turnbull et al. 2000) might help determine the impact sweetclover has to specific functional groups or species.

Shading as a Mechanism Underlying Sweetclover Impacts

Sweetclover has altered the physical structure of floodplain habitats by shading areas that were previously open to light. Common Alaskan species adapted to early-successional habitats were each shown to be shade-intolerant (i.e. increased shading led to etiolation, decreased biomass, skewed shoot biomass allocation, and/or increased over-wintering mortality). Clearly, shading by sweetclover has the potential to stress and, when seedlings were over-wintered, kill the recruits of early-successional floodplain plants. However, I found no relationship between shading and growing season mortality in the greenhouse. Therefore, competition for light alone does not appear to explain observations from the removal experiment.

Though I isolated light as a potential mechanism through which sweetclover could impact plant communities, sweetclover likely limited native recruitment through competition for several additional resources including space, water, and soil nutrients. Sweetclover can produce 350,000 seeds per plant (Turkington *et al.* 1978). Such copious seed production may saturate available sites for establishment, decreasing the number of native germinates that survived during the growing season (sensu Brown & Fridley 2003). Furthermore, the rapid growth of sweetclover may reduce soil moisture and nutrients below a threshold that can support native seedlings. For instance, a study in Rocky Mountain National Park indicated that areas with a similar invasive species (*Melilotus officinalis*) had less soil moisture, phosphorous, and nitrogen than areas without *M. officinalis* (Wolf *et al.* 2003).

Although sweetclover competition was shown to affect native seedlings, invasive plants are also known to facilitate recruitment (Tecco *et al.* 2006). Sweetclover could both suppress and facilitate native seedling recruitment. For instance, sweetclover shading can stress native plant species during its two-year life cycle and, after mortality, may add nitrogen to soils that could benefit seedling recruitment in the future (sensu del Moral & Bliss 1993; Callaway & Walker 1997). Sweetclover, adding nitrogen in floodplain habitats, may also facilitate the invasion of other non-native plant species (sensu Maron & Conners 1996). J. Conn *et al.* (*in review*) found that the non-native plants *Crepis tectorum* and *Taraxacum officinale* were positively correlated with sweetclover in riparian habitats of Alaska, suggesting sweetclover may be facilitating the invasion of select non-native species. The differences in shade tolerance among common floodplain species suggest sweetclover competition will affect some species more then others.

When results from the greenhouse shading experiment are put in context of floodplain succession in interior Alaska, the findings suggest sweetclover will only impact early-successional plant communities. The majority of common floodplain species I tested were not tolerant of moderate levels of shading and are likely floodplain pioneer species (i.e. *H. alpinum*, *H. mackenzii*, *C. latifolium*, *S. alaxensis*, *O. campestris*, and *D. drummondii*). Floodplain pioneers are typically replaced from the community as succession progresses and light becomes a limiting factor. Of the species I consider to be floodplain pioneers, only *S. alaxensis* is considered a dominant species and it only dominates the earliest stages of succession (Van Cleve & Viereck 1981). Compared to pioneer species, *A. tenuifolia* and *P. balsamifera* had a higher tolerance to shading. Both species eventually replace *S. alaxensis* and dominant later stages of floodplain succession (Van Cleve & Viereck 1981). If shading by sweetclover is a major factor limiting recruitment, then I believe sweetclover will have the largest impacts on pioneer species that occur in the earliest stages of floodplain succession.

While both of my studies were short-term experiments, results obtained indicate sweetclover may have long-term impacts to floodplain habitats. Sweetclover is among the three most abundant species in both of my study sites and, subsequently, has affected the composition of plant communities along the Healy and Nenana Rivers. However, as no data exist for my sites regarding conditions prior to invasion, it is difficult to determine if sweetclover has already impacted biodiversity along either river's floodplains. Regardless, sweetclover has altered the physical structure of early-successional habitats through shading and is currently limiting the recruitment of native plant species. Since recruitment limitation was an important factor that structured plant communities in other ecosystems (Clark *et al.* 1998; Hubbell *et al.* 1999; Foster & Tilman 2003), I believe sweetclover will have long-term impacts within floodplain habitats of Alaska. However, the impacts of sweetclover will likely be focused in early-successional floodplain habitats.

Conclusions

I found that sweetclover impacted recruitment within floodplain habitats of Alaska. Often researchers fail to determine the underlying mechanisms associated with an invasive species altering the structure of an invaded community (Parker & Reichard 1998; Levine *et al*. 2003). Knowledge regarding mechanisms that change communities is vital if the goal of a land manager is to restore native species to systems dominated by invasive plant species (Levine *et al.* 2003). I demonstrated that shading is a mechanism through which sweetclover can stress seedlings of early-successional floodplain species. However, recruitment limitation was likely caused by competition for several limited resources. My study represents a first step toward understanding the complicated interactions among sweetclover and floodplain vegetation of Alaska.

Results gained from these two complimentary experiments can be used by land managers to enhance public awareness and direct policy towards protecting the natural habitats of Alaska. I hope these results will be used to generate questions for future research. For instance, are native species seed limited, competitively suppressed by sweetclover, or both? If a plant is a superior competitor but seed limited, broadcasting that species' seed within floodplain habitats might be an approach to control sweetclover. In the end, more research is required to understand the short and long-term impacts sweetclover has within Alaska’s floodplain habitats and to explore effective restoration strategies.

Table 2.1. The 20 most abundant plant species along the Healy River. The cover of each species was visually estimated in three floodplain transects. Species are ranked by mean percent cover. Standard errors are in parentheses.

Species	Percent Cover
Melilotus alba	7.60 (1.1)
Populus balsamifera	7.51 (1.0)
Alnus sinuata	3.93 (0.9)
Salix alaxensis	1.26 (0.2)
Oxytropis campestris	1.20 (0.2)
Chamerion latifolium	1.08 (0.2)
Hedysarum boreal **spp.** ***mackenzii***	0.95 (0.2)
Shephardia canadensis	0.84 (0.3)
Salix niphoclada	0.63 (0.3)
Elaeagnus commutata	0.59 (0.3)
Hedysarum alpinum	0.58 (0.1)
Picea glauca	0.51 (0.3)
Rosa acicularis	0.33 (0.2)
Chamerion angustifolium	0.28 (0.1)
Elymus trichocarpa	0.26 (0.1)
Achillea millefolium	0.20 (0.04)
Salix setchelliana†	0.18 (0.1)
Calamagrostis canadensis	0.15 (0.04)
Potentilla fruiticosa	0.11 (0.1)
Astragalus alpinus	0.10 (0.04)

Species in bold were used in a greenhouse shading experiment.

† *S. setchelliana* is endemic to Alaska.

+ Among the 20 most abundant plants, *M. alba* is the only non-native species. Other non-native species surveyed were *Bromus inermus*, *Elymus sibiricus*, *Hordeum jubatum*, *Taraxicum officinalis*, *Crepis tectorum*, and *Melilotus officinalis*.

Table 2.2. Results regarding the recruitment of native seedlings in a removal experiment. Data was collected along the Healy and Nenana Rivers during 2006 and 2007.

Source	DF	F	P	Source	DF	F	P
percent survival				number of recruits			
Block(Year*Site)	36	1.38	0.13	Block(Year*Site)	36	5.95	<**0.0001**
Year	1	43.70	< **0.0001**	Year	1	86.28	< **0.0001**
Site	1	5.87	**0.02**	Site	1	31.18	< **0.0001**
Year*Site	1	7.66	**0.007**	Year*Site	1	5.75	**0.02**
Treatment	3	7.00	**0.004**	Treatment	3	5.00	**0.003**
Year*Treatment	3	0.00	0.99	Year*Treatment	3	1.77	0.16
Site*Treatment	3	0.47	0.70	Site*Treatment	3	0.14	0.93
Year*Site*Treatment	3	1.64	0.19	Year*Site*Treatment	3	2.06	0.11
Error	64			Error	64		

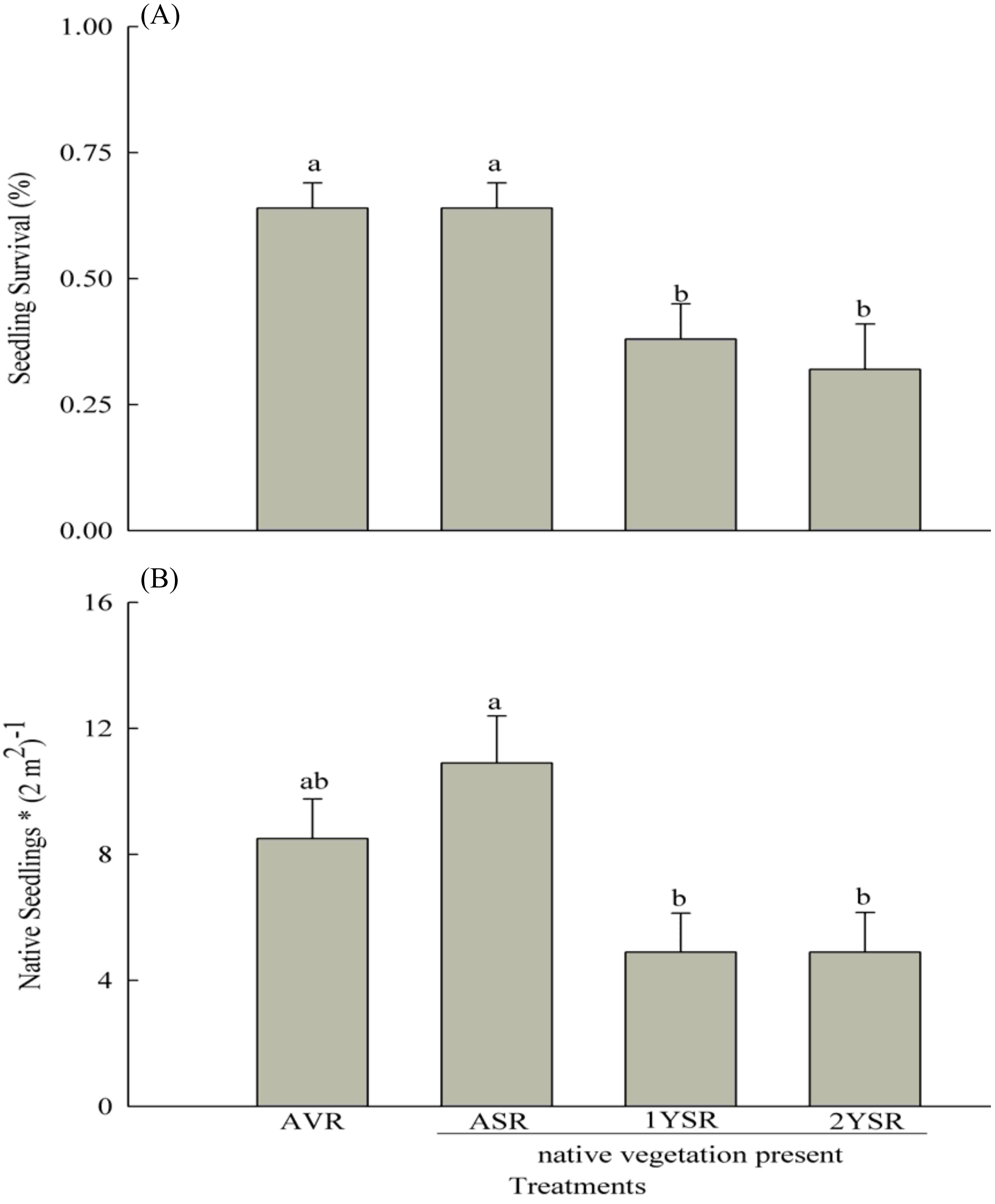

Fig. 2.1. (A) The percentage of native seedlings and (B) number of native recruits that survived in the removal experiment. Data are least-square means and bars indicate standard errors. Different letters indicate treatment means differed significantly ($p < 0.05$).

Table 2.3. Mean native recruits grouped by functional group. Data was collected along the Healy and Nenana Rivers during 2007. Standard errors are in parentheses.

		Functional Groups			
Treatment	n	trees and shrubs	graminoids	forbs	legumes
AVR	16	2.6 (2.6)	2.5 (1.1)	15.6 (7.5)	1.6 (1.0)
ASR	16	6.3 (6.1)	16.1 (6.9)	10.3 (4.3)	2.8 (2.0)
1YSR	9	0.3 (0.2)	5.6 (2.2)	10.2 (3.7)	1.1 (0.7)
2YSR	7	0.7 (0.7)	11.4 (5.2)	4.7 (2.3)	2.4 (2.3)

* No observed statistical differences.

Table 2.4. Mean native recruits grouped by genus and/or species. Data was collected along the Healy and Nenana Rivers during 2007. Standard errors are in parentheses.

Functional Group	Species	Treatments			
		AVR (n=16)	ASR (n=16)	1YSR (n=9)	2YSR (n=7)
Tree/Shrub	*Populus balsamifera*	0.1 (0.1)	0.6 (0.5)	0.1 (0.1)	0.3 (0.3)
	Alnus sinuata	0.1 (0.1)			
	Salix sp.	2.4 (2.4)	5.7 (5.6)	0.2 (0.2)	0.4 (0.4)
Graminoid	*Hordeum jubatum*		0.2 (0.2)		
	Elymus sibiricus		0.1 (0.1)	0.1 (0.1)	
	Elymus trachycaulus	1.7 (0.7)	2.6 (1.8)	3.6 (1.7)	9.4 (5.4)
	Festuca rubra	0.8 (0.4)	13.2 (6.6)	1.9 (1.2)	2.0 (0.7)
Forb	*Crepis elegans*	13.7 (6.9)	7.9 (4.4)	9.1 (3.8)	2.7 (1.8)
	Chamerion latifolium		0.1 (0.1)		0.1 (0.1)
	Achillea millefolium	0.3 (0.2)	0.1 (0.1)	0.1 (0.1)	
	Aster sibiricus	0.2 (0.1)	0.3 (0.2)	0.1 (0.1)	0.6 (0.4)
	Artemisia tillesii	0.1 (0.1)	0.1 (0.1)		
	Antennaria sp.	1.3 (1.0)	1.8 (1.2)	0.9 (0.6)	1.3 (1.3)
	Erigeron sp.	0.1 (0.1)	0.1 (0.1)		
Legume	*Hedysarum alpinum*	0.4 (0.2)	0.6 (0.3)	0.6 (0.6)	0.1 (0.1)
	Hedysarum boreal spp. *mackenzii*	0.6 (0.4)	2.1 (1.8)	0.6 (0.6)	2.3 (2.3)
	Oxytropis campestris	0.6 (0.6)	0.2 (0.1)		
	Totals	22.3 (0.6)	35.6 (10.4)	17.2 (4.6)	19.3 (5.2)

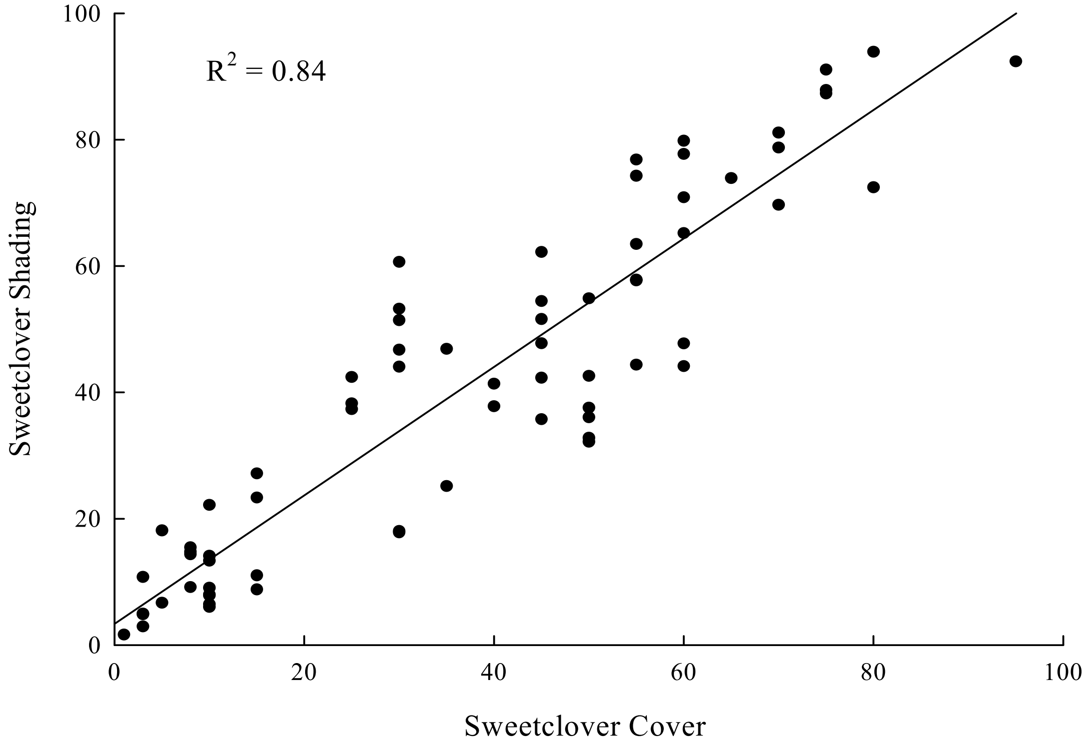

Fig. 2.2. The relationship between sweetclover shading and sweetclover cover. Data was collected along the Healy River in Alaska. Shade value equation: [1- (PAR below sweetclover/PAR above sweetclover)]*100.

Table 2.5. Results regarding the growth of native species under five shade treatments.

Species	Growth Parameters		
	Height	Final Biomass	Root : Shoot Ratio
H. alpinum 2006	0.9($_{4,68}$)	23.8($_{4,68}$) ***	6.0($_{4,68}$) **
H. alpinum 2007	2.4($_{2,41}$)	43.9($_{2,41}$) ***	10.4($_{2,41}$) **
H. mackenzii	14.0($_{4,65}$) ***	76.2($_{4,65}$) ***	6.1($_{4,65}$) **
O. campestris	4.2($_{4,68}$) **	32.4($_{4,68}$) ***	6.5($_{4,68}$) **
C. latifolium	4.2($_{4,68}$) **	39.4($_{4,68}$) ***	3.2($_{4,68}$) *
D. drummondii	44.0($_{4,69}$) ***	6.7($_{4,69}$) ***	27.4($_{4,69}$) ***
S. alaxensis	2.7($_{4.70}$) *	34.9($_{4.70}$) ***	20.0($_{4.70}$) ***
A. tenuifolia	2.8($_{4,70}$) *	4.8($_{4,70}$) **	2.4($_{4,70}$)
P. balsamifera	5.8($_{4,66}$) **	16.7($_{4,66}$) ***	6.6($_{4,66}$) **

* Values are observed F from the ANOVA model and the corresponding numerator and denominator degrees of freedom. Asterisks indicate significant p-values: (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.0001$).

[†] *H. alpinum* was grown during 2006 and 2007.

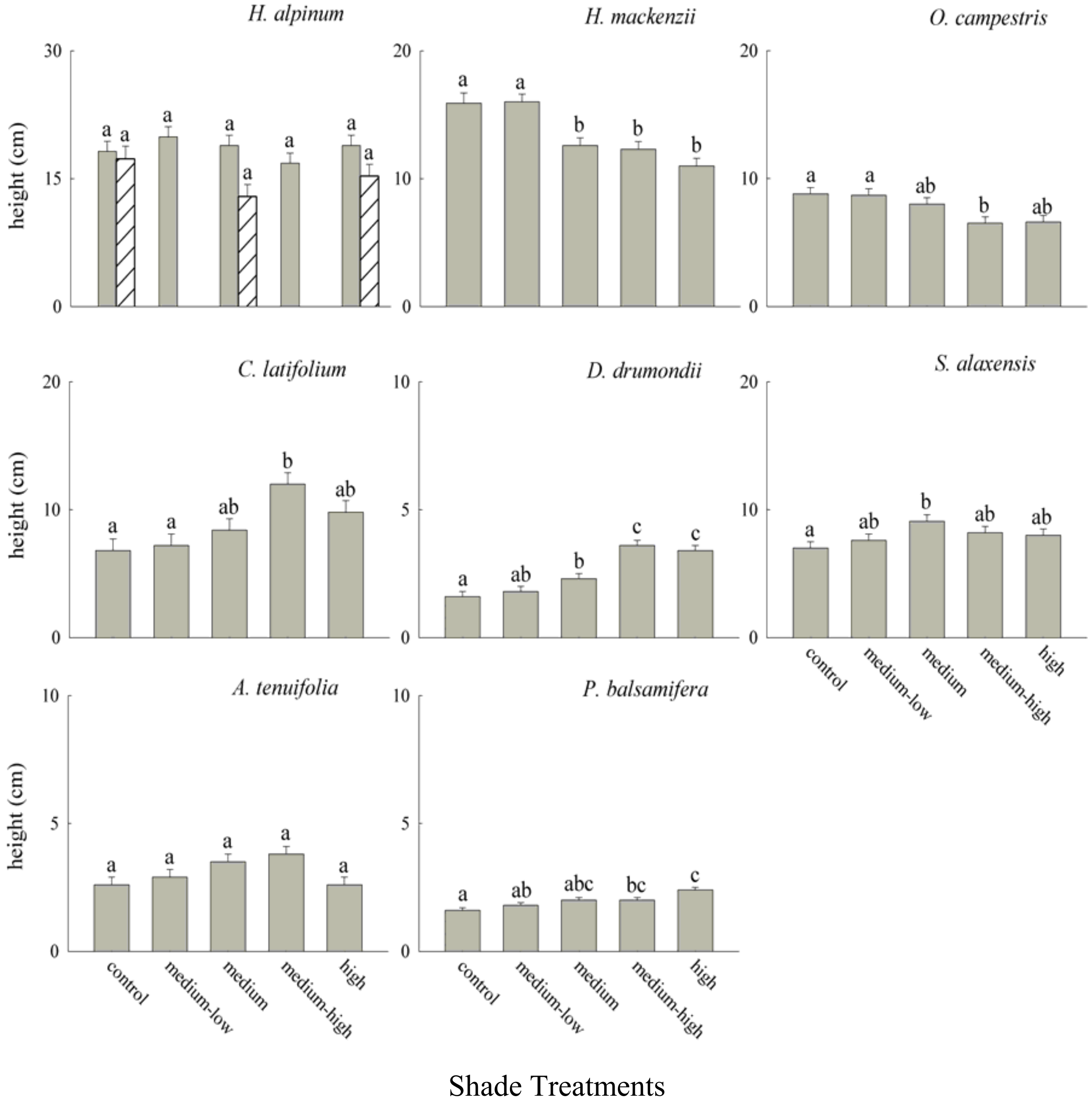

Fig. 2.3. The height of native species grown under five levels of shading. Bars indicate standard errors. For *H. alpinum*, grey bars indicate seedlings were grown during 2006 and hatched bars during 2007. Means for *H. alpinum* were not compared across years. Different letters indicate treatment means differed significantly ($p < 0.05$).

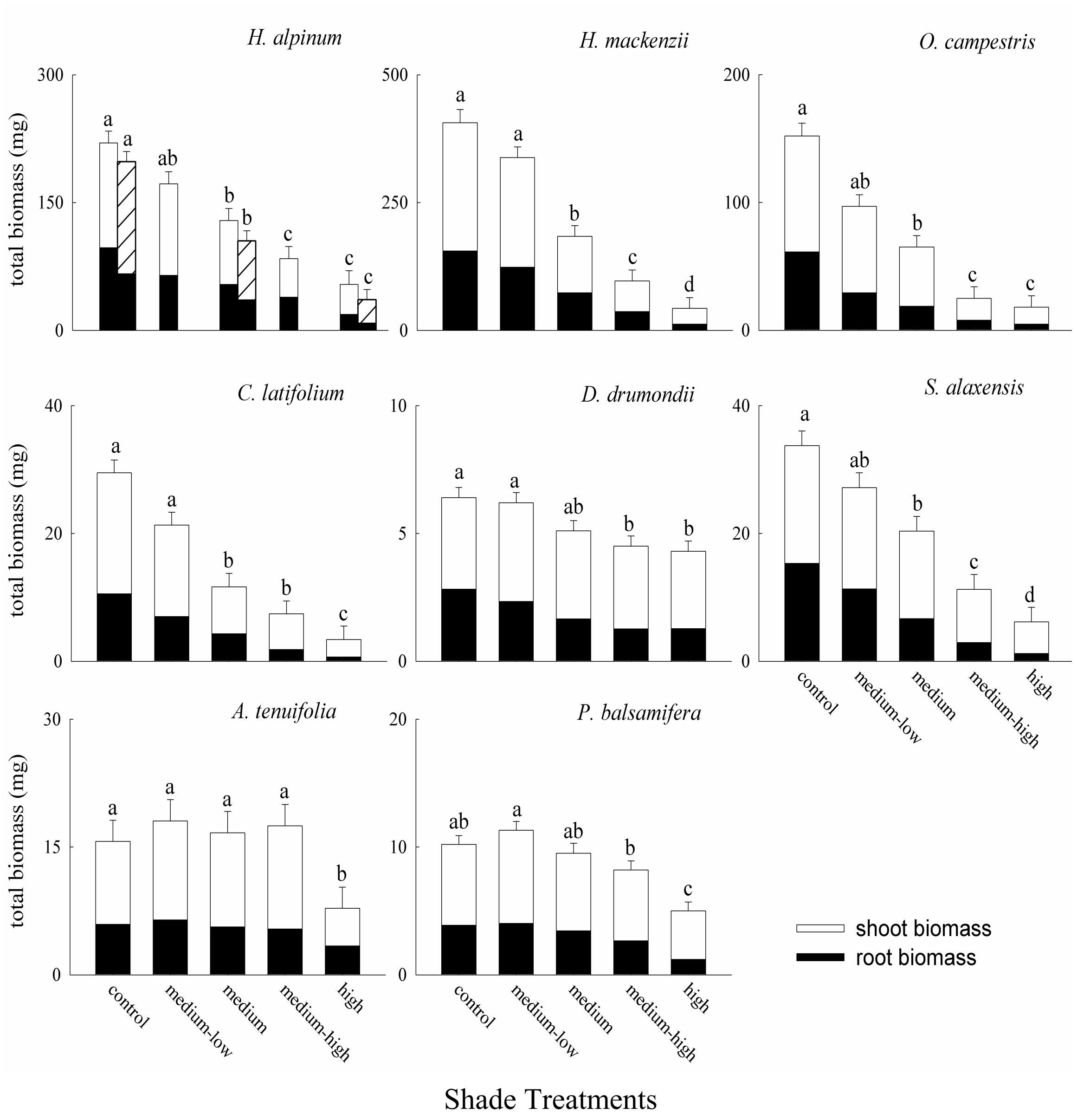

Fig. 2.4. The root, shoot, and total biomass of native species grown under five levels of shading. Bars indicate standard errors for total biomass. For *H. alpinum*, bars without hatching were grown during 2006, while bars with hatching were grown during 2007. Means for *H. alpinum* were not compared across years. Different letters indicate treatment means for total biomass differed significantly ($p < 0.05$).

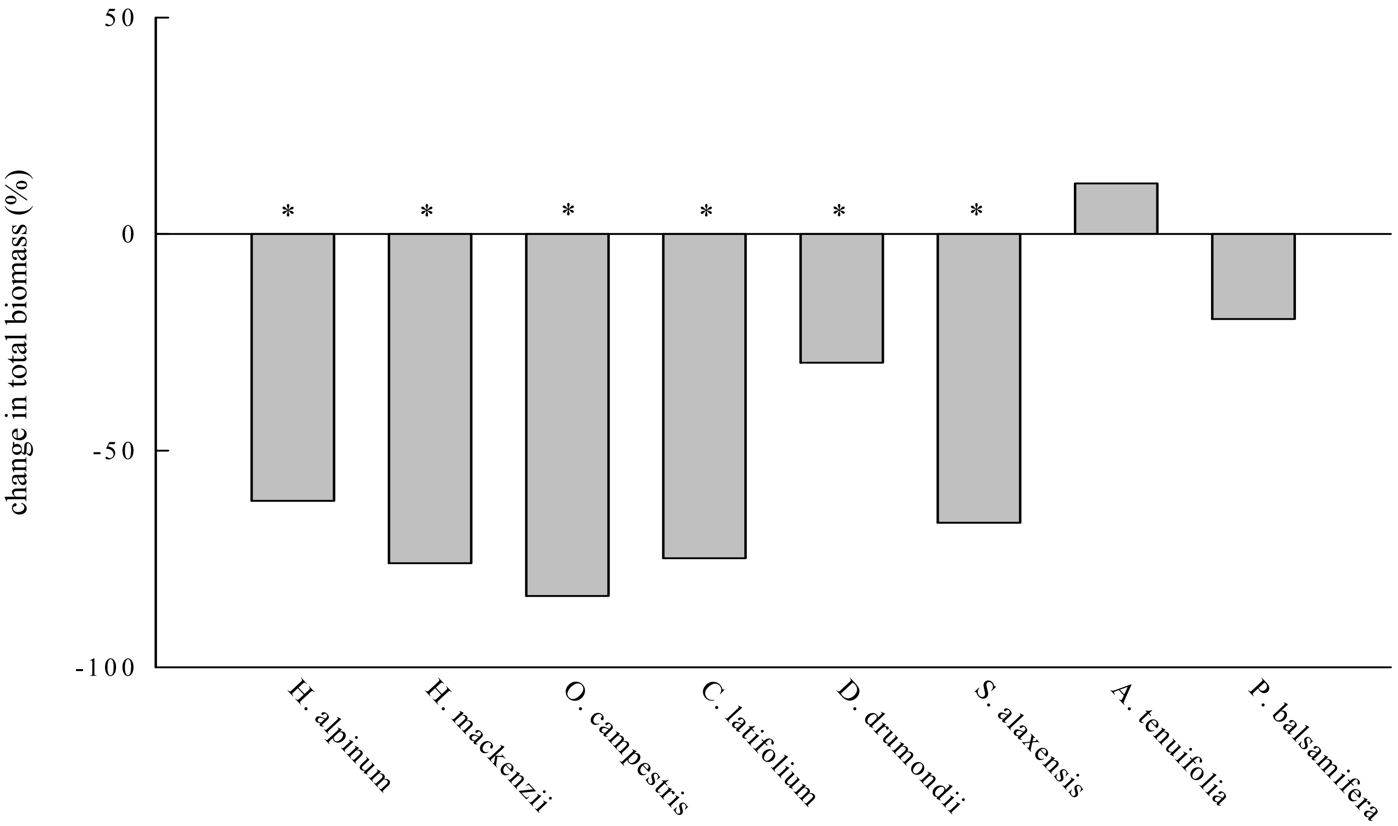

Fig. 2.5. The relative change in total biomass for species grown under low and high shading. Data are from the control and medium-high shade treatments. An asterisk indicates the treatment means were significantly different ($p < 0.05$). Relative change equation: [1 – (medium-high/control)] * 100.

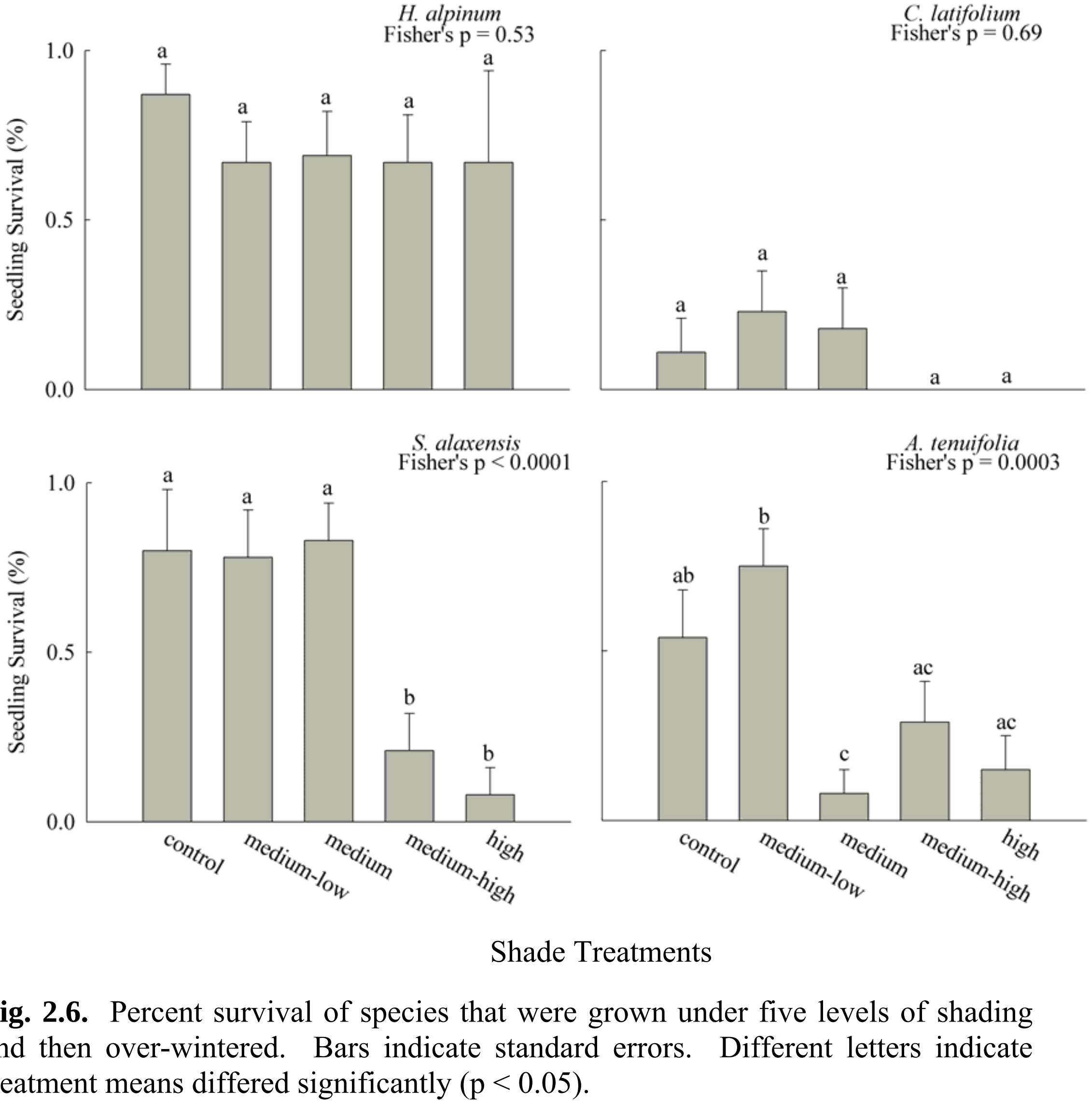

Fig. 2.6. Percent survival of species that were grown under five levels of shading and then over-wintered. Bars indicate standard errors. Different letters indicate treatment means differed significantly ($p < 0.05$).

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Chapter 3. Seedling interactions between an invasive legume (*Melilotus alba)* and two legumes native to Alaska[1]

Introduction

The rapid increase of non-native plants found in boreal forests of North America (Rose & Hermanutz 2004; Sumners & Archibold 2007; Carlson & Shephard 2007) has outpaced research regarding their impacts in boreal ecosystems. In the past, a cold climate and small human population were likely strong barriers against non-native plants establishing within boreal ecosystems. Recent warmer winters (Chapman & Walsh 1993), longer growing seasons (Myneni *et al.* 1997), and the potential of greater propagule pressure through increased human disturbances and commerce (Carlson & Shephard 2007) have likely altered these barriers and increased the potential of non-native plant invasion. For instance, between 1941 and 2006, the number of non-native plants recorded in Alaska has increased by 46% (Carlson & Shephard 2007). In select cases, non-native plants have invaded and begun to form extensive populations in natural habitats of Alaska (e.g. Conn *et al. in press*). Since invasive plants can dramatically alter ecosystem processes and the structure of plant communities (Wilcove *et al.* 1998; Mack *et al.* 2000; Levine *et al.* 2003), land managers and researchers are concerned that invasive plant species might be affecting natural habitats in the state. To address this concern, I conducted the first study of the ecological impacts of an invasive plant in floodplain habitats of Alaska.

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[1] Spellman, B.T. Seedling interactions between an invasive legume (*Melilotus alba)* and two legumes native to Alaska. Prepared for submission in *The Journal of Ecology*.

In other boreal ecosystems, riparian plant communities are highly vulnerable to invasion (Rose & Hermanutz 2004), and several floodplains in Alaska now support non-native plant species (e.g. seven non-native plant species were found along the Healy River of interior Alaska, Table 2.1). *Melilotus alba* Medik. (Fabaceae) is an invasive plant that has formed dense and extensive patches along several rivers in Alaska (Conn *et al. in press*). *M. alba*, hereafter referred to as sweetclover, is a biennial legume that grows 90-200 cm in height and can produce up to 350,000 seeds per plant (Turkington *et al.* 1978). Sweetclover is widely distributed along roadsides in Alaska (Wurtz *et al.* 2005), where it may have been sown as a vegetative cover to stabilize road-side soils after construction. Sweetclover growing along roadsides, which often parallel and cross waterways in Alaska, likely provided the propagules sweetclover required to invade riparian habitats. Because the seed of sweetclover floats (Turkington *et al.* 1978), it has the ability to spread to new floodplain habitats far removed from human disturbances (Wurtz & Macander 2007). Sweetclover is now common along extensive portions of the Healy, Stikine, Matanuska, and Nenana Rivers of Alaska (Table 2.1; Conn *et al. in press*). Sweetclover has become one of the most widespread invasive species along roadsides and along several rivers of Alaska (Wurtz *et al.* 2005; Conn *et al. in press*), yet nothing was known about the potential for it to impact riparian plant communities.

The objective of this study was to address the potential of sweetclover to impact floodplain plant communities of Alaska. While invasive species may affect habitats through numerous mechanisms (Levine *et al.* 2003), I focused solely on the potential for sweetclover to competitively suppress native species. I examined competitive interactions between sweetclover and two native legumes: *Oxytropis campestris* (L.) and *Hedysarum alpinum* (L.). Sweetclover competition could potentially affect mature native legumes, seedlings of native legumes, or both. However, in this study, I examined the interactions between seedlings of sweetclover and seedlings of native legumes. Seedling interactions are important as slight differences in competitive ability during the initial stage of colonization can grow in magnitude with time and determine the outcome of competition between species (Harper 1977; Newberry & Newman 1978; Gerry & Wilson 1995).

I chose *O. campestris* and *H. alpinum* because research in other ecosystems suggested functionally similar species have stronger interactions than functionally dissimilar species (Prieur-Richard *et al.* 2000; Fargione *et al.* 2003; Turnbull *et al.* 2005). Sweetclover, *O. campestris*, and *H. alpinum* are each legumes (Fabaceae) that associate with soil *Rhizobia sp.* that fix atmospheric nitrogen (Hultén 1968, Turkington *et al.* 1978). In Alaska, early-successional habitats along glacial rivers have low amounts of soil nitrogen (Van Cleve & Viereck 1981; Chapin *et al.* 2006). The ability of legumes to cope with limited nitrogen likely allows these species to colonize early-successional floodplain habitats. Sweetclover, *O. campestris*, and *H. alpinum* were the three most common legumes and among the ten most abundant floodplain species along two river floodplains in Alaska (i.e. Healy and Nenana Rivers, Chapter 2).

While similarities exist between species, there are also differences in their life strategies and heights. Sweetclover is a biennial, while both *O. campestris* and *H. alpinum* are perennials (Hultén 1968). Because annual and perennial n-fixing plants can have different affects in ecosystems (Yelenik *et al.* 2007), it would have been ideal to compare sweetclover to a short-lived leguminous species. However, there are no annual or biennial legumes native to Alaska (Hultén 1968). In addition, sweetclover grows larger than any native legume along floodplains in interior Alaska (*pers. obs.*). Sweetclover grows 90-200 cm in height, *O. campestris* grows 10-20 cm in height, and *H. alpinum* grows 20-70 cm in height (Turkington *et al.* 1978; Johnson *et al.* 1995; Graham 2002). Both native legumes are being overtopped by dense patches of sweetclover along several floodplains in Alaska (*pers. obs.*).

Since sweetclover can overtop these native legumes, I hypothesized that differences in height will result in sweetclover dominating competitive interactions between the species. Early-successional floodplain habitats in Alaska are highly disturbed and sparsely vegetated (Chapin *et al.* 2006). As a result, plants that are common in early-successional habitats are adapted to high light availability. For example, both *O. campestris* and *H. alpinum* are both shade-intolerant (Chapter 2). I predicted seedlings of sweetclover would overtop seedlings of *O. campestris* and *H. alpinum*, and as native legumes are shade-intolerant, I hypothesized that sweetclover would competitively suppress both native species.

To test my hypothesis, I grew legumes in additive series experiments where seedling density and species mixtures were varied independently. I used final height and biomass as indicators of a species' dominance within mixture. I addressed three questions: (1) Does varying seedling density or species mixture affect the growth of tested species? (2) Is the growth of sweetclover, *O. campestris*, and *H. alpinum* limited by intra- and/or interspecific competition? (3) Does sweetclover competitively suppress either *O. campestris* or *H. alpinum*?

The questions I addressed here present the first step toward understanding the ecological impacts of an invasive plant in Alaska.

Methods

The study was conducted outdoors at the University of Alaska Fairbanks during the growing season of 2007. Seed of each species was collected from three locations in interior Alaska. Seed of sweetclover was collected along the Nenana River floodplain (64°13'N, 149°16'W). Seed of *O. campestris* and *H. alpinum* was collected and supplied by the Alaska Plant Materials Center (APMC). The APMC collected seed of *O. campestris* from the Black rapids Glacial Area, while seed of *H. alpinum* was collected near the town of Paxson, Alaska.

To examine competitive interactions between seedlings of sweetclover, *O. campestris*, and *H. alpinum*, I conducted two additive series experiments (Law & Watkinson 1987; Sher *et al.* 2000). In these experiments, there were three seedling densities: "low density" had 4, "medium density" had 20, and "high density" had 40 seedlings per pot. Each density had five mixtures of species at ratios of 1:0, 3:1, 2:2, 1:3, and 0:1 (Fig. 3.1). The purpose of creating a range of densities and mixtures was to have a gradient of intra- and interspecific competition from low to high. Herein, a unique level of density and mixture will be termed a "combination". Each experiment had 15 combinations (i.e. 3 seedling densities x 5 species mixtures) resulting in a total of 30 combinations (i.e. 15 combinations for sweetclover and *O. campestris* and 15 combinations for sweetclover and *H. alpinum*).

Seedling densities used in the experiments were based on sweetclover seedling counts from the field. During the summer of 2006, I counted sweetclover seedlings in six 2 m x 1 m plots along the Nenana River floodplain of interior Alaska. The counts ranged from 407 to 1307 sweetclover seedlings per plot. However, within these plots, sweetclover seedlings were highly clustered and often exceeded 60 seedlings per 20 cm x 20 cm areas, which corresponds to ≥ 6000 seedlings per 2m x 1m area. For my experiments, low density corresponded to 400 seedlings, medium density 2000 seedlings, and high density 4000 seedlings per 2m x 1m area. In a separate experiment that I conducted along two river floodplains in Alaska, I counted the seedlings of native species within 64 2 m x 1 m plots. I never found *O. campestris* and *H. alpinum* exceeding 10 seedlings per plot.

Before the experiments began, I collected sediment from the Nenana River floodplain to use as a growth medium. As test species were common along the Nenana River (Chapter 2), this substrate likely had *Rhizobia* sp. required to inoculate the roots of each legume. I placed rock wool in the bottom of 150 experimental pots (20 cm wide x 46 cm deep, 9.63 L) and filled these pots 1 cm below the brim with floodplain substrate. I created five wooden boxes (4 m x 8 m x 0.5 m) and placed 30 pots in each box. I used a randomized complete block design to assign each pot a combination. Seed of each legume was scarified with sand paper to break dormancy and facilitate germination. During 3-5, June 2007, three times the required seed for each combination was sown on the surface of pots. Seed was sown at this date to reflect the emergence of vegetation along floodplains in interior Alaska (*pers. obs*.). After two weeks, seedlings were either transplanted or pulled so that species were growing at the desired combinations.

Seedlings were grown in full light outside and were subjected to ambient conditions. Throughout the growing season, reverse osmosis (R/O) water was added to each box so that all pots were immersed in approximately 10 cm of water. To prevent leaking, each box had a water-proof liner. Therefore, seedlings received water through natural precipitation or capillary rise from the pools of water within each box. This form of watering likely reduced water stress and minimized disturbance to plants on the surface of pots. Every three weeks, I applied fertilizer to the top of pots. Fertilizer was dissolved at a ratio of 1:13:50 ppm of N:P:K, which is representative of soil nutrient levels along the Nenana River floodplain (J. Conn *unpubl. data*).

At the end of one growing season (14-16, September 2007), I randomly selected the 10 centermost plants from each pot to be harvested. If there were fewer then 10 plants to select, all plants were harvested. While harvesting plants, I observed the roots of each species had nodules. Each harvested plant was cut at the cotyledon scar to divide root and shoot biomass. Harvested plants were dried at 70^{o} C for two weeks. Measured growth parameters were shoot height and biomass (root, shoot, and total). Due to high seedling mortality in eight experimental pots, three of the 75 pots were removed from the sweetclover and *O. campestris* experiment, while five of the 75 pots were removed from the sweetclover and *H. alpinum* experiment.

Statistical Analysis

All statistical analyses were conducted with SAS 9.1 (SAS institute, North Carolina, USA). I conducted t-tests to determine if significant differences ($\alpha = 0.05$) existed among the height and biomass of sweetclover and both native legumes. To perform these analyses, I pooled the mean response from all combinations and compared data solely by species. When necessary, I log transformed data to meet model assumptions of normality. When data had constant variance I used a pooled t-test and if data had heterogeneous variance I used a Satterthwaite t-test.

To address research question one, I used two-way analysis of variance (ANOVA) models to determine if density, mixture, or their interaction affected the height and biomass of tested species. When necessary, I log transformed data to meet model assumptions of normality and homogeneity of variance. When significant differences existed among density or mixture ($\alpha = 0.05$), I used pair-wise Tukey tests to determine differences among factor levels.

To address research questions two and three, I conducted regression analyses to determine (1) if either intra- or interspecific competition affected the height or biomass of tested species and (2) which form of competition was most important. I fit the data to a linear (Spitters 1983) and generalized linear two-species reciprocal yield model (Watkinson 1981, Park *et al.* 2002):

$$W_i^{-1} = W_o + B_i N_i + B_j N_j \qquad [3.1]$$

$$W_i = W_o(1 + B_i N_i + B_j N_j)^{-1} \qquad [3.2].$$

When necessary, I log transformed data to meet model assumptions of normality and homogeneity of variance. For both models, W_i represented the mean response per individual of species i, W_o represented the response of species i at no competition, N_i was the density of species i, N_j was the density of species j, B_i and B_j were parameters that represent intra- and interspecific competition of species i and j respectively. Analysis of species j was performed by rearranging the models:

$$W_j^{-1} = W_o + B_j N_j + B_i N_i \qquad [3.3]$$

$$W_j = W_o(1 + B_j N_j + B_i N_i)^{-1} \qquad [3.4].$$

For the linear model, I used multiple linear regression to estimate W_o, B_i, and B_j. I tested significance of parameters with t-tests ($\alpha = 0.05$). For the generalized linear model, I used the Levenberg-Marquardt method to estimate W_o, B_i, and B_j (Park et al. 2002). Parameters were considered significant if the 95 percent confidence intervals did not span 0. I chose the model that met the assumptions of normality and constant variance. If both models met these assumptions, then I chose the model with the highest R^2 value.

Results

At the end of one growing season, sweetclover grew taller than both native species and had more biomass than *O. campestris*. When compared to *O. campestris*, sweetclover grew taller and had more root, shoot, and total biomass (Table 3.1). When compared to *H. alpinum*, sweetclover grew taller and had more shoot biomass; however, the root and total biomass did not differ significantly (Table 3.2).

Effects of Density and Mixture

For each species, root and shoot biomass were highly correlated with total biomass ($R > 0.84$, $P < 0.0001$). Due to the high correlation between these growth parameters, I discuss biomass accumulation solely in terms of total biomass.

In the sweetclover and *O. campestris* experiment, *O. campestris* had no clear relationship with density or mixture while sweetclover was affected by both factors. The height of *O. campestris* was affected by an interaction between density and mixture but no clear trend existed in the data (Table 3.3, Fig. 3.2a). *O. campestris* biomass was not affected by density or mixture (Table 3.3, Fig. 3.2b). When grown with *O. campestris*, density and mixture affected the height and biomass of sweetclover (Table 3.3). As density increased, sweetclover height and biomass decreased (Fig. 3.2c and 3.2d); however, the medium and high density had a similar response for sweetclover height. The mixture that had the least amount of sweetclover grew tallest and had the greatest biomass (Fig. 3.2c and 3.2d).

In the sweetclover and *H. alpinum* experiment, *H. alpinum* was affected by mixture while both density and mixture affected sweetclover. The height of *H. alpinum* had a significant interaction between density and mixture (Table 3.4, Fig. 3.3a). The biomass of *H. alpinum* was not affected by density but was affected by mixture (Table 3.4). The mixture with equal parts *H. alpinum* and sweetclover (i.e. 2 : 2 species ratio) had less biomass than the monoculture and other mixtures (Fig. 3.3b). When grown with *H. alpinum*, density and mixture affected the height and biomass of sweetclover (Table 3.4). The height of sweetclover was affected by an interaction between density and mixture (Table 3.4, Fig. 3.3c). Sweetclover biomass was greatest at low density but did not differ at medium and high densities (Fig. 3.3d). Furthermore, the mixture that had the least amount of sweetclover had the greatest biomass (Fig 3.3d).

Effects of Intraspecific and Interspecific Competition

For the reciprocal yield models, the parameters of competition (i.e. B_i or B_j) explain the effect that the independent variables (i.e. density of species i or j) had on the response. Intra- or interspecific competition occurred if the estimated parameters of competition were significantly different from zero. When B_i or B_j estimates were positive, the response decreased when density increased. When B_i or B_j estimates were negative, the response increased when density increased. The value of B_i or B_j estimates determined competitive ability of a species, where larger positive values indicate greater competition.

While interspecific competition had minimal impacts on tested species, intraspecific competition affected the height and/or biomass of sweetclover, *O. campestris*, and *H. alpinum*. The presence of sweetclover, at any density, did not significantly affect the height and biomass of *O. campestris* (Table 3.5, Fig. 3.4a and 3.4b) and *H. alpinum* (Table 3.6, Fig. 3.5a and 3.5b). For both *O. campestris* and *H. alpinum*, intraspecific competition increased shoot length but did not affect the accumulation of biomass (Table 3.5 and 3.6, Fig. 3.4a, 3.4b, 3.5a, and 3.5b). Of note, regression models explained a marginal amount of variance for either native legume (i.e. $R^2 < 0.14$). The presence of *O. campestris* or *H. alpinum*, at any density, did not significantly affect the height and biomass of sweetclover (Table 3.5 and 3.6, Fig. 3.4c, 3.4d, 3.5c, and 3.5d). For sweetclover, intraspecific competition significantly decreased shoot length and biomass (Table 3.5 and 3.6, Fig. 3.4c, 3.4d, 3.5c, and 3.5d).

Discussion

Despite sweetclover clearly overtopping both native legumes, there was no evidence that sweetclover competitively suppressed either *O. campestris* or *H. alpinum*. The height and biomass response of *O. campestris* and *H. alpinum* was independent of the density of sweetclover. As native legume density increased, the effect of intraspecific competition increased *O. campestris* and *H. alpinum* height but not biomass. Native legumes likely increased shoot length as a physiological response to capture more light (Grime 1979). Since densities were based on field observations, these findings suggest both native legumes are tolerant of sparse or dense mixtures of sweetclover in floodplain habitats. When compared to native legumes, sweetclover had a morphologically plastic response to seedling density.

The response of sweetclover was clearly limited by increases in plant density. The response of sweetclover was largely independent of the density of *O. campestris* or *H. alpinum*. Increased sweetclover density caused the height and biomass of sweetclover to decrease significantly, suggesting intraspecific competition was the major factor limiting sweetclover growth. However, sweetclover generally grew tallest and had the most biomass in low density plant mixtures. These findings suggest sweetclover grows optimally in sparsely vegetated areas and would not be as tolerant as native legumes to dense vegetation in floodplain habitats. My findings are supported by a field study that indicated sweetclover was a floodplain pioneer; its abundance decreases as cover of surrounding vegetation increases (Conn *et al. in review*).

While the tested species here likely affect ecosystem processes similarly (i.e. n-fixing legumes), differences in traits likely allow for sweetclover and native legumes to occupy separate niche space in floodplain habitats. The assumption that tested species would have stronger interactions because they shared a functional group proved to be erroneous. Though the two native species and sweetclover are legumes, they differ in many respects. Sweetclover has a short lifecycle that emphasizes rapid growth and copious seed production, while *O. campestris* and *H. alpinum* are perennial species adapted to low-nutrient environments. As a result, the growth strategies and tolerances to competition between species likely differ. For instance, sweetclover was clearly limited by density. Increases in plant density likely decreased the amount of light and soil resources required for sweetclover seedlings to achieve optimal growth. In contrast, *O. campestris* and *H. alpinum* were not limited by density. Perennial species adapted to nutrient-poor habitats tend to grow slowly and, subsequently, require few resources (Chapin *et al.* 1986; Chapin 1991). Therefore, in comparison to sweetclover, native legumes likely require less light and soil resources to reach optimum growth. Sharing similar functional effects in ecosystems does not equate to having similar functional responses to pressures such as competition or nutrient limitations (Diaz & Cabido 2001). In theory, both sweetclover and native legumes can co-occur because they both take up and require different amounts of resources. Because of the differences in growth and resource requirements, I believe sweetclover is filling a novel niche for legumes within glacial floodplain habitats of Alaska.

On the other hand, results might have differed if the experiments were conducted over a two-year period or if seedlings of native legumes were grown in competition with mature sweetclover. At the end of one growing season, sweetclover was taller than both native legumes and had more biomass than *O. campestris*. Connelly & Wayne (1996) found that initial differences in size between plants can cause smaller plants to experience asymmetric relationships with larger species, resulting in competitive suppression. If the experiment had been allowed to carry over to the next growing season, the initial size advantage of sweetclover might have resulted in sweetclover competitively suppressing both native legumes. Furthermore, since mature sweetclover can shade up to 94 percent of photosynthetically active radiation and *O. campestris* and *H. alpinum* are shade-intolerant (Chapter 2), I believe shading by mature sweetclover would have a negative effect on the growth of native legumes.

Results from the seedling competition experiments were consistent with a sweetclover removal experiment conducted along the Healy and Nenana Rivers of interior Alaska (described in Chapter 2). In the removal experiment, I determined seedling recruitment of native species in plots with sweetclover and plots where sweetclover was removed. While sweetclover limited overall recruitment of native species, it was not found to affect the recruitment of native legumes (Chapter 2). In fact, native legumes appeared propagule-limited. For instance, in 64 2 m x 1 m removal plots, *O. campestris* and *H. alpinum* never exceeded 10 seedlings per plot. Due to the lack of legume propagules in the removal experiment, I was unable to determine whether sweetclover competitively suppressed native legumes, whether native legumes were seed-limited, or both. When combining results from the seedling competition and removal experiments, data suggest *O. campestris* and *H. alpinum* are more likely to be seed-limited than competitively suppressed by sweetclover.

I found that seedlings of sweetclover did not competitively suppress seedlings of the native legumes *O. campestris* and *H. alpinum*. Results gained from my short-term experiments can be used to generate questions for future research. For instance, are Alaskan floodplain endemics (e.g. *Salix setchelliana*) or functional groups other than legumes (e.g. graminoids or forbs) competitively suppressed by sweetclover? If so, do those species have growth and resource requirements similar to sweetclover? More research is needed to understand the effect that sweetclover has on floodplain habitats in Alaska.

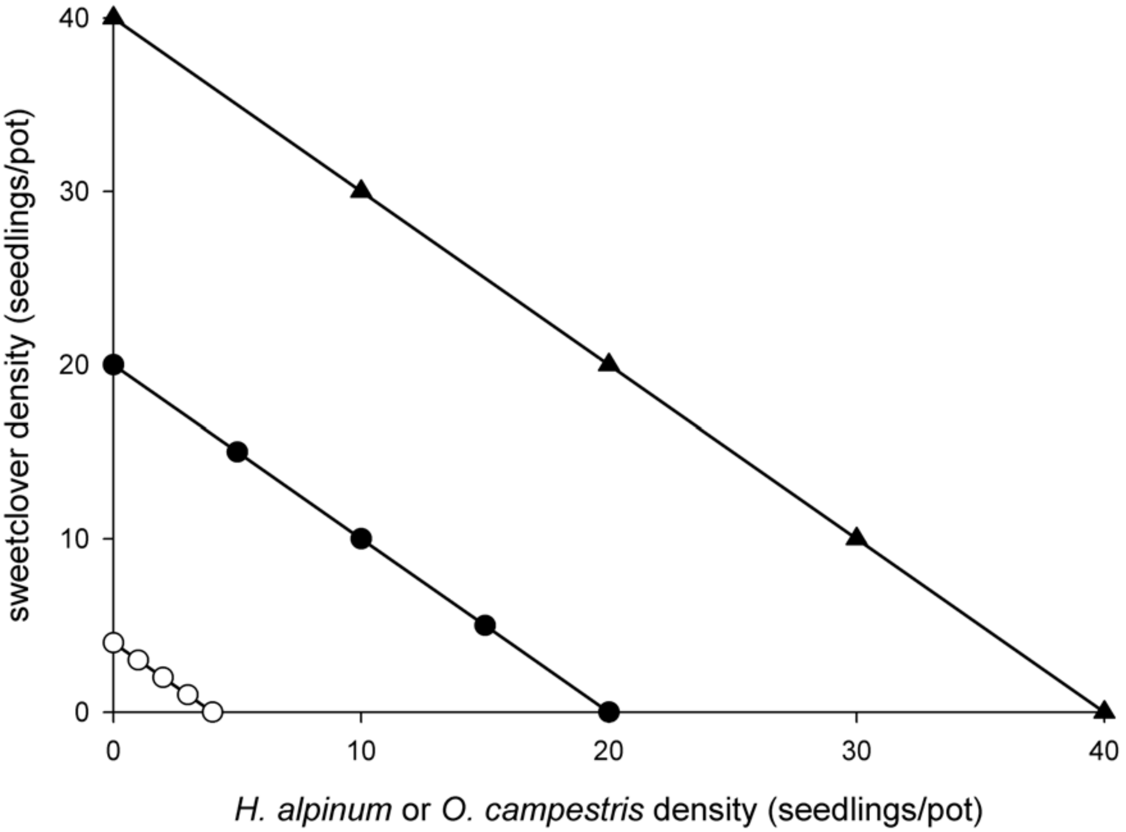

Fig. 3.1. Design of seedling competition experiments (sweetclover vs. *O. campestris* and sweetclover vs. *H. alpinum*). The low density (open circles) had 4 seedlings per pot, medium density (closed circles) had 20 seedlings per pot, and high density (triangles) had 40 seedlings per pot; each density had 3 mixtures and 2 monocultures.

Table 3.1. Results comparing the final biomass and height of *O. campestris* and sweetclover. Standard errors are in parentheses.

Growth Parameters	*O. campestris* (n=56)	sweetclover (n=68)	DF	t-value	p
height (cm)	9.0 (0.4)	18.3 (0.8)	105†	11.38	< 0.0001*
shoot biomass (mg)$^{+}$	193.7 (17.6)	348.3 (45.8)	123	2.66	0.009*
root biomass (mg)$^{+}$	117.1 (10.6)	226.4 (33.1)	119†	2.35	0.02*
total biomass (mg)$^{+}$	310.8 (27.6)	574.7 (76.7)	121†	2.60	0.01*

* Asterisk indicates t-test was significant after a Bonferroni multiple comparison test. Family error rate in Bonferroni test was $\alpha = 0.10$.

$^{+}$ Data were log transformed for analyses.

† Data had non-constant variance and I used a Satterthwaite t-test. Otherwise, I used a pooled t-test.

Table 3.2. Results comparing the final biomass and height of *H. alpinum* and sweetclover. Standard errors are in parentheses.

Growth Parameters	*H. alpinum* (n=54)	sweetclover (n=68)	DF	t-value	p
height (cm)	12.6 (0.5)	17.8 (0.6)	119†	6.23	0.0001*
shoot biomass (mg)$^{+}$	175.6 (14.6)	316.7 (43.8)	118†	2.85	0.005*
root biomass (mg)$^{+}$	156.3 (11.3)	204.3 (32.4)	112†	-0.41	0.69
total biomass (mg)$^{+}$	332.0 (24.9)	521.0 (75.3)	116†	1.49	0.14

* Asterisk indicates t-test was significant after a Bonferroni multiple comparison test. Family error rate in Bonferroni test was $\alpha = 0.10$.

$^{+}$ Data were log transformed for analyses.

† Data had non-constant variance and I used a Satterthwaite t-tests.

Table 3.3. The importance of density and mixture on the biomass and height responses of *O. campestris* and sweetclover. Values are observed F-values from the ANOVA model and the corresponding numerator and denominator degrees of freedom.

Growth Parameters	Species	block	density	mixture	interaction
Height (cm)	*O. campestris*	0.9 (4, 40)	1.4 (2, 40)	0.6 (3, 40)	2.8 (6, 40)*
	sweetclover	1.1 (4, 52)	13.5 (2, 52)**	4.5 (3, 52)*	1.4 (6, 52)
Shoot biomass (mg)+	*O. campestris*	0.9 (4, 40)	2.6 (2, 40)	0.3 (3, 40)	1.3 (6, 40)
	sweetclover	1.4 (4, 51)	47.3 (2, 51)**	8.4 (3, 51)*	1.2 (6, 51)
Root biomass (mg)+	*O. campestris*	0.7 (4, 40)	2.2 (2, 40)	0.2 (3, 40)	1.6 (6, 40)
	sweetclover	1.9 (4, 51)	42.9 (2, 51)**	7.7 (3, 51)*	1.3 (6, 51)
Total biomass (mg)+	*O. campestris*	0.5 (4, 40)	1.4 (2, 40)	0.2 (3, 40)	1.8 (6, 40)
	sweetclover	1.4 (4, 51)	48.9 (2, 51)**	8.7 (3, 51)**	1.3 (6, 40)

* Asterisks indicate significant p-values (* = $p < 0.05$ and ** = $p < 0.0001$).

+ Data were log transformed for analyses.

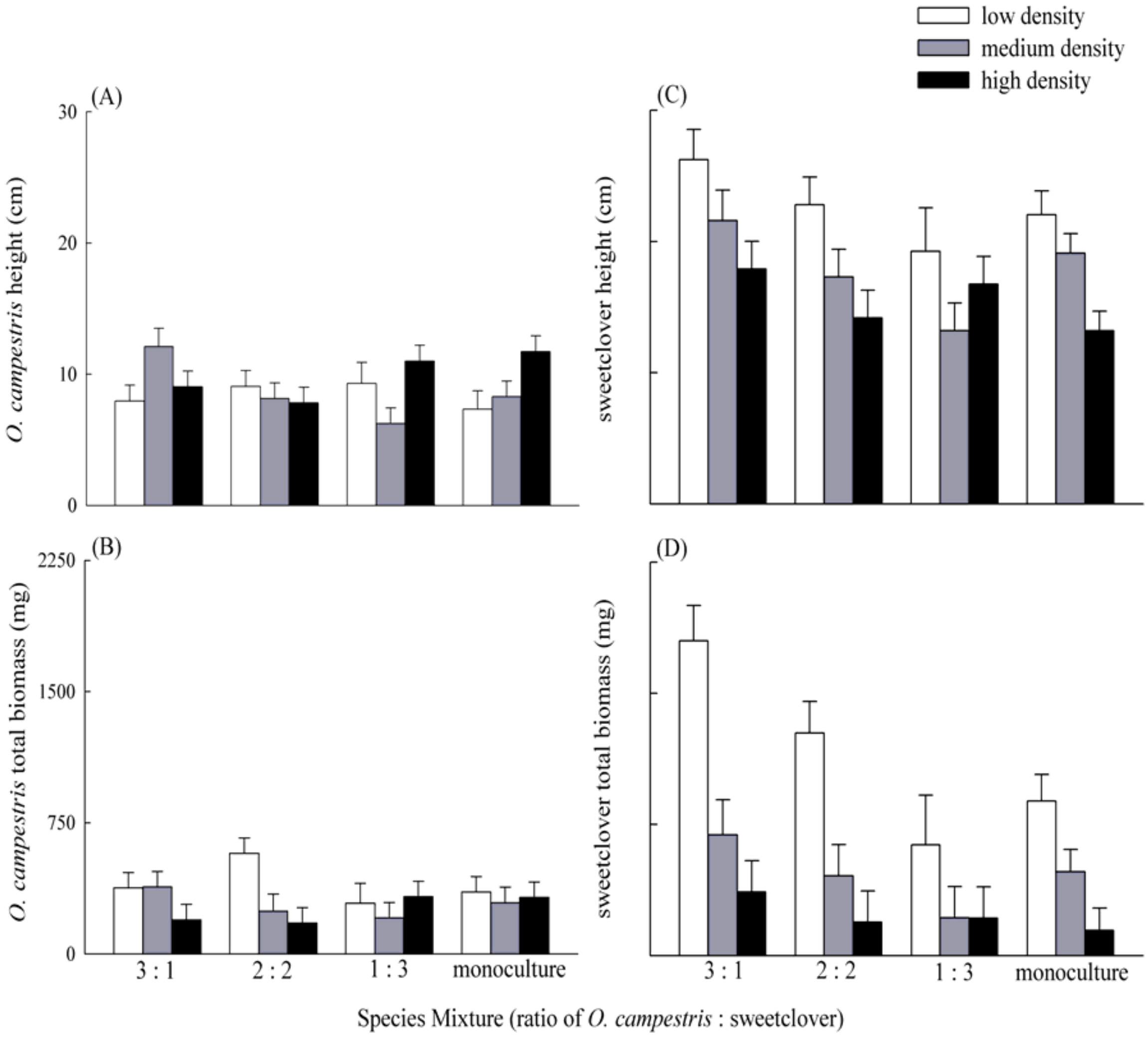

Fig. 3.2. Mean height and biomass of *O. campestris* (A, B) and sweetclover (C, D) grown at several densities and mixtures. Bars indicate standard errors.

Table 3.4. The importance of density and mixture on the biomass and height responses of *H. alpinum* and sweetclover. Values are observed F-values from the ANOVA model and the corresponding numerator and denominator degrees of freedom.

Growth Parameters	Species	block	density	mixture	interaction
Height (cm)	*H. alpinum*	2.3 (4, 38)	1.3 (2, 38)	4.0 (3, 38)*	3.6 (6, 38)*
	sweetclover	2.8 (4, 51)*	2.7 (2, 51)	3.2 (3, 51)*	3.9 (6, 51)*
Shoot biomass (mg)$^+$	*H. alpinum*	4.5 (4, 38)*	0.6 (2, 38)	5.1 (3, 38)*	3.3 (6, 38)*
	sweetclover	0.2 (4, 51)	9.6 (2, 51)*	3.4 (3, 51)*	1.2 (6, 51)
Root biomass (mg)$^+$	*H. alpinum*	4.8 (4, 38)*	0.6 (2, 38)	4.5 (3, 38)*	1.3 (6, 38)
	sweetclover	3.8 (4, 50)*	16.4 (2, 50)**	2.3 (3, 50)	1.4 (6, 50)
Total biomass (mg)$^+$	*H. alpinum*	4.7 (4, 38)*	0.7 (2, 38)	5.1 (3, 38)*	2.3 (6, 38)
	sweetclover	1.5 (4, 51)	17.0 (2, 51)**	3.4 (3, 51)*	1.6 (6, 51)

* Asterisks indicate significant p-values (* = $p < 0.05$ and ** = $p < 0.0001$).

$^+$ Data were log transformed for analyses.

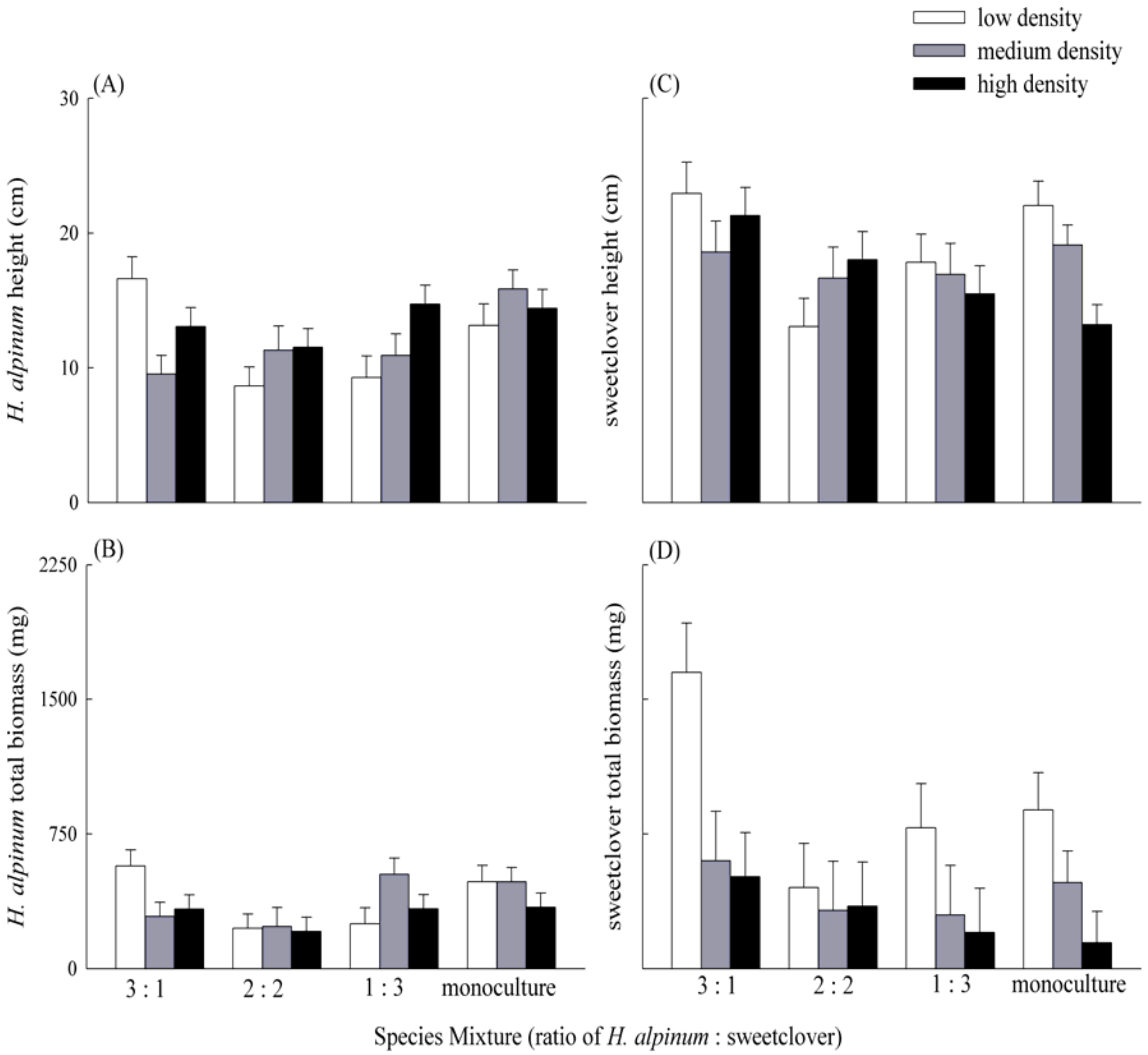

Fig. 3.3. Mean height and biomass of *H. alpinum* (A, B) and sweetclover (C, D) grown at several densities and mixtures. Bars indicate standard errors.

Table 3.5. The importance of competition on the height and biomass responses of *O. campestris* and sweetclover. Standard errors are in parentheses.

Growth Parameters	Species	W_o	Model Parameters intraspecific competition	 interspecific competition	R^2
Height (cm)	*O. campestris*	0.88 (0.04)*	-0.003 (0.002)*	0.0001 (0.002)	0.06
	sweetclover	1.35 (0.03)*	0.005 (0.001)*	0.002 (0.001)	0.28
Shoot biomass (mg)	*O. campestris*	2.29 (0.08)*	0.001 (0.002)	0.004 (0.002)	0.05
	sweetclover	2.81 (0.07)*	0.01 (0.002)*	0.003 (0.002)	0.53
Root biomass (mg)	*O. campestris*	2.07 (0.07)*	0.002 (0.02)	0.003 (0.002)	0.05
	sweetclover	2.59 (0.08)*	0.01 (0.002)*	0.004 (0.003)	0.44
Total biomass (mg)	*O. campestris*	2.50 (0.07)*	0.001 (0.001)	0.003 (0.002)	0.05
	sweetclover	3.02 (0.07)*	0.01 (0.002)*	0.003 (0.002)	0.51

* Parameters were significant in the two species reciprocal model (alpha=.05).

† Data were analyzed with the linear reciprocal yield model. Otherwise data were analyzed with the generalized reciprocal yield model.

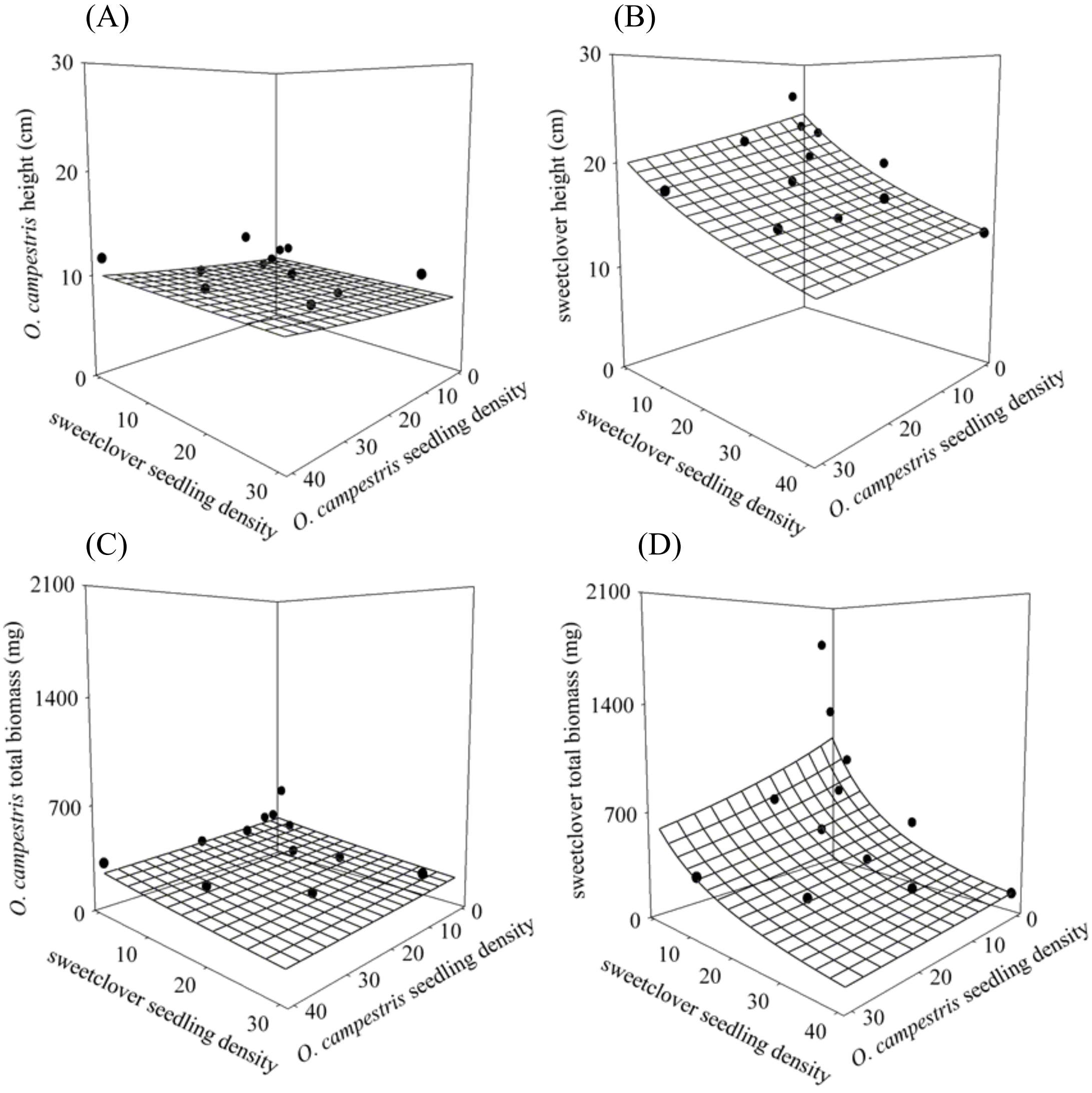

Fig. 3.4. Modeled height and biomass of *O. campestris* (A, B) and sweetclover (C, D) grown at several seedling densities and mixtures. Filled circles represent means for each density and mixture combination. Note that y-axes have different scales between species.

Table 3.6. The importance of competition on the height and biomass responses of *H. alpinum* and sweetclover. Standard errors are in parentheses.

Growth Parameters	Species	Model Parameters			
		W_o	intraspecific competition	Interspecific competition	R^2
Height (cm)	*H. alpinum*	1.01 (0.82)*	-0.004 (0.001)*	-0.001 (0.001)	0.14
	sweetclover	1.30 (0.02)*	0.004 (0.001)*	-0.001 (0.001)	0.31
Shoot biomass (mg)$^+$	*H. alpinum*	2.19 (0.06)*	-0.001 (0.001)	0.003 (0.002)	0.06
	sweetclover[†]	0.38 (0.01)*	0.004 (0.001)*	0.001 (0.001)	0.49
Root biomass (mg)$^+$	*H. alpinum*	2.15 (0.06)*	-0.001 (0.001)	0.002 (0.002)	0.05
	sweetclover[†]	0.40 (0.01)*	0.005 (0.001)*	0.001 (0.001)	0.45
Total biomass (mg)$^+$	*H. alpinum*	2.47 (0.06)*	-0.001 (0.001)	0.002 (0.002)	0.05
	sweetclover[†]	0.35 (0.01)*	0.003 (0.0004)*	0.001 (0.001)	0.46

* Parameters were significant in the two species reciprocal model (alpha=.05).

[†] All data were analyzed with the generalized reciprocal yield model.

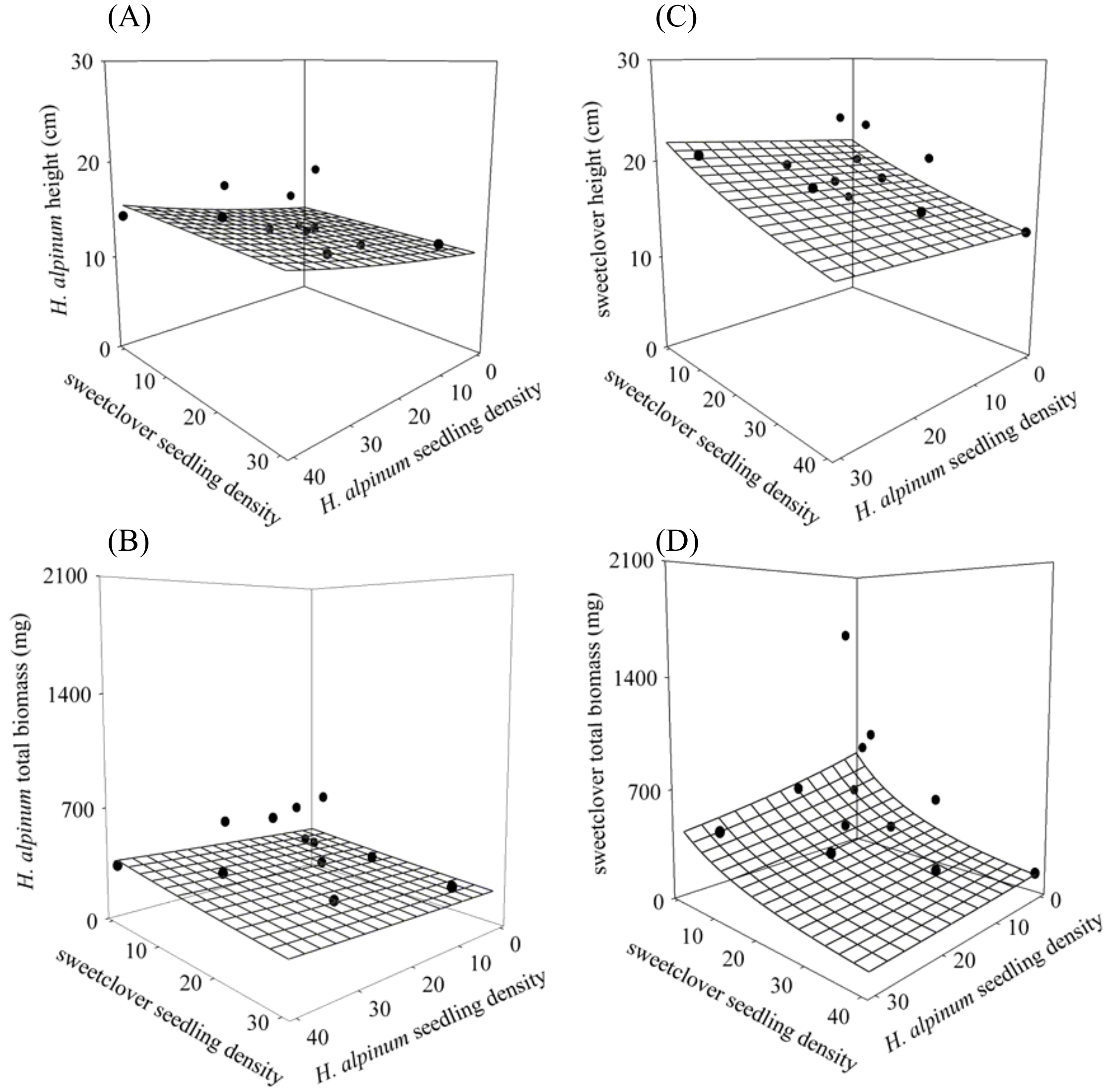

Fig. 3.5. Modeled height and biomass of *H. alpinum* (A, B) and sweetclover (C, D) grown at several seedling densities and mixtures. Filled circles represent means for each density and mixture combination. Note that y-axes have different scales between species.

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Chapter 4. General Conclusions

In recent years, the number of non-native plant species in Alaska has increased dramatically (Carlson & Shephard 2007), yet little information exists regarding their impacts on ecosystems in the state. One non-native plant, *Melilotus alba*, has invaded natural habitats in Alaska and currently has extensive populations along portions of the Healy, Nenana, Matanuska, and Stikine Rivers (Chapter 2; Conn *et al. in press*). Since invasive plants can dramatically alter ecosystem processes and the structure of plant communities (Parker & Reichard 1998; Mack *et al.* 2000; Wilcove *et al.* 1998; Levine *et al.* 2003), land managers and invasive species biologists were concerned that sweetclover might be affecting Alaska's floodplain habitats. To address this concern, I conducted research to determine if sweetclover was impacting recruitment of native plants in early-successional riparian habitats.

I found that sweetclover does impact Alaskan floodplain plant communities during the early stages of floodplain succession. In chapter two, I presented findings from a removal experiment that indicated sweetclover had two impacts on floodplain habitats: it altered the physical structure of early-successional plant communities and limited the recruitment of native species. Sweetclover alters the physical structure of floodplain habitats by overtopping native vegetation and shading areas that are generally open to light. In the removal experiment, areas in which sweetclover was not removed had half as much light as areas where sweetclover was removed. Furthermore, seedlings of native species in areas with sweetclover were 50 percent more likely to die than seedlings in areas where sweetclover was removed. Subsequently, there were half as many native seedlings in areas with sweetclover. I proposed two underlying mechanisms to explain the observed reduction in recruitment of native species: (1) native species are intolerant of sweetclover shading, and (2) sweetclover is competitively superior to native species.

Shading by sweetclover can stress the seedlings of native species common in early-successional floodplain habitats. In chapter two, I presented findings from a greenhouse shade experiment where I grew eight native species under a range of lighting conditions that were representative of shading under sweetclover patches in the field. Plant species were chosen because they were among the most common plants in early-successional floodplain plant communities invaded by sweetclover. The eight tested species were: *Hedysarum alpinum*, *Hedysarum boreale* spp. *mackenzii*, *Oxytropis campestris*, *Chamerion latifolium*, *Dryas drummondii, Salix alaxensis*, *Alnus incana* spp. *tenuifolia*, and *Populus balsamifera*. Each common early-successional plant species was shown to be shade-intolerant (i.e. increased shading led to etiolation, lower biomass, skewed root to shoot biomass ratio, and/or increased over-wintering mortality). However, *A. tenuifolia* and *P. balsamifera* were more tolerant of shading than the other tested species. Shading by sweetclover clearly has the potential to stress seedlings of native plants common to early-successional floodplain habitats. Yet, I found no relationship between shading and growing season mortality of native species. Therefore, I concluded that sweetclover shading can not solely explain decreased recruitment of native species that occurred in the removal experiment.

When compared to two native legumes, sweetclover was not competitively superior. In chapter three, I presented findings regarding the competitive interactions between seedlings of sweetclover and two native legumes: *O. campestris* and *H. alpinum*. I chose native legumes because research in other ecosystems suggested that functionally similar species are likely to have stronger interactions than functionally dissimilar species (Prieur-Richard *et al.* 2000; Fargione *et al.* 2003; Turnbull *et al.* 2005). I conducted two additive series experiments in which I manipulated seedling densities and species' mixtures independently. I found that sweetclover did not competitively displace or suppress native legumes. In fact, for each tested species, I found that intraspecific competition had a larger impact on growth than interspecific competition. Furthermore, in one growing season, sweetclover was clearly limited by seedling density while both native legumes were not. This finding suggests sweetclover grows optimally in sparse vegetation while native legumes can grow in sparse or dense mixtures of sweetclover. Field observations support these findings. In my removal experiment, sweetclover was not found to limit the recruitment of native legumes (Chapter 2). Due to the lack of interspecific interactions and differences in growth and resource requirements between species, I concluded that sweetclover is likely filling a novel niche for legumes within glacial floodplain habitats of Alaska.

The underlying mechanisms I proposed do not fully address how sweetclover limited recruitment of native species in floodplain habitats. Though I isolated light as a potential mechanism by which sweetclover could impact plant communities, competition for several additional resources, including space, water, and soil nutrients, is also likely to be important. While sweetclover competition affected recruitment of native species, it is unlikely, based on my results, that seedlings of sweetclover are affecting the recruitment of either *O. campestris* or *H. alpinum*. Sweetclover may have stronger interactions with plants that share similar growth traits and resource requirements. One native species, *Festuca rubra,* clearly had reduced recruitment in the presence of sweetclover (Chapter 2). Perhaps *F. rubra* requires similar amounts of nutrients but is a weaker competitor than sweetclover. To more fully understand how sweetclover limited native recruitment, more research is required regarding the impacts of sweetclover on other limited resources in early-successional floodplain habitats and the response of native species to those impacts.

Sweetclover is likely abundant in early-successional floodplain plant communities because of its ability to produce copious amounts of seed that are readily dispersed into unoccupied habitats. The early-successional surfaces along glacial rivers in interior Alaska are highly disturbed, sparsely vegetated, and open to light (Chapin *et al.* 2006). These habitats are ideal for sweetclover because it is shade-intolerant (Turkington *et al.* 1978) and was shown to be stressed when grown in dense plant mixtures (Chapter 3). Because sweetclover produces copious amounts of seed that are readily dispersed by water (Turkington *et al.* 1978), it has the potential to densely colonize sparsely vegetated riparian habitats. For instance, sweetclover counts ranged from 407 to 1307 seedlings in six 2 m x 1 m plots along the Nenana River (Chapter 3). In contrast, I found that native species often had few seedlings. For instance, in 64 2 m x 1 m removal plots, I found that *O. campestris* and *H. alpinum* never exceeded 10 seedlings per plot. This may be due to competition, limited seed output, or both. However, when combining results from the seedling competition and removal experiments, my data suggest *O. campestris* and *H. alpinum* are more likely to be propagule-limited than competitively suppressed by sweetclover. Therefore, even though sweetclover was more abundant than almost all native species along the Healy and Nenana Rivers (Chapter 2), it might not be competitively displacing all native species. Rather, the propagule pressure and/or dispersal ability of sweetclover could be greater than that of native species, which would allow sweetclover to colonize floodplain habitats more effectively than native species. I believe the extensive distribution of sweetclover along several rivers in Alaska may be a result of its superior ability to produce and disperse seed.

While my thesis research involved short-term experiments, results indicate that sweetclover may have long-term impacts on floodplain habitats. Sweetclover is among the three most abundant species in both of my study sites and, subsequently, has affected the composition of plant communities along the Healy and Nenana Rivers. Furthermore, sweetclover has altered the physical structure of early-successional habitats through shading and is currently limiting native recruitment of some native plant species. Since recruitment limitation was an important factor that structured plant communities in other ecosystems (Clark *et al.* 1998; Hubbell *et al.* 1999; Foster & Tilman 2003), I believe sweetclover will have long-term impacts within floodplain habitats of Alaska. These impacts will likely be focused in early-successional plant communities.

It seems unlikely that sweetclover will affect the trajectory of succession in floodplain habitats of Alaska. J. Conn *et al.* (*in review*) found that the abundance of sweetclover in riparian habitats decreases as the cover of surrounding vegetation increases. Such floodplain pioneers are typically replaced as succession progresses and light becomes a limiting factor. The majority of common floodplain species tested in the shading experiment were also floodplain pioneers (i.e. *H. alpinum*, *H. mackenzii*, *C. latifolium*, *S. alaxensis*, *O. campestris*, and *D. drummondii*). Species that dominate later stages of floodplain succession, *A. tenuifolia* and *P. balsamifera* (Van Cleve and Viereck 1983), had a higher tolerance to shading than the native pioneer species. Due to differences in tolerance of shading, pioneer species are more likely to be stressed and displaced by sweetclover than either *A. tenuifolia* or *P. balsamifera*. Since plant species that dominate later stages of succession are less likely to be impacted by sweetclover, I believe it is unlikely that sweetclover will impact the trajectory of succession in floodplain habitats.

My thesis findings offer researchers and land managers insight into the impacts of sweetclover on native vegetation and suggests mechanisms through which sweetclover can alter Alaskan floodplain plant communities. Results gained from my thesis experiments can be used by land managers to enhance public awareness of invasive plants and direct policy towards protecting the natural habitats of Alaska. I also hope that results gained will be used to generate questions for future research. Several questions would be interesting and important to address: (1) Does sweetclover impact mature floodplain vegetation? (2) Does sweetclover alter soil conditions in early-successional habitats? If so, (3) How do seedlings and/or mature native plants respond to these effects? (4) Are other functional groups or species more likely to be competitively suppressed by sweetclover? (5) Are native species seed-limited in early-successional floodplain habitats? Finally, (6) What are the long-term impacts of sweetclover on the floodplain plant communities of Alaska? In the end, more research is required to understand the short- and long-term impacts of sweetclover in Alaska's floodplain habitats.

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