DOES AN EXOTIC INVASIVE GRASS FACILITATE THE INVASION OF A WOODY SPECIES INTO REMNANT PRAIRIES? A STUDY OF THE NATIVE, *PROSOPIS GLANDULOSA* AND THE ALIEN, *SORGHUM HALEPENSE*

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ABSTRACT

DOES AN EXOTIC INVASIVE GRASS FACILITATE THE INVASION OF A WOODY SPECIES INTO REMNANT PRAIRIES? A STUDY OF THE NATIVE, *PROSOPIS GLANDULOSA* AND THE ALIEN, *SORGHUM HALEPENSE*

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The native tree, *Prosopis glandulosa* (honey mesquite), and the exotic grass, *Sorghum halepense* (Johnsongrass), have been successfully invading native prairies in the Southwest U.S. since the 1800s. Although both species employ complementary life history traits in order to establish and flourish in grasslands, a correlation between the two has yet to be established. MacDougall and Turkington's (2005) "driver" or "passenger" model of invasive species was applied to explore mechanisms of invasion and impacts on community structure of these two species. My first objective was to determine if *S. halepense* was driving shifts in the abiotic and biotic structure of a native prairie community. Assuming that *S. halepense* was in fact altering both the resources and the plant neighborhood of the community, my second objective was to determine if *S. halepense* was facilitating the invasion of *P. glandulosa*. I predicted that in an invaded prairie zone, *S. halepense* A) increased light levels, B) decreased soil nitrogen (N) and increased soil carbon (C), and C) decreased soil moisture relative to conditions in a prairie without this species, and thus D) created a less diverse plant community, comprised of different plant species, and E) facilitated the invasion of P. *glandulosa*, a known N-fixer. In 2005 a field experiment was established in a remnant tallgrass prairie in North Texas comprised of three distinct zones: a native zone dominated by the native grass *S. scoparium*, an invaded zone of *S. halepense*, and a mixed zone where both native and exotic grasses were present. A greenhouse competition experiment followed in 2006 comparing *P. glandulosa's* germination and growth in two soil types, native and invaded, with three levels of competition: no competition, *S. scoparium,* and S. *halepense*. To test predictions regarding the first objective, light levels, soil N and soil C were examined in both the field and the greenhouse while soil gravimetric moisture and plant community composition were measured in the field only. The presence of *S. halepense* significantly lowered light levels and increased soil N and soil moisture in the field plots relative to native prairie. However, the lowest light levels in the greenhouse experiment occurred in pots with *S. scoparium* owing to the presence of standing dead. Somewhat surprisingly, plant species diversity and the number of woody species were higher in the invaded zone than the native zone.

To address the second objective, *P. glandulosa* germination and seedling growth were measured in both the field and greenhouse. Ambient litter inhibited *P. glandulosa* germination in the field regardless of neighbors, although a correlation with decreased light was not established. Significantly more seeds germinated in the invaded zone then either the mixed or native zones in the field, while seeds planted in greenhouse pots with *S. halepense* germinated better then those planted alone or with *S. scoparium*, regardless of soil type. Contrary to the field germination results, there was no effect of litter on seedling growth, while in both the field and greenhouse competition from live neighbors inhibited seedling growth. In the field seedlings in the native zone without competition grew the tallest, and seedling mortality caused by herbivores was significantly higher in the invaded zone (60-80%) than the native zone (20%). In the greenhouse seedling growth was equally inhibited by the presence of *S. halepense* and *S. scoparium.*

These results suggest that the soil abiotic resources and community structure were being altered in a way that facilitated seedling recruitment but not growth of *P. glandulosa,* and the shift from grassland to woodland was multivariate in origin. Anthropogenic influences, such as disturbance, fragmentation, and land management, may have caused the low diversity in the native zone and may have interacted with *S. halepense's* indirect effects on soil moisture, light, and N availability to drive community level changes in this remnant prairie.

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CHAPTER 1

BACKGROUND

1.1 Tallgrass prairies

While the loss of biodiversity due to anthropogenic causes is a focus of researchers worldwide, less attention is being placed on the conservation of North America's grasslands (Sampson and Knopf 1994). Since European settlement, the area of open grassland that supported native grasses, forbs, 60 million bison, prairie dog colonies, and up to 330 bird species has declined 99%. Unique interactions among herbivores, grasses and environmental factors have created the tallgrass prairie's community structure.

Due to the dominant grassy vegetation and open flat structure, a majority of the research on Texas prairies has focused on the prairie as a rangeland resource for cattle and other domestic livestock (e.g., Archer et al 1988, McPherson et al. 1988, Bush and Van Auken 1989, 1995, Pyke and Archer 1991, Zitzer et al. 1996, Brown and Archer 1999, and Tiedmann and Klemmedson 2004,). Fewer studies, however, have focused on causes of vegetation extinction, grassland community structure and conservation in native Texas prairies (Dyksterhuis 1946, Dyksterhuis and Schmutz 1947, Diamond and Smeins1985, Polley et, 1994, 2005, Seimann and Rogers 2003). Dyksterhuis (1946) was perhaps the first to quantify the detrimental effects of grazing and overgrazing on species composition in the Fort Worth Grand Prairie in North Central Texas. More recently, however, studies have focused on mechanisms of exotic and native species invasion into Texas prairies, composition of restored versus remnant prairies, species richness, and the effects of global warming on Texas grasslands (e.g., Diamond and Smeins 1985, Polley et al. 1994, 2005, Seimann and Rogers 2003). My research attempted to look at the abiotic and biotic interactions that shape both a remnant tallgrass prairie and a prairie community dominated by an exotic invasive grass.

Perennial grasses such as *Schizachyrium scoparium* (little bluestem), *Sorghastrum nutans* (Indian grass), *Andropogon gerardii* (big bluestem), *Bouteloua curtipendula* (sideoats grama), and *Sporobolus drummondi* (meadow dropseed) make up much of the tallgrass prairie plant community (Diamond and Smeins 1985). *S. scoparium* is a bunchgrass that dominates the vegetation of tallgrass prairies in North Texas and is often considered an indicator of the health of the prairie. The growth habit of a bunchgrass consists of clumps of standing dead and living biomass interspersed with open areas that allow for the establishment of annual forbs. The standing dead biomass and litter accumulation not only provide fuel for periodic fires, but also may inhibit germination of some species or provide necessary shelter or moisture for other species (Foster 1999, Wilsey and Polley 2003). The bunchgrass growth form and complex interactions with fire, herbivory, and climate are thought to be the major influences that shape the tallgrass prairie communities (Knapp and Steastedt 1998). Both direct and indirect anthropogenic disturbances threaten these interactions.

1.2 Threats to tallgrass prairie communities

Human encroachment and fragmentation of prairies has been occurring since the arrival of Europeans and the agricultural boom in the Great Plains. While studies of forest ecosystems have shown that fragmentation often leads to an increased susceptibility to invasive species, grassland researchers have found conflicting results (Harrison and Bruna 1999, Cully et al. 2003). Increases in exotic invasives in Australian grasslands have been attributed not only to high fragmentation, but also domestic livestock and surrounding agricultural lands (Hobbs 2001). Also, the size of a remnant prairie can affect the species associated with the community. As the size of a prairie decreases, not only are rare species at risk, but dominant species are negatively affected due to their inability to disperse to new communities (Tilman et al. 1994). This in turn can negatively impact the herbivores that often rely on the dominant species as a food source (Kostova et al. 2004). In addition, habitat fragmentation in prairies provides barriers such as roads and neighborhoods that suppress natural fire cycles.

The suppression of both naturally occurring and human mediated fires has long been cited as a reason for the decline of native species in prairies (Anderson 1990). The standing dead and litter accumulated by native prairie plants like *S. scoparium,* acts as fuel for necessary fire cycles (Tilman, Wedin 1991). Fire is necessary to release stores of nutrients and encourage vigorous germination and plant growth of other forbs and grasses by removing the litter and tall standing dead, thereby increasing the diversity and species richness of the grassland (Brockway et al 2002). Periodic burning of prairies may further maintain the community structure by reducing the amount of invasive woody species (Brockway et al. 2002). Although a prairie's role in carbon sequestration has yet to be clearly defined, infrequent burning of prairies may help alleviate increases in atmospheric carbon dioxide (CO_2) levels associated with global warming by increasing the productivity of the grasses that are able to sequester carbon in both above and below ground litter. (Arnold et al. 2000, Kucharik et al. 2006).

The changing climate and increased CO_2 levels, if left unchecked, will not only disrupt global weather patterns but also affect regional fire and rainfall cycles, alter community structure by favoring the growth of woody plant species, and increase the growth of invasive species in prairies (Walther et al. 2002). The C_4 grasses that dominate the tallgrass prairies at the Konza Prairie Long Term Ecological Research (LTER) site in Kansas have increased in biomass in response to elevated CO_2 levels during dry or normal rainfall years, but grass productivity did not change in wet years (Ham et al. 1995). This suggests that C_4 grasses may be able to respond to a changing climate if that climate is dry, but growth may be hindered if rainfall increases across the Great Plains due to global warming. Woody species also respond positively to increased CO_2 levels and may be able to out-compete grass species in arid and semi-arid ecosystems (Brown et al.1997). Even though native plants have the capacity to store carbon, exotic invasive clonal species may be better able to sequester and utilize CO_2 and higher levels of this gas may only fuel the takeover of native habitats by these invaders (Thompson et al. 1995).

Both native and exotic invasives may employ similar mechanisms to invade and modify community and ecosystem structure (Thompson et al., 1995) and are both the result of prairie degradation and also a major cause of species extinction in grasslands and other ecosystems around the world (McPherson et al. 1988, DiTomaso 2000). In urban areas the native *Typha* spp. and the exotic *Lythrum salicaria* employ rapid vegetative growth and habitat versatility to out-compete and eventually displace other native wetland species (Rachich and Reader 1999, Woo and Zedler 2002). Other similar life history traits are shared by two invasive trees in the southwest: the native *Prosopis glandulosa* (honey mesquite) and non-native *Tamarix ramosissima* (salt cedar). Both species are facultative phreatophytes (can access water from the water table via extremely long roots), have long lasting seeds, and can establish quickly due to extremely fast growing roots (Sala et al. 1996, Rogers, 2000). Allelopathy is another important mechanism of invasion sometimes employed by exotic species in introduced habitats. *Centuarea diffusa* and *Sorghum halepense* (Johnsongrass) are two noxious weeds in the U.S. that are able to exude chemicals that inhibit or disrupt the growth of native species in grasslands (Callaway and Aschehoug 2000, Rout 2005). All of these mechanisms lead to a decrease in native plant cover, creations of monocultures, a decrease in biodiversity, habitat loss, alteration of nutrient cycling, and potential change in community structure, i.e. grassland to woodland (Archer 1989, D'Antonio and Vitousek 1992, Thompson et al. 1995). Due to the already diminished land area of native prairies in the United States the impact of invasives may be amplified in these ecosystems.

1.3 Life history of Sorghum halepense: *a possible "driver" of ecosystem change*

Both native woody species and exotic invasive grasses threaten the existing tallgrass prairies in the United States. One of these exotic grasses, *S. halepense,* was introduced as a forage grass in the Southern United States in the 1800's, but by 1900 it had escaped cultivation and was characterized as a weed by the USDA (McWhortor 1981). Historically, *S. halepense* was believed to be native to the Mediterranean (Holm et al. 1977). however, this species is actually a hybrid of two *Sorghum* species, the cultivated *S. bicolor* and the noxious weed *S. propinguum* (Patterson et al. 1995). *S. halepense* can be found across most of the North American continent but is particularly a problem in the southern U.S. where mild winters allow its rhizomes to survive underground unharmed (Oyer et al. 1959, USDA 2006). The introduction of *S. halepense* has proven to be a problem for ranchers, land managers, and conservationists alike in North America. *S. halepense* has an arsenal of life history traits that contribute to its role as a ferocious invasive and make management of this weed costly and difficult (Baker 1974, McWhorter 1981).

S. halepense's ability to produce a massive amount of biomass each growing season is one life history trait that helps it out-compete local species for resources. Each ramet can grow 3 or more meters tall, and twelve rhizomes can produce anywhere from 80 to 90 ramets (Anderson et al. 1960, McWhorter 1981). Substantial belowground and aboveground growth in early spring has the potential to decrease the amount of sunlight, moisture, and nutrients available to neighboring plants (Mitskas et al. 2003). Even in extremely dense monocultures of Johnsongrass the aboveground shoots are able to produce sexually reproductive flowers (Williams and Ingber 1977).

Throughout the summer one *S. halepense* ramet can produce thousands of wind distributed seeds. The small seeds are easily transported among highly fragmented ecosystems allowing for recruitment into new communities (Holm et al 1977). Rapidly growing rhizomes develop only three to four weeks after seedling emergence (McWhorter 1981). These underground stems function as carbohydrate storage during the winter for shoots emerging from nodes in the spring (Anderson et al. 1960). One *S. halepense* plant can produce up to 5,000 rhizomatous nodes during one growing season making it an intense competitor for both aboveground and belowground resources (McWhorter 1971). Rhizomes typically fill the first 5-10 cm of soil but can also be found in much (120 cm) deeper soils (Holm et al. 1977). This coupled with the persistence of seeds in the seed bank make removal of *S. halepense* by tilling, mowing or burning difficult.

S. halepense rhizomes produce roots that exude an allopathic chemical, sorgoleone, through their root hairs (Yang et al 2004). Sorgoleone chemically disrupts and suppresses neighboring plant growth (Nimbal et al. 1996). Sorgoleone affects neighboring plant species by disrupting Photosystem II (Czarnota et al. 2001, Gonzalez 1997). A negative effect on growth or biomass of sorgoleone has been documented in greenhouse and field studies on crop, weedy, and native species (Einhelling and Rasmussen 1989, Czaronta et al. 2001). The ability of *S. halepense* to resist its own allopathic chemical, however, has not been documented (Gonzalez et. al. 1997). This may also suggest that other species have a mechanism to resist the effects of sorgoleone and might be able to survive in a *S. halepense* invaded habitat. Conversely, the capacity of this plant to grow rapidly and tolerate its own allelochemical has the potential to alter plant communities by creating a monoculture of *S. halepense*.

Another life history trait that improves the invasive nature of *S. halepense* is an anitherbivory chemical, dhurrin, produced in the aboveground biomass (Abdul-Wahab and Rice 1967, Nicollier et al. 1983). The initial production of dhurrin is genetically regulated, and the plant stores the cyanide compound as a bound nontoxic cyanogenic glucoside (Busk and Moller 2002). Once the plant is damaged (herbivory) or stressed (drought) the cyanogenic glucoside bond is broken and a highly toxic hydrogen cyanide compound is released (Nicollier et al. 1983). This mechanism helps *S. halepense* maintain high levels of aboveground biomass throughout the growing season by making the plant unpalatable to mammals and insects. Immense biomass and production of a cyanide compound would suggest that this plant has a high nitrogen requirement to support these mechanisms.

S. halepense can invade a broad range of habitats and effective control in these communities has been limited. Agricultural fields, pastures, prairies, forest edges, and wetlands have all been successfully invaded by *S. halepense*. Evidence suggests that periodic burning of native prairies or rangelands during the spring and summer could slow the growth of *S. halepense* (Grace et al. 2001). Controlled burning during these seasons in the southern U.S. is often not feasible due to the hot dry climate and the proximity of human habitation to remnant prairies. The control of *S. halepense* by herbicide is often employed and has shown limited success (Newman 1993). Unfortunately, herbicide is often costly and must be applied by hand in agricultural fields. Herbicide control is also not feasible in wetlands or stream banks due to possible pollution from runoff.

All of the above life history traits or mechanisms of invasion employed by *S. halepense* have the potential to alter community functioning or "drive" community change in an invaded area. Its capacity to out-compete native plants for light, water, and nutrients allows it to reduce the diversity and species richness in an ecosystem by creating a monoculture. This rapid growth coupled with its ability to deter herbivores and suppress native grass growth allows it to potentially change community composition in more then one trophic level (McWhortor 1981, Costa-Arbulu et al. 2001). *S. halepense* also has the potential to change the abiotic functions of a community. Prairies are known to have soils low in nitrogen and extremely slow nutrient turnover rates. An invader such as *S. halepense* that may require a large amount of nitrogen to support production of both biomass and cyanide compound could radically lower the nitrogen available in the community, but to date this effect has not been examined.

1.4 Growth of Prosopis*: a possible "passenger"*

Currently, the USDA recognizes 36 species and several varieties in the genus *Prosopis* (USDA Plants Database, 2006). Only four species occur in the Southwestern United States: *Prosopis pubescens, Prosopis velutina*, *Prosopis reptans,* and *Prosopopis* *glandulosa. Prosopis* species can vary widely in growth from low growing shrubs to trees reaching up to 40 feet in height (Johnston1962, Meyer et al. 1971, Morton and Howard 1975.) Native to Texas, *Prosopis glandulosa* var. *glandulosa* Torr. (honey mesquite) typically grows in arid to semi arid ecosystems as a deciduous, multi-stemmed shrub or single trunked tree (Meyer et al. 1971). Parallel to *S. halepense's* invasion, *P. glandulosa* trees have been increasing in density in grasslands, and a conversion from grassland to woodland has been occurring in the Southwestern United States since the 1800's (Archer 1989).

Similar to *S. halepense, P. glandulosa* has several life history traits that are often associated with weedy or invasive species. After about three years of age, adult trees produce a copious amount of seeds in long, green pods. The sweet taste and nutritious value of these pods allow the seeds to be dispersed long distances by herbivores. Not only is this mechanism important for seedling recruitment into new communities, but the herbivores promote germination since the extremely hard seed coat is then scarified in their digestive tract (Rogers 2000). While deer, rodents and other wild browse animals disperse *P. glandulosa* seeds, horses and cattle are perhaps the best known dispersers. Fisher et al. (1973) found that 97% of seeds fed to horses passed through the digestive tract intact, and 79% of seeds were viable after being eaten by cattle. Once the seeds are scarified either by weather or exposure to a digestive tract they are able to take up water and develop into seedlings. While aboveground tissues of *P. glandulosa* seedlings are highly susceptible to predation and fire, the belowground root collar and vast root system can resist most environmental pressures once the tree has matured (Roger 2000).

P. glandulosa trees are deeply rooted phreatophytes allowing them to access ground water unavailable to other grassland plants (Nilsen et al. 1986, Rogers 2000). *P. glandulosa* trees can invade and flourish in communities with low rainfall and soil which impedes percolation due to their ability to retrieve deep underground stores of water (Archer 1995, Miller et al 2001). Although most southern prairies and savannahs are water limited, P. *glandulosa* has the capacity to establish seedlings successfully in these environments (Brown and Archer 1999). However, Bush and Van Auken (1991) found that in ungrazed grasslands this was not a competitive advantage. In these communities the underground growth of *Bouteloua curtipendula* was able to effectively prevent the early establishment *P. glandulosa.* In the absence of grazing, grasses were able to devote 90% of their biomass to belowground structures that can inhibit the establishment of phreatophitic, N fixing trees such as *P. glandulosa* (Bush and Van Auken 1995, Van Auken and Bush 1988, 1997).

The association with N fixing bacteria is common in most legumes including *P. glandulosa*. All *Prosopis* species form relationships with nodulating species in the genus *Rhizobium* (Allen 1981). *Rhizobium's* ability to fix gaseous nitrogen (N_2) into ammonium (NH_4), a form usable by plants, alters the environment beneath *P. glandulosa* canopies, facilitating the invasion of other woody species that are able to take advantage of increased nitrogen in the soil (Seimann and Rogers 2003). The association with *Rhizobium* allows *P. glandulosa* a competitive advantage, the ability to grow in nitrogen poor soils (Zitzer et al. 1996).

These life history traits are not the cause of *Prosopis* species expansion, only tools that make these trees successful once they have invaded a new, often previously disturbed area. *P. glandulosa* modifies a grassland community by acting as a catalyst for the conversion of grassland to woodland. *P. glandulosa* alters the light and nitrogen levels under its canopy recruiting other woody species into the grassland. Both Whittaker et al. (1979) and Archer et al. (1988) described the conversion of a Rio Grande Plains, south Texas grassland as a two-phased pattern. Distinct shrub clusters comprised of many evergreen and deciduous species surround a *P. glandulosa* nucleus to form the intermediate phase, a mixed community, before a dense thorn woodland becomes the final phase (Archer et al. 1988, Whittaker et al 1979.). Initial seedling recruitment of lone *P. glandulosa* trees into grasslands facilitates a cluster of other shade tolerant, woody species such as *Opuntia lindheimeri, Zanthoxylum fagara,* and *Juniperus pinchotii* under its canopy, and later recruits other species, such as *Diospyros texana* or *Cletis pallida* outside the canopy (Archer et al. 1988, McPherson et al. 1988). It is well agreed upon that the conversion from grassland and establishment of woody species is recent, occurring within the past 100 -150 years (Archer et al. 1989, 1990, Bahre and Shelton 1993, Whittaker et al. 1979). However, many different reasons have been cited regarding what initially drove *P. glandulosa* to invade grasslands.

Grazing pressure by domestic animals has a significant effect on the species composition and forage quality in a grassland. Domestic livestock may affect *Prosopis* species by: increasing dispersal relative to wild species, scarifying seeds, supplying dung as a nutrient rich medium for young seedlings, compressing soil favoring the growth of trees with extensive root systems, and reducing forage grass cover thereby decreasing competition and fire frequency (Bahre and Shelton 1993). However, *P. glandulosa* continues to increase in density even after livestock have been removed (Brown and Archer 1989, Glendening 1952). Detrimental damage to perennial grass cover and changes in climate have been cited as possible reasons for this continued invasion (Polley et al. 1994, Brown and Archer 1989).

As with other invasive species, both exotic and native, climate change and associated increases in CO_2 levels favor *P. glandulosa* growth. *P. glandulosa* responded to higher levels of CO_2 with increased N fixation and better N and water use efficiency when compared to the C_4 grass, *Schizachyrium scoparium* (Polley et al. 1994). Vegetational shifts to shrub-tree ecosystems in arctic ecosystems and alpine communities in both Europe and New Zealand have also been attributed to increases in CO_2 levels and subsequent global climate change (Kullman 2002, Van Wijk et al. 2004, Wardle and Coleman 1992). Regional weather patterns associated with climate change such as increases in prolonged droughts and changes to fire cycles are also influencing the expansion of *P. glandulosa*. Many native perennial grasses survive on light rain events typical during the spring and summer in the Southwest. When these rain events do not occur, deeply rooted species similar to *P. glandulosa* have a competitive advantage (Leopold 1951, Price and Gunter 1942). Still, conflicting analyses of weather data have suggested that aridity has not been increasing in the southwest, and P.

glandulosa has been driven into new ecosystems primarily by human disturbance (Bahre and Shelton 1993). The success of prescribed burning at controlling young trees has indicated that suppression of naturally occurring fires, both climatic and human mediated, may also contribute to woody plant encroachment (Martin 1975).

While fire is successful at controlling the establishment of young trees and new seedlings, mature established *P. glandulosa* stands are more difficult and costly to control (Martin 1975, Kupfer and Miller 2005 and Ansley and Castellano 2006). Kupfner and Miller (2005) suggest that invasive grasses present in a *P. glandulosa* community change fire intensity and increase tree sprouting following a burn. Control by herbicide treatment is often more successful than burning, and native grasses respond with more growth and diversity when tree cover is reduced by an aerial spray of herbicide. The significant amount of branching and spouting exhibited by mature trees post-fire inhibits the growth of native grasses (Ansly and Castellano 2006). Mechanical removal is the most common form of control, but it is unsuccessful in reducing the recruitment of juvenile *P. glandulosa* trees (Tiedemann and Klemmedson 2004). Regardless, most methods used to control *P. glandulosa* have proved ineffective and costly to both ranchers and land managers.

1.5 Current hypotheses regarding invasive species

The problem of invasive species is a global phenomenon that occurs across most ecosystems and trophic levels. Even as the majority of studies on invasive species have highlighted the effects on community structure or a single species, new research trends are emerging. More recently the focus has shifted and studies are being conducted to observe the mechanisms of invasion, species interactions, and more specific effects on the underlying abiotic and microbial functions in a community (Shea and Chesson 2002).

One of the most common hypotheses associated with invasive species is the enemy release hypothesis (ERH). The ERH predicts that the establishment of nonnative invasive species in new habitats is due to the fact they have escaped their natural predators or herbivores (Keane and Crawley 2002). While this may apply to some species and their mechanisms of invasion, it does not explain species lacking controlling predators in their native range or qualities of invasives that emerge once they have occupied a new community (Colautti et. al. 2004, Keane and Crawley 2002). For instance, *Centaurea diffusa,* a noxious weed in North America, is able to radically disrupt the growth of neighboring plants in new communities but does not exhibit this behavior in its native environment (Callaway, 2000). The ERH also does not account for native U.S. plants that escape their natural range such as *Prosopis* and *Typha* that increase in density and move into new habitats without direct human mediated introduction. More innovative hypotheses, however, are attempting to addresses some of the gaps in the ERH by focusing on how invasive species interact in their new environment and how they affect critical ecosystem functions, such as resource availability and nutrient cycling (e.g., Tilman 2004, Davis et al. 2000, MacDougall and Turkington 2005).

One idea, introduced by MacDougall and Turkington in 2005, focused on invasive species and their ability to alter ecosystem functioning. The driver and passenger hypotheses question the role that exotic invasive species play in ecosystem change. The driver hypothesis suggests that exotic invasive species are “drivers” of ecological change if their competitive dominance is the direct cause of native species reduction. Conversely, exotic invasive species may be considered “passengers” if other factors, such as fragmentation or altered fire regimens, are limiting native species cover. In an oak savannah ecosystem MacDougall and Turkington (2005) found exotics to be merely passengers. Shifts in the plant community were not a direct result of the invasive species and were instead caused by reductions in seedling recruitment. They failed to examine however, any roles the invasive may have played in altering fire regimen or changing nutrient cycling that might have been the original “driving” force behind the ecosystem change (Didham et al. 2005). Nonetheless, they offer testable predictions for the role of both native and invasive species in other ecosystems including prairies, savannahs, and rangelands.

Although both the exotic *S. halepense* and the native *P. glandulosa* have been invading the same ecosystems since the late 1800’s, a correlation between the two species has yet to be established. Defining these species as either a “driver” or “passenger” allows me to explore the role native and exotic invasives employ in ecosystem change within a remnant prairie. Studying both an exotic and native invasive species allows not only for a comparison of their mechanisms of invasion but also a look at the impacts they have on local community structure. The goal of my research was to determine if *S. halepense* acts as a "driver" of community change and decreases the soil nitrogen availability in a native tallgrass prairie and in doing so facilitates the invasion of a "passenger" *P. glandulosa.*

1.6 Study objectives

Two objectives structured my thesis research. My first objective was to determine if *S. halepense* was altering the biotic and abiotic structure of a native prairie community. The abiotic resources I examined in the field included light levels, soil C, soil N and soil gravimetric moisture in invaded (dominated by *S. halepense*) and native (dominated by *S. scoparium*) prairie zones. Plant community composition, litter and standing dead heights were examined in both of these zones to determine the biotic structure. I measured a similar set of variables in a greenhouse experiment in which I established pots without grasses, with *S. halepense*, or with *S. scoparium* in two soil types: invaded and native. The annual dieback of *S. halepense* along with its ability to create a monoculture and produce a cyanide compound, led me to four distinct predictions for areas dominated by *S. halepense* when compared with native prairie without this species: A) Light levels in the invaded zone would be greater due to *S. halepense's* annual dieback and predicted lower litter and standing dead heights compared to *S. scoparium*, B) Soil N is lower and total C higher in the invaded zone soil compared to the native zone soil, C) less gravimetric moisture is present in the invaded zone soil relative to the native zone, and D) the invaded zone has a less diverse plant community, comprised of different plant species compared to the native zone.

Assuming that *S. halepense* is in fact altering the abiotic resources of the community, the second objective in my research was to determine if *S. halepense* facilitates the invasion of *P. glandulosa*. In the field, *P. glandulosa* seeds were planted in plots in which effects of both litter and invasive vs. native plant competition were manipulated. In the greenhouse, *P. glandulosa* seeds were planted in pots with one of two soil types, native and invaded, and with three levels of competition: *S. halepense, S. scoparium*, and no competition. I predicted that if *S. halepense* was decreasing soil N, it was creating a niche for *P. glandulosa*, a known N-fixer. Thus *P. glandulosa* would be a better competitor in the invaded zone soil when planted with *S. halepense* compared to competing with *S. scoparium* in native zone soil in both the field and greenhouse.

CHAPTER 2

METHODS

2.1 Study site field studies

The Fort Worth Nature Center and Refuge (FWNC&R) (Latitude: 32˚ 49' N; Longitude: 97˚ 21' W) is an ecotone where remnant Fort Worth and Blackland Prairies and the Eastern and Western Crosstimbers converge in Northwest Tarrant County, Texas. The 12 hectare study site was within FWNC&R and consisted of both remnant and invaded prairie/savannah. The gently sloping prairie was also surrounded by an encroaching tree-line comprised of trees typical of the Western cross timbers.

The Fort Worth Prairie has a thin layer of calcareous, alkaline clay soil with an underlying layer of soft limestone rock (Dyksterhus 1946), while the soil of the Western Cross Timbers can be described as mildly acidic, reddish, sandy, clay soil layered over sandstone bedrock (Dyksterhus 1948, Fort Worth Parks and Community Services Dept. 2002). The vegetation in the study site may be considered as three distinct zones: a native zone dominated by *Schizachyrium scoparium* (little bluestem), an invaded zone of *S. halepense,* and a transition or mixed species zone where *S. halepense, S. scoparium,* and *Sorghastrum nutans* (Indian grass) coexist. Other common native grass species in the prairie include *Bouteloua curtipendula* (sideoats grama), *Sporobolus compositus* (tall dropseed), *Bouteloua hirsuta* (hairy grama), and

Andropogon gerardii (big bluestem). Interspersed in the prairie are many woody species including *Prosopis, Diospyros texana, Symphoricarpos orbiculatus* (coral berry), *Ulmus crassifol* (cedar elm), and *Celtis laevigata* (hackberry). The last three are species native to the Western Cross Timbers.

The eastern side of the study site is bordered by Lake Worth and the western side is bordered by pavement. Currently, a walking trail divides the area approximately in half. Previously, however, the study site was divided into northern and southern sections by a fence that was removed approximately twenty years ago. The fence likely kept livestock and forage crops in the northern half while the southern portion remained native prairie (Rout 2005). Different land management practices have been applied to this field in the past decade, including mowing and haying, and the field was burned in 2000.

2.2 Field studies experimental design

2.2.1 Competition experiment

A competition experiment was established to examine the ability of *P. glandulosa* to invade the three prairie zones: native, invaded and mixed. This experiment had a 2x2x3 factorial design with two missing cells. The design had two levels of litter manipulation (+: ambient, -: removed), two levels of competition (+: ambient, -: removed), and three different zones (invaded, native, and mixed) (Table 2.1). In April of 2005, two 40 meter transects were established in each zone and 50 0.25 m^2 plots, spaced 3-12 m apart, were erected along each transect. Manipulations were randomly assigned within transects. The (-) litter removal manipulation was implemented (n=10 in native and invaded zones, n=5 in the mixed zone) by first measuring the height of the litter and the standing dead biomass and then removing all of the ground litter and a majority of the standing dead in each plot. Litter removal was conducted April 14 and 16, 2005 (Julian day 104 and 105), and was maintained throughout the course of the experiment. Litter and standing dead height were also measured in the ambient (+) litter plots (n=10 native and invaded zones, n=5 mixed zone). These plots were established by leaving all ground litter and standing dead intact. Additionally, 10 plots in the native zone and 10 in the invaded zone were randomly selected to become no (-) competition plots. Within the (-) competition plots, both the aboveground and belowground competition was inhibited by tying back all aboveground plant biomass and inserting 15cm (diameter) x 20 cm (height) PVC root excluders (Fig 2.1)(Van Auken and Bush 1997). Prior to the start of the experiment all living roots and rhizomes were removed from within the root excluders.

Table 2.1: Factorial design and number of replicates for the field experiment.

Treatment	**Competition**	+	+	-	-
	Litter	+	-	+	-
Zone	**Invaded**	5	5	5	5
	Native	5	5	5	5
	Mixed	5	5	0	0

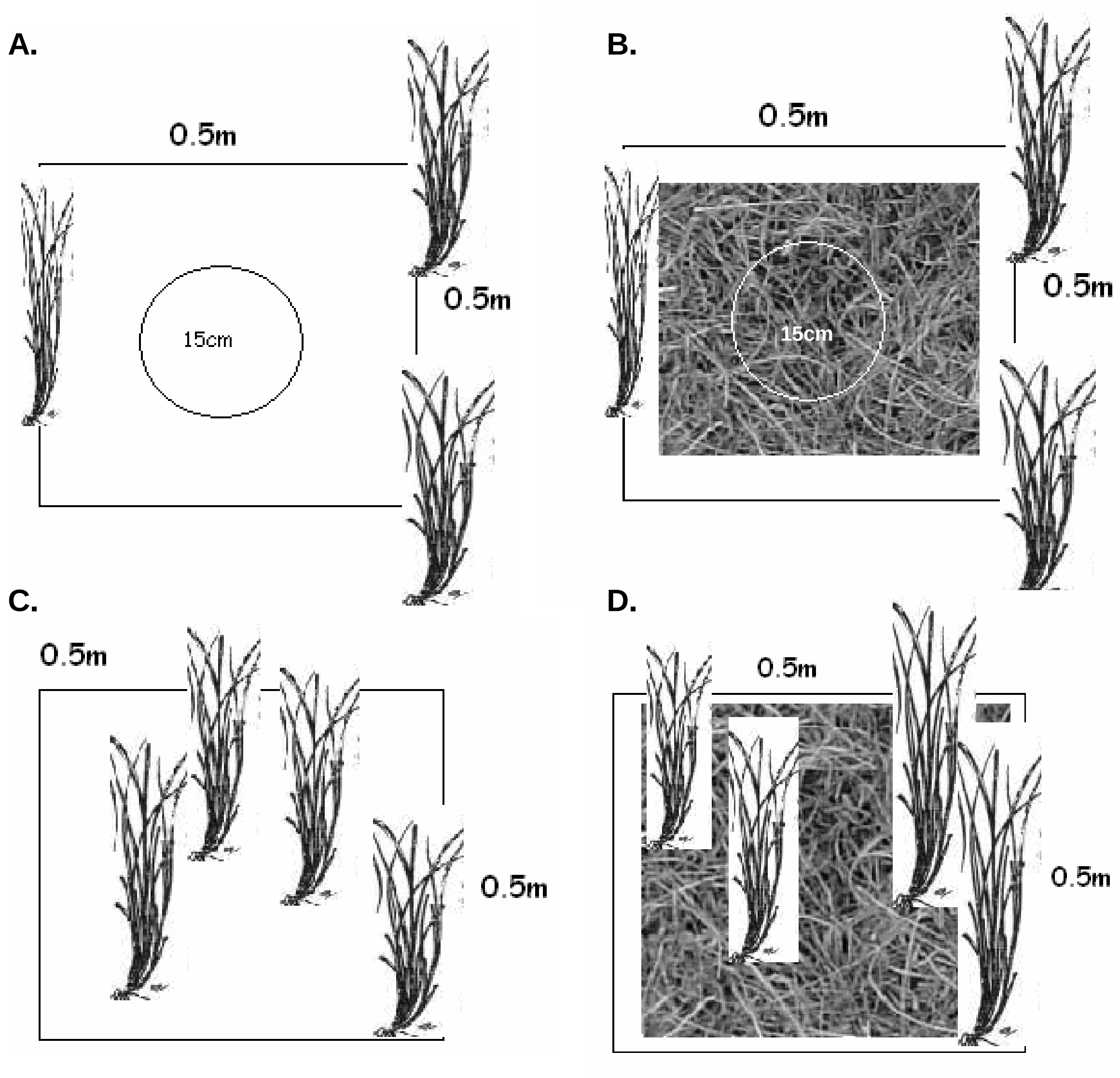

Fig 2.1: Example of field plots. A. – competition, - litter plot with 15 cm root excluder, B. – competition, + litter plot with 15 cm root excluder (A&B were established in the native & invaded areas only), C. + competition, - litter plot, D. + competition, + litter plot (C&D were in all three vegetation zones).

P. glandulosa seeds, purchased from a local nursery, were mechanically scarified by clipping the seed coat, and three seeds were planted in each plot on April 24, 2005. The number of seeds germinated and seedling survivability were recorded on days 6, 9, 12, 15, and 21. On day 33, seedlings were thinned and transplanted (if needed) to one per plot. Extra seedlings were relocated within zone (if possible) to plots that had no seeds geminate or severe mortality of all seedlings. Height of seedlings was measured weekly from the cotyledons or cotyledon scars to the tip of the tallest true leaves. Within each (+) competition plot, 6 grass ramets or tillers closest to the seedling were tagged and monitored weekly for growth starting 40 or 42 days after the litter manipulations were applied. In some cases, in the mixed zone plots, ramets/tillers were not located near the seedling because they were the only plant of the required species in that plot. Grass species tagged were dependant on the zone: 6 *S. halepense* ramets in the invaded zone, 6 *S. scoparium* tillers in the native zone, and 2 *S. halepense* ramets, *2 S. scoparium* tillers and 2 *S. nutans* tillers in the mixed zone .

The presence and type (insect or mammal) of herbivory on *P. glandulosa* seedlings and all tagged grass tillers were monitored in all plots, on each sample date. Herbivory was coded by severity; 0 = no herbivory, 1 = slight herbivory (top leaves of seedling or top of grass leaves or inflorescence removed), 2 = severe herbivory (majority of leaves or inflorescence removed but not detrimental), 3= severe herbivory resulting in the death of the seedling, ramet or tiller.

Light (Li-COR LI-250) measurements were taken midmorning to determine differences in light availability among treatments. Light measurements were taken in all plots at the base of the *P. glandulosa* seedling once a week, midmorning, for 10 weeks. In (+) litter treatment, the meter was placed beneath the litter to determine light effects on seedling emergence. This measurement was taken once a week, midmorning, for the first four weeks prior to transplanting.

2.2.2 Community structure

The effect of altering litter and the introduction of *P. glandulosa* were examined over the period of one year in each zone. Aerial percent cover of all plant species was recorded in all plots prior to the beginning of the (-) competition treatment and subsequently in all plots except for the (-) competition treatment plots in April, June and September 2005, and April 2006. In all cases species abundance was recorded to the nearest percent using a 0.25 m^2 quadrat. The majority of plant species were taxonomically identified to species level. Species diversity was calculated using the Shannon-Weiner diversity index (Gotelli and Ellison 2004):

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

Where;

H’ = Shannon's diversity index

S = total number of species in the community (richness)

p_i = proportion of total abundance made up by the ith species

2.2.3 Soil gravimetric moisture, C, and N

Several soil abiotic resources in the native, invaded, and mixed zones were determined. Coring tubes (2.5 cm in diameter and 20 cm long) were fabricated from PVC pipe. Extremely dry conditions made it impossible to core the hard soils during most of the study, consequently soil cores were collected the day after rain events. On July 8, 2005 and July 28, 2005, 30 soil cores were taken near all ten mixed zone plots and ten plots randomly selected in the invaded and the native zones each. The litter layer was removed and discarded, and the coring tube was pushed into the ground to 30 cm in depth and removed with soil intact. The soil was pushed out of the coring tube in the field, separated by depth (0-15 cm,15-30 cm), placed into a labeled, sterilized soil bag, and transported on ice back to the lab for immediate gravimetric soil moisture analysis.

Prior to being frozen (-10˚) approximately 20 – 25 g of soil was aseptically removed from each core, weighed, and placed in open soil tins. Soils were dried at 60˚C and repeatedly weighed until weight remained constant. Gravimetric moisture was calculated as equal to (g of moist soil – g of dry soil)/g of dry soil.

Frozen soil cores were thawed in February of 2006 and prepared for total C and N analysis by dry combustion. Each core was dried for 48 hours in a clean, sterilized soil tin, lightly ground with a mortar and pestle, and all plant and animal material was removed from the soil. Soil was then homogenized by grinding until it could pass through a 500 μm screen. C and N analysis was performed on cores removed on July 8, 2005 to further investigate differences in the soils; analysis was only performed on the 0 to 15 cm depth. Five replicates of 2 to 5 g samples were analyzed from each soil core for C and N content using a Perkin-Elmer CHN analyzer (Series 2400).

2.3 Greenhouse studies experimental design

2.3.1 Soil preparation

Soil for the greenhouse experiment was collected from the FWNC&R over a period of 10 months from April 2005 through December 2005. Soil from both the invaded zone and a native prairie near the study site was collected and brought back to the lab for processing. All soil was air dried overnight in a thin layer at room temperature. Soil was homogenized by removing all large rocks (>5cm), plant material, and debris.

2.3.2 Competition experiment

Dormant *S. scoparium* plants and *S. halepense* rhizomes were harvested from the study site in January, 2006, maintained in the greenhouse in the soil in which they were collected, and subsequently divided into smaller plants in February, 2006. All *S. scoparium* rhizomes were divided into 70 similar sized clumps with standing dead from the previous growing season left intact. Thirty-five *S. scoparium* plants were placed in 5 cm pots containing invaded zone soil, and 35 plants were placed in the same size pots containing native zone soil. Seventy similar sized *S. halepense* rhizomes were also divided and placed in 5 cm diameter pots: 35 rhizomes in the invaded soil and 35 in the native soil. All plants were allowed to acclimate in the greenhouse for a period of two weeks in February 2006.

This experiment also had a 2x3 factorial design with 2 levels of soil type (native and invaded) and 3 levels of competition (no competition, *S. scoparium* competition, and *S. halepense* competition (Table 2.2)). Eight replicates of each combination of competition and soil type were assembled. Pots with no competition were initially just filled with soil. For pots with *S. halepense* competition, three *S. halepense* plants were transplanted from the small 5 cm pots into the larger pots and placed in a 7 cm triangle in the new pots. *S. scoparium* competition pots were assembled the same as *S. halepense* but using previously planted *S. scoparium* instead. Grass species were allowed to acclimate to the larger pots for one week. All pots were watered once a week with DI water until saturated until the maximum temperature in the greenhouse rose above 32˚ C at which point pots were watered twice a week.

Table 2.2: Factorial design and number of replicates for the greenhouse competition experiment.

Treatment	Competition	No competition	*S. scoparium* competition	*S. halepense* competition
Soil Zone	Invaded	8	8	8
	Native	8	8	8

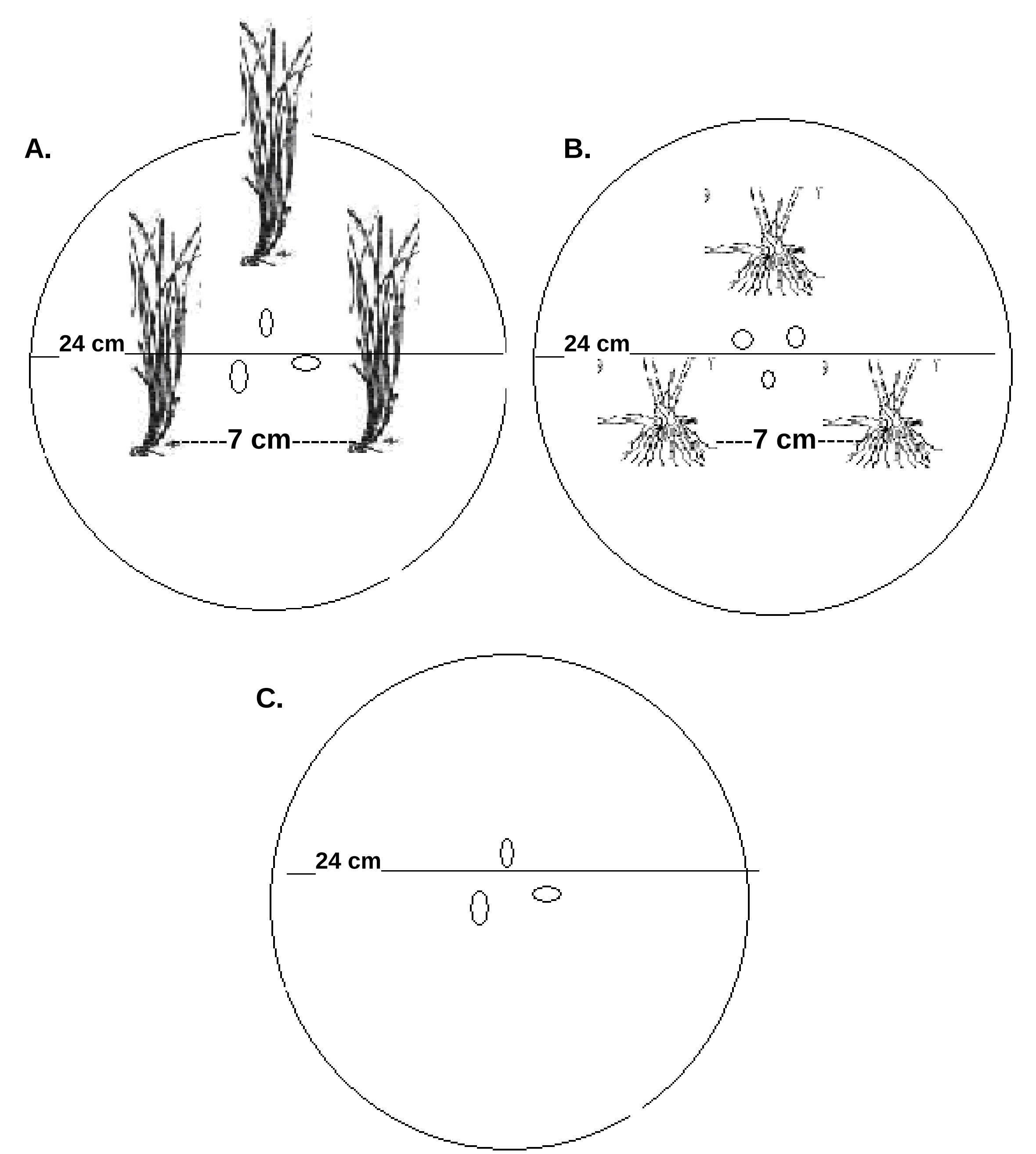

Fig 2.2: Example of greenhouse pots. A. competition with *S. scoparium*, B. competition with *S. halepense* C. no competition. All combinations of soil type (native & invaded) and competition were assembled (n = 8).

On March 8, 2006 three mechanically scarified *P. glandulosa* seeds were planted in the center of each pot 5 cm apart. All *P. glandulosa* seedlings were allowed to grow for 21 days after which seedlings were thinned to one per pot. Initial germination rate and survivability of the seedlings were determined. After thinning, weekly height from the point of cotyledonary attachment to the tip of the tallest true leaves was measured. An average tiller/ramet count per plant per pot along with average tiller/ramet height per pot and overall number of inflorescences per pot were also measured weekly for *S. halepense* and *S. scoparium*

Light levels were measured weekly within each pot both at the base of the seedling and above the grass or standing dead biomass. Pots were individually moved to a single location for light measurement. Light levels were always collected between 1200 and 1400 Central Standard Time.

After 10 weeks, *P. glandulosa* seedlings were harvested from pots. Final aboveground height measurements were taken from the cotyledon scars to the tip of the tallest true leaves and a belowground length measurement was taken from the cotyledon scars to the bottom of the longest lateral root. Roots were inspected for the presence of nodules, and all nodules were counted. Above and belowground biomass was separated after all measurements were taken and dried at 60˚C for seven days and then weighed.

2.3.3 Soil C and N

Before harvesting, soil samples were extracted from each pot. Two 1 cm cores were taken near the rhizosphere of the seedling, and two 1 cm cores were sampled towards the outside of the pot away from the seedling. Similar soil cores were homogenized within each pot and then dried at 60˚ C for 72 hours in a clean, sterilized soil tin. After drying, soil was lightly ground with a mortar and pestle and all plant and animal material was extracted from the soil. Each sample was then homogenized by grinding until it could pass through a 500 µm mesh screen. Five replicates of 2 to 5 g samples were analyzed from each pair of soil cores within each pot (1 rhizosphere sample and 1 away from rhizosphere sample) for CHN content using a Perkin-Elmer CHN analyzer (Series 2400).

2.4 Statistical analysis

2.4.1 Field statistical analysis

A one-way ANOVA with three levels of zone was used to analyze litter and standing dead differences at the start of the experiment. Analysis of light, *P. glandulosa* germination and growth data required two separate factorial ANOVA's due to missing cells (Table 2.1): 1) 3-way ANOVA with zone (invaded, native), competition (+,-), and litter (+,-), and 2) 2-way ANOVA with zone (invaded, mixed, native) and litter (+,-) for plots with competition only. The same approach (2) was used to analyze gravimetric moisture, grass growth, diversity, and evenness. When appropriate, repeated measures were utilized. Soil C and N data were analyzed with an additional nested component of replicate nested within core. Cumulative logic analysis, using generalized estimating equations, was employed to determine the effects of zone, competition, and week on herbivory (Fahrmeier and Tutz 1994).

2.4.2 Greenhouse statistical analysis

A complete two-by-three factorial design with main effects of soil type and competition was used to analyze germination, growth, biomass, light, and tiller/ramet and inflorescence data collected from the greenhouse experiment. When appropriate, repeated measures were utilized. A Poisson regression was required for the *Rhizobium* nodule count data. C and N were further analyzed using a nested design with replicate nested within pot.

2.4.3 Common statistical approaches

Post hoc means comparisons were conducted using Tukey's HSD. Unless otherwise noted, an α value of 0.05 was used to determine significant differences. Data were transformed as appropriate to meet model assumptions. Normality and homogeneity of variances were examined using Shapiro-Wilks'-test, normality plots, and residual plots. All statistical analyses were conducted using SAS (Version 9.1, SAS Institute, Cary, NC).

CHAPTER 3

RESULTS

The results are organized into two sections: field results and greenhouse results. Within the field results, I first present results describing the environmental conditions followed by the biological conditions and plant growth data. The greenhouse results begin with an examination of the light data, followed by plant growth and biomass, and end with effects of the treatments on the soil environment.

3.1 Field results

3.1.1 Environmental conditions

3.1.1.1 Litter and light levels

Mean litter height (Fig. 3.1) was initially significantly higher in the mixed and invaded zones than in the native zone (main effect of zone: $F_{3, 46} = 12.00$, $P < 0.0001$). In contrast, the standing dead biomass of the native plants (Fig.3.1), found in both the native and mixed zones, was significantly taller than that of invaded zone plants ($F_{3,46} = 51.85$, $P < 0.0001$).

Light levels were low when litter was left intact at all levels of competition and in all zones but were greater in the native zone plots without competition (Fig. 3.2) (significant zone*competition interaction, Table 3.1A). Light was generally higher in the native zone (significant zone effect) and in plots without competition (significant competition effect). Litter treatment did not significantly affect light levels. Many of these effects differed over the course of the season, leading to significant interactions with sampling day (Table 3.1A). Similarly, when all three zones were examined, light availability differed with the greatest light available in the native zone (Fig. 3.2, Table 3.1B).

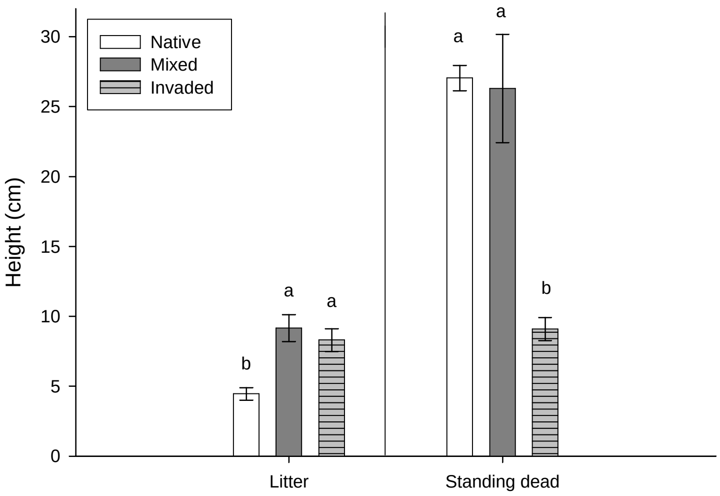

Fig 3.1: Mean litter and mean standing dead height in each vegetation zone May 2005. In all plots all zones in May 2005 prior to litter manipulation. Bars represent the mean and one standard error. Different lowercase letters indicate significant differences among zones. Means comparisons based on Tukey's HSD (Mixed n = 10, Native and Invaded n = 20).

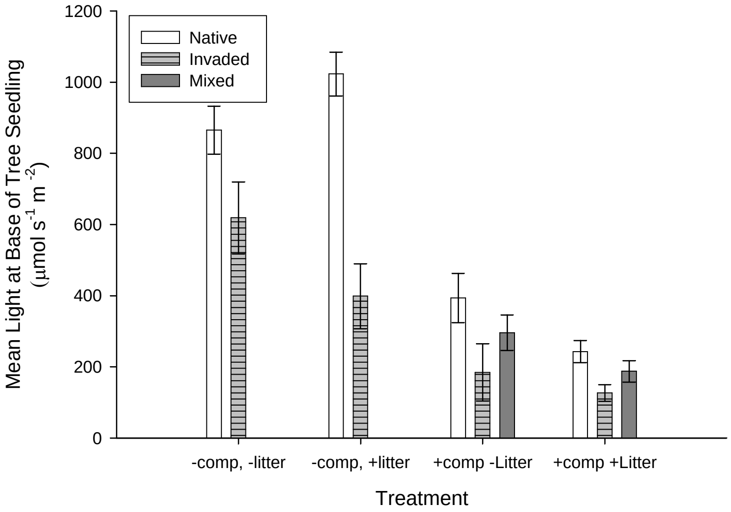

Fig 3.2: Mean light measurements taken at the base of each seedling, averaged over 9 weeks. Bars represent mean and one standard error.

Table 3.1: Repeated Measures MANOVA Light measured at the base of *P. glandulosa* seedlings. A. 3-way MANOVA invaded vs. native zone, competition and litter; B. 2-way MANOVA three zones, litter Significant P-values are in bold italics.

A) Invaded vs. Native: **Competition and Litter** Source of variation	df	MS/Wilks' Lambda	F	P
A1) Between-subjects				
Transect	1	3069.67	0.02	0.89
Litter	1	159263.14	1.00	0.32
Zone	1	6868025.29	43.15	***<.0001***
Zone*Litter	1	338615.82	2.13	0.15
Comp	1	20227128.78	127.09	***<.0001***
Litter*Comp	1	85733.86	0.54	0.47
Zone*Comp	1	934124.69	5.87	***0.02***
Litter*Zone*Comp	1	342008.53	2.15	0.15
Error	31			
A2) Within-subjects				
Day	8,24	0.24602260	9.19	***<.0001***
Day*transect	8,24	0.67092043	1.47	0.22
Day*litter	8,24	0.50323674	2.96	***0.02***
Day*zone	8,24	0.11528193	23.02	***<.0001***
Day*zone*litter	8,24	0.78526656	0.82	0.59
Day*comp	8,24	0.53136036	2.65	***0.03***
Day*comp*litter	8,24	0.81359958	0.69	0.70
Day*zone*comp	8,24	0.33250924	6.02	***0.0003***
Day*litter*zone*comp	8,24	0.49683900	3.04	***0.02***
B) All Zones: **Litter** Source of variation	df	MS/Wilks' Lambda	F	P
B1) Between-subjects				
Transect	1	10112.951	0.05	0.82
Litter	1	415965.981	2.17	0.15
Zone	2	670084.513	3.49	***0.05***
Zone*litter	2	1674.269	0.01	0.99
Error	23			
B2) Within-subjects				
Day	8,16	0.28876505	4.93	***0.003***
Day*transect	8,16	0.63036303	1.17	0.37
Day*litter	8,16	0.62274836	1.21	0.35
Day*zone	16,32	0.29606296	1.68	0.10
Day*zone*litter	8,16	0.45154505	0.98	0.50

3.1.1.2 Soil moisture and nutrient levels

Soils in the native zone were hard, making core removal more difficult compared to soils of the invaded zone. The light sand-colored native soil appeared to contain a significant amount of gravel, while the soil in the invaded zone seemed to have almost no gravel and was a dark rich color. The mixed zone soil's color and texture varied but was similar overall to the native zone soil (personal observation).

Invaded zone soils contained almost 30% more total N then the native zone soil and almost twice as much as the mixed zone (main effect of zone: $F_{2,73}$= 9.16, P=0.0003; Fig. 3.3A). Total C was significantly lower in the invaded zone than either the mixed or native zones (main effect of zone: $F_{2,78}$=7.67, P=0.0009; Fig 3.3B). The C:N molar ratio was significantly lower in the invaded zone than either the native or mixed zones (Fig 3.3C main effect of zone: $F_{2,73}$= 28.62, P <0.0001).

Soils from the invaded zone had significantly higher moisture content when compared to those of the native zone (Fig 3.4; main effect of zone: $F_{7,112}$ = 3.40, P = 0.04). In all zones, moisture content was significantly higher closer to the surface (0-15 cm) compared to deeper (15-30 cm) soil ($F_{7,112}$ = 34.35; P <0.0001). Gravimetric moisture was higher in soils collected on July 28, 2006 than soils collected July, 8 2006 (main effect of day: $F_{7,112}$ = 11.79, P = 0.0008).

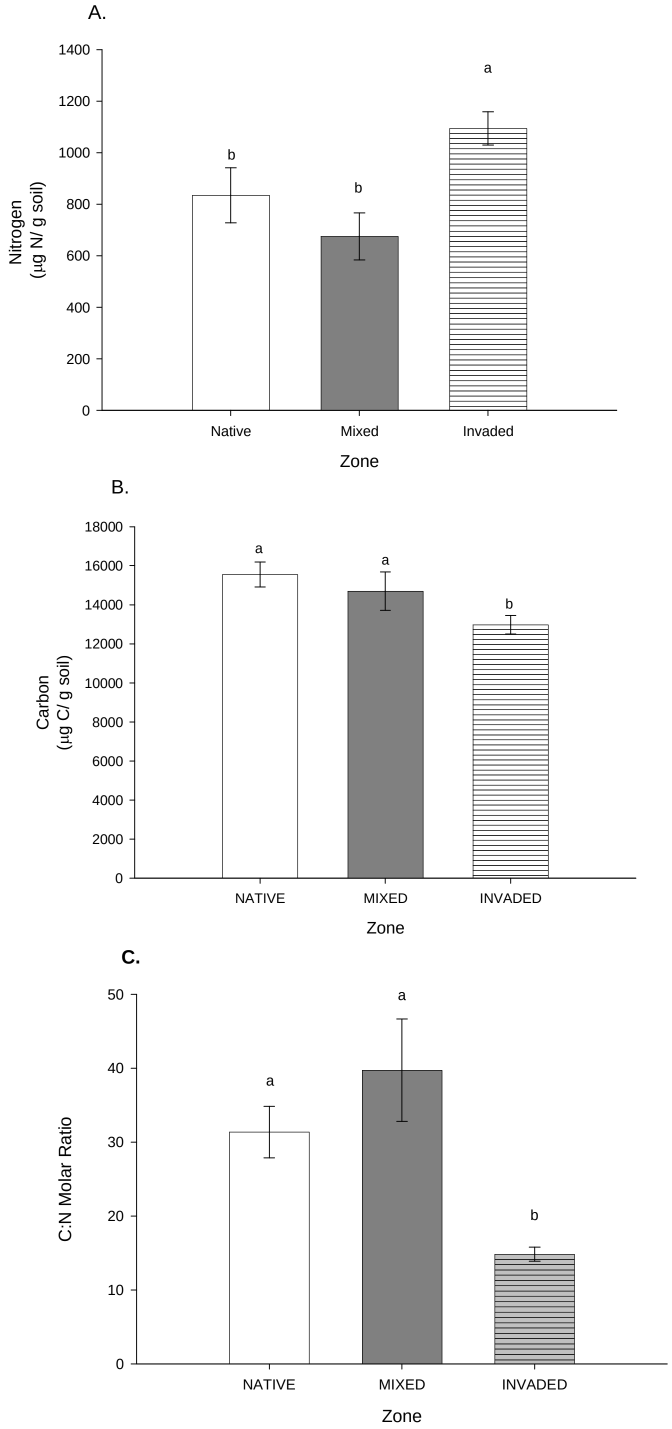

Fig 3.3: Mean soil nutrients. A) total N B) total C and C)C:N molar ratio. All cores sampled on 8 – July -2005 in all three prairie zones Bars represent the mean and standard error. Different lowercase letters refer to significant differences among zones. Means comparisons based on Tukey's HSD (n = 10).

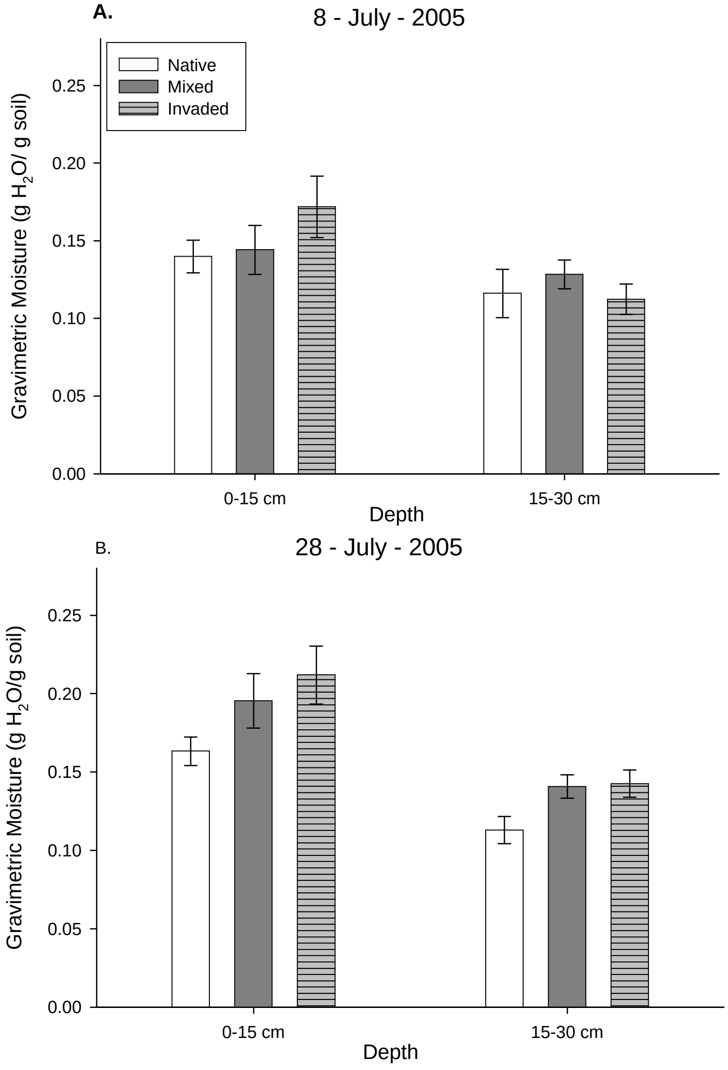

Fig 3.4: Mean gravimetric moisture at two separate depths, in all three zones. A. 8-July-2005, B. 28-July-2006.

3.1.2 Community species composition

3.1.2.1 Species diversity and richness

S. scoparium dominated most of the native prairie zone throughout the growing season (Table 3.2). *S. scoparium* and *S. nutans* were equally abundant in the mixed zone and more frequent than *S. halepense*. In early spring another exotic, invasive grass species, *Bromus japonicus*, contributed equally to the percent plant cover of the invaded zone. During the summer, however, *S. halepense* dominated plots in the invaded zone.

Plant species diversity, as calculated by the Shannon-Weiner index (H'), was consistently higher in both the mixed and invaded zones then in the native zone (Fig. 3.5: main effect of zone: $F_{2, 23}$= 39.56, P <0.0001). Litter manipulation did not affect diversity. Mean species richness was also highest in the invaded zone, (+)litter) manipulation and lowest in the native zone, (-)Litter manipulation (Table 3.3)

Much of the increased diversity in the invaded and mixed zones can be explained by the contribution (percent) of woody species to H' (the ratio of H' woody species: H' overall where manipulated additions of trees were excluded) (Fig 3.6). Litter removal decreased woody species H' in the mixed zone and increased the woody H' in the invaded zone (significant litter*zone interaction: $F_{2, 23}$= 10.92, P = 0.0005). Native zone plots had the lowest percentage of woody species: no woody species were found in native (+ litter) plots (Fig. 3.6). As with overall species diversity, woody species contributed the most to diversity in the invaded zone compared to the native zone (main effect of zone: $F_{2, 23}$= 16.92, P <0.0001).

Table 3.2: Mean (±1 S.E.) contribution (%) of dominant grasses to total plant cover in each zone. Spring season data were taken from data samples collected in April (2005 & 2006), while summer season was June and September (2005) (n=5).

	Native Zone		Mixed Zone		Invaded Zone	
Dominant Grasses	Spring	Summer	Spring	Summer	Spring	Summer
S. Scoparium	41±3	50±2	14±2	29±3	4±2	4±3
S. nutans			10±2	18±3	2±1	1±1
S. halepense			4±2	6±2	23±4	32±2
B. japonicus		0.2±0.1	3±1	6±2	20±4	5±2

Table 3.3: Mean (±1 S.E.) species richness in each vegetation zone over a 13 month period (n=5).

Zone/treatment	Native	Mixed	Invaded
Litter	4.4±0.4	6.7±0.5	5.4±0.8
No Litter	3.8±0.6	5.7±0.3	7.4±1.2

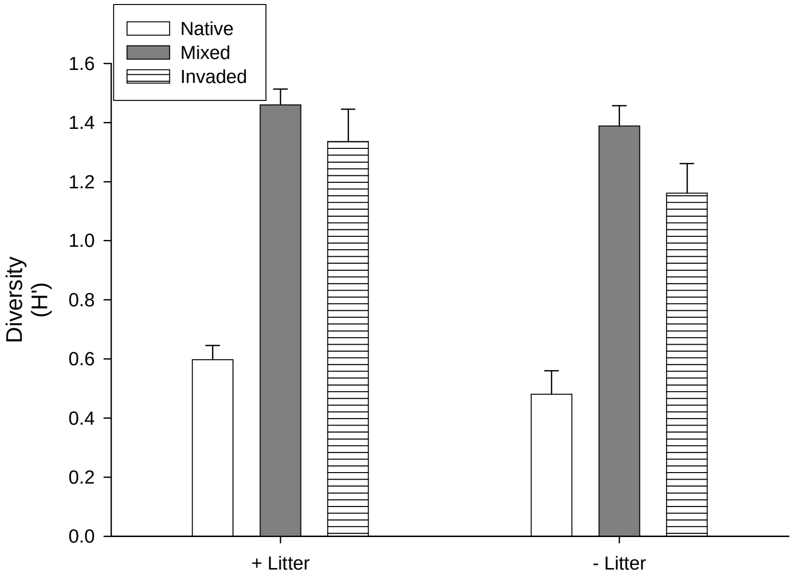

Fig 3.5: Mean diversity (H') of all plant species averaged over 13 months in all three zones. Plots with competition only (n=5). Data points represent means and bars one standard error.

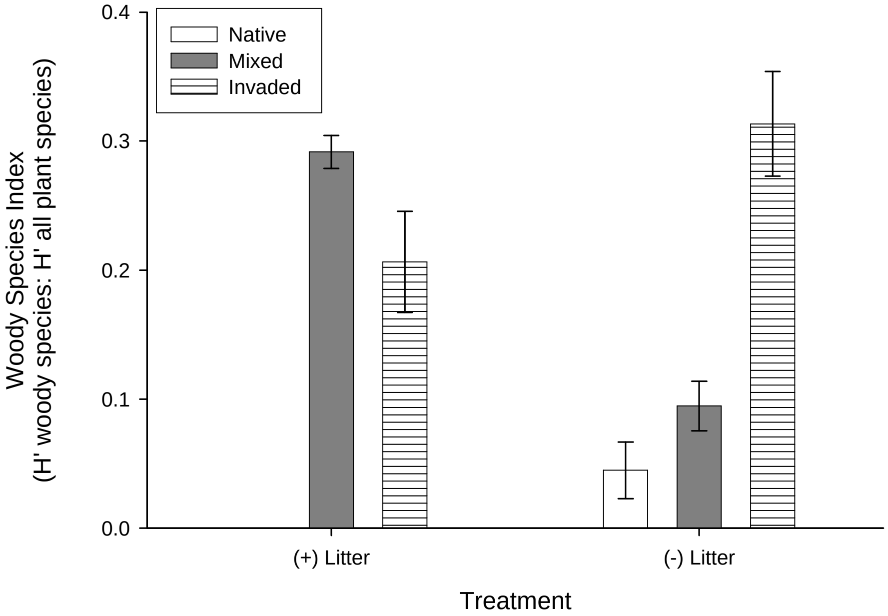

Fig 3.6: Mean diversity due to woody species over 13 months in all three zones. Plots with competition only (n=5). Calculated as the ratio of Shannon-Weiner index due to woody species: Overall Shannon-Weiner diversity index per plot. Data points represent means and bars represent one standard error.

3.1.3 Growth and germination of observed species

3.1.3.1 Grass growth

All three dominant grasses, *S. scoparium, S. nutans,* and *S. halepense*, exhibited a change in height over the course of the study (measured in the +competition plots) (Table 3.4AandB). Since there were no significant litter effects on the growth of *S. nutans,* it was not included in the ANOVA table; the mean height of *S. nutans* after 12 weeks of growth was 48.6 ±5.0 cm, and growth of this grass was unaffected by litter manipulation. Removing litter had a negative effect on *S. scoparium* height in the mixed zone and in the native zone, however, the impact was greater in the mixed zone (Fig 3.7; significant zone by litter interaction: Table 3.4A). Along with an overall, inhibitory effect of litter removal on the height of *S. scoparium* (main effect of litter: Table 3.4A), plants were taller in the mixed zone (main effect of zone). The height of *S. scoparium* tended to decrease over time, particularly in the native zone (Fig. 3.7). *S. scoparium* in the mixed zone, however, appeared to increase in height during the last two weeks regardless of litter manipulation (Fig 3.7)

Height of *S. halepense* slightly increased over time in all zones and treatments except the mixed zone litter removal treatment (Fig 3.8). A marginal interaction between zone and litter indicated *S. halepense* was taller in the mixed zone plots where the ambient litter was left in place (Fig 3.8, Table 3.4B1). The height of *S. halepense* varied over time (significant week effect: Table 3.8B2).

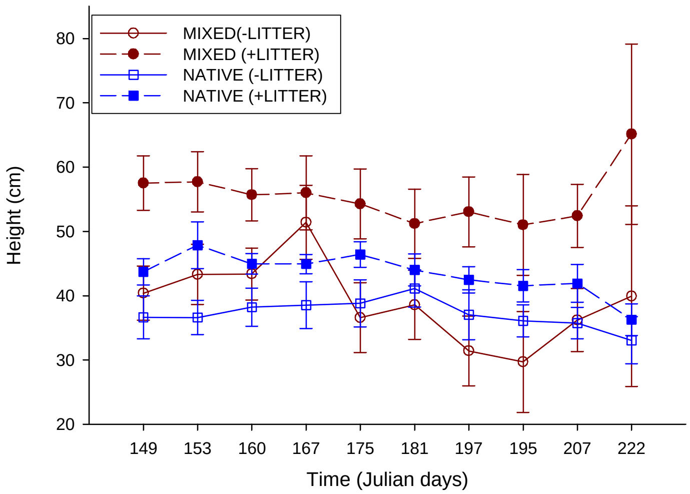

Fig 3.7: *S. scoparium* mean height over 12 weeks. Plots with (+) competition, both litter treatments (+ and -) in the native and mixed zones (n=5). Data points represent means and bars represent one standard error.

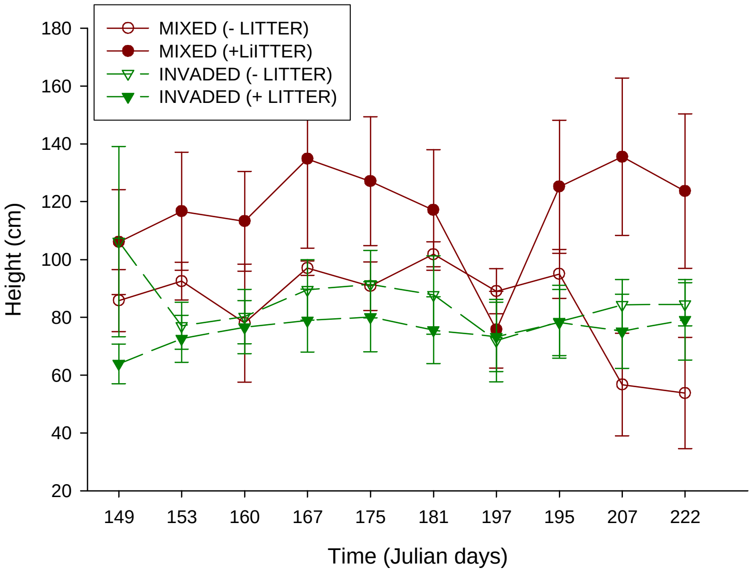

Fig 3.8: Mean *S. halepense* height over 12 weeks. Plots with (+) competition , both litter treatments (+ and -) in the native and invaded zones(n=5) Data points represent means and bars represent one standard error.

Table 3.4: Multivariate repeated measures ANOVA for height of *S. scoparium* and *S. halepense* A. Height of *S. scoparium* ramets tagged in the mixed and invaded prairie zones. Significant P-values are in bold italics. B.Height of *S. halepense* tillers tagged in the mixed and native zones. Significant P-values are in bold italics.

LBS growth				
Source of variation	df	MS/Wilks' Lambda	F	P
A1) Between-subjects				
Zone	1	7789.62668	12.41	***0.0008***
Transect(zone)	2	991.58587	1.58	0.21
Litter	1	15802.36859	25.18	***<.0001***
Zone*Litter	1	4366.56725	6.96	***0.01***
Error	63	627.45388		
A2) Within-subjects				
Week	9,55	0.53585690	5.59	***<.0001***
Week*zone	9,55	0.72288305	2.34	***0.03***
Week*transect(zone)	18,110	0.47575901	2.75	***0.0006***
Week*litter	9.55	0.77767797	1.75	0.10
Week*zone*litter	9,55	0.67423363	2.95	***0.006***
JG growth				
Source of variation	df	MS/Wilks' Lambda	F	P
B1) Between-subjects				
Zone	1	13347.7890	1.83	0.18
Transect(Zone)	1	31752.7617	4.35	***0.04***
Litter	1	23778.1794	3.26	0.08
Zone*Litter	1	7301.7073	2.80	0.10
Error	45	7301.7073		
B2) Within-subjects				
Week	9,37	0.28975903	10.08	***<.0001***
Week*zone	9,37	0.76119851	1.29	0.27
Week*transect(zone)	9,37	0.85914960	0.67	0.73
Week*litter	9,37	0.61370248	2.59	***0.02***
Week*zone*litter	9,37	0.63898772	2.32	***0.03***

3.1.3.2 P. glandulosa

3.1.3.2.1 Germination of P. glandulosa

P. glandulosa seedlings emerged faster in the invaded and mixed zones than in the native zone (data not shown). Some *P. glandulosa* seeds successfully germinated in each of the three zones (Fig. 3.9). Germination in invaded plots was significantly lower when litter was present. In native and mixed plots litter manipulation had no effect on germination (zone by litter interaction and main effect of litter; Table 3.9). Competition had no effect on germination success.

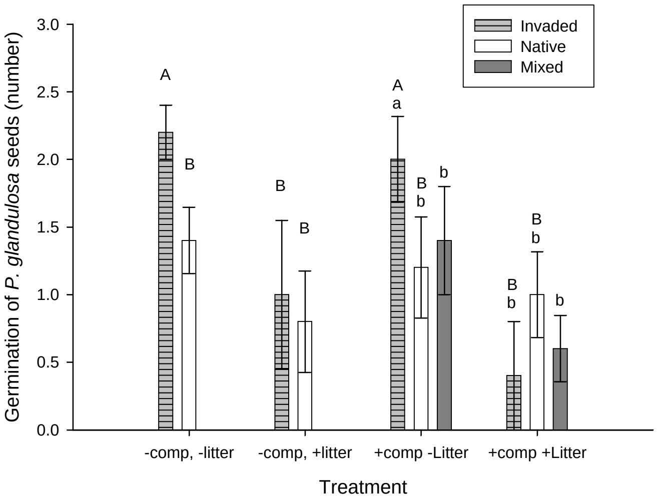

Fig 3.9: Number of *P. glandulosa* seeds that germinated in plots in all three zones. Averages calculated from data collected 15 days after sowing or date of maximum germination. Bars represent the mean and one standard error. Different uppercase and lowercased letters refer to significant differences among zones from 3-way ANOVA of the Native vs. Invaded (n=5) and 2-way ANOVA all three zones (n=5), respectively. . Means comparisons based on Tukey's HSD.

Table 3.5: ANOVA for germination of *P. glandulosa* seeds in the field. A. 3-way germination of seeds planted in the native and invaded prairie zones, all levels of competition and litter. B. 2-way ANOVA for seeds planted in all three prairie zones all levels of litter. Significant P-values are in bold italics.

Source of variation	df	MS	F	P
A) 3- way ANOVA **Invaded vs. Native** **Competition and Litter**				
Transect	1	0.066622	0.28	0.60
Comp	1	0.314157	1.49	0.23
Zone	1	0.072824	0.31	0.58
Litter	1	2.774745	11.78	***0.002***
Comp*Zone	1	0.259522	1.10	0.30
Comp*Litter	1	0.000116	0.00	0.98
Zone*Litter	1	1.067711	4.53	***0.04***
Comp*Zone*Litter	1	0.678775	2.88	0.10
B) 2-way ANOVA **All Zones Litter**				
Transect	1	0.066581	0.22	0.64
Zone	2	0.039020	0.13	0.88
Litter	1	1.819864	6.02	***0.02***
Zone*Litter	2	0.917512	3.04	*0.07*

3.1.3.2.2 Growth of P. glandulosa

P. glandulosa seedlings grew significantly taller in the native zone when competition with neighbors was inhibited compared to growth in all other combinations of zones and treatments (Fig 3.10; significant competition by zone interaction: Table 3.6A1). Since there was no effect of litter on seedling height, means were pooled across litter treatments for presentation (Fig 3.11). An overall zone effect indicated that seedlings grew taller in the native zone (Table 3.6A1). Seedlings in the native zone, (-) competition plots, suffered the least mortality and grew taller than seedlings in native zone (+) competition plots (competition*zone interaction, Fig 3.11). The low average height of seedlings in the invaded zone was due to a spike in seedling mortality caused by herbivore activity within that zone during the 2nd and 3rd weeks of study (Fig 3.11).

In native and mixed plots with competition and ambient litter (+comp,-litter), mean *P. glandulosa* height decreased over time (Fig. 3.12A). When both neighbors and litter were present (+comp, +litter) seedlings were shorter over time in the native and invaded zones but slightly taller in the mixed zone (Fig3.12B). The change in *P. glandulosa's* height over time was statistically significant (Table 3.6 B2)

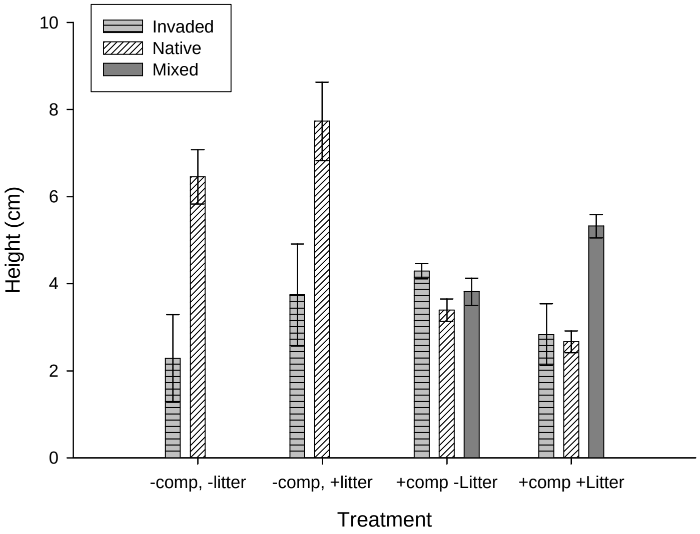

Fig 3.10: *P. glandulosa* height averaged over 12 weeks. Bars represent means and standard error.

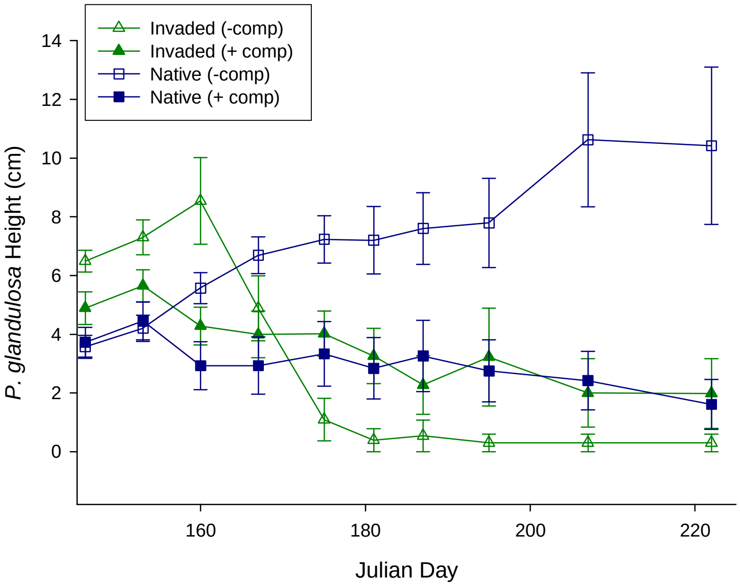

Fig 3.11: Comparison of mean height of *P. glandulosa* in the native and invaded zones only. Both levels of competition. Means pooled across litter treatments (n=10). Data points represent means and bars represent one standard error.

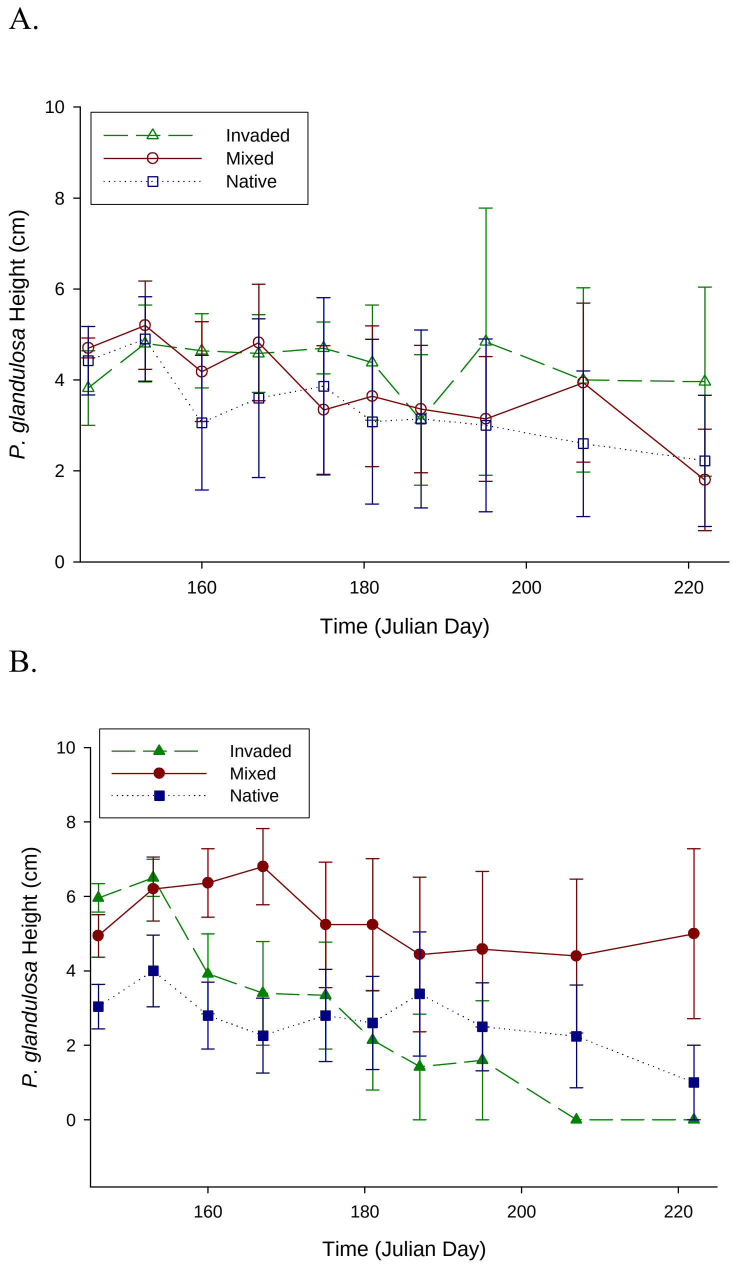

Fig 3.12: Height of *P. glandulosa* in all plots with competition in all three zones : A. + competition, - litter plots B. + competition, + litter plots (n=5). Data points represent means and bars represent standard error.

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Table 3.6: Multivariate repeated measures ANOVA for height of *P. glandulosa* seedlings in the field A. planted in the native and invaded prairie zones all levels of competition and litter. B. seedlings planted in all three prairie zones plots having both levels of litter. Significant P-values are in bold italics.

Source of variation				
3- way ANOVA **Invaded vs. Native** **Competition and Litter**				
A1) Between-subjects	df	MS/Wilks' Lambda	F	P
Transect	1	54.541350	0.77	0.39
Comp	1	350.676450	4.93	***0.03***
Zone	1	314.175625	4.41	***0.04***
Litter	1	1.890625	0.03	0.87
Comp*Zone	1	530.611225	7.45	***0.01***
Zone*Litter	1	1.863225	0.03	0.87
Comp*Litter	1	150.921225	2.12	0.15
Comp*Zone*Litter	1	5.221225	0.07	0.79
Error	31	71.179169		
A2) Within-subjects				
Week	9,23	0.36258495	4.49	***0.002***
Week*transect	9,23	0.79710012	0.65	0.74
Week*Comp	9,23	0.38296346	4.12	***0.003***
Week*Zone	9,23	0.2329062	8.42	***<.0001***
Week*Comp*Zone	9,23	0.28734020	6.34	***0.0002***
Week*Litter	9,23	0.82189472	0.55	0.82
Week*Comp*Litter	9,23	0.70197016	1.08	0.41
Week*Zone*Litter	9,23	0.65696474	1.33	0.27
Week*Zone*Litter*Comp	9,23	0.66231786	1.30	0.29
2-way ANOVA **All Zones Litter only**				
B)Between-subjects	df	MS/Wilks' Lambda	F	P
Transect	1	61.383200	0.91	0.35
Zone	2	68.842464	1.02	0.37
Litter	1	1.986197	0.03	0.86
Zone*Litter	2	67.311543	1.00	0.38
Error	23	67.257704		
B1) Within-subjects				
Week	9,15	0.40064103	2.49	***0.057***
Week*transect	9,15	0.51838179	1.55	0.21
Week*zone	9,15	0.35536778	1.13	0.37
Week*Litter	9,15	0.58612870	1.18	0.37
Week*Zone*Litter	9,15	0.33286135	1.22	0.30

3.1.4 Herbivory data

The probability of an herbivore causing *P. glandulosa* mortality was significantly higher in the invaded zone then the native or mixed zones ($\chi^2 = 13.24$, P=0.001; Fig.3.13). Mortality due to herbivore activity on *P. glandulosa* was pronounced in the absence of competition, affecting eighty percent of seedlings in the invaded zone plots without competition (Fig.3.12).

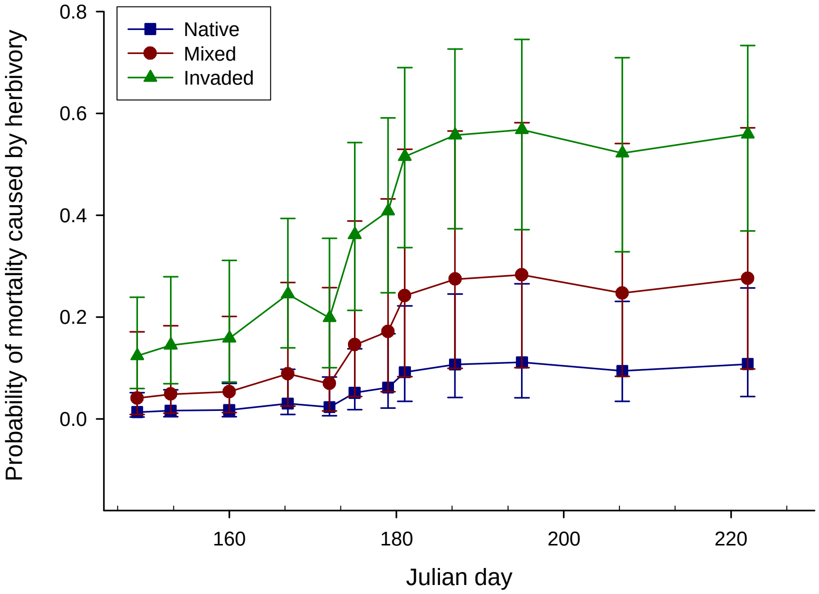

Fig 3.13: Probability of *P. glandulosa* mortality caused by herbivory in all three zones. Responses were pooled across litter and competition treatments (n=20, native and invaded zones and n=10 mixed zone). Bars represent 95% confidence intervals.

3.2 Greenhouse results

3.2.1 Environmental conditions

3.2.1.1 Light

Light data collected at the base of each seedling highlighted the differences in growth forms between *S. scoparium* and *S. halepense* (Fig. 3.14) Not surprisingly, the no competition treatments had the greatest amount of light while *S. scoparium* blocked more light than *S. halepense* (main effect of light; F= 109.36, P<0.0001). This was most likely due to the greater amount of standing dead associated with *S. scoparium*. . Since light levels varied over the course of the summer, a significant sampling day and day by competition interactions were also found.

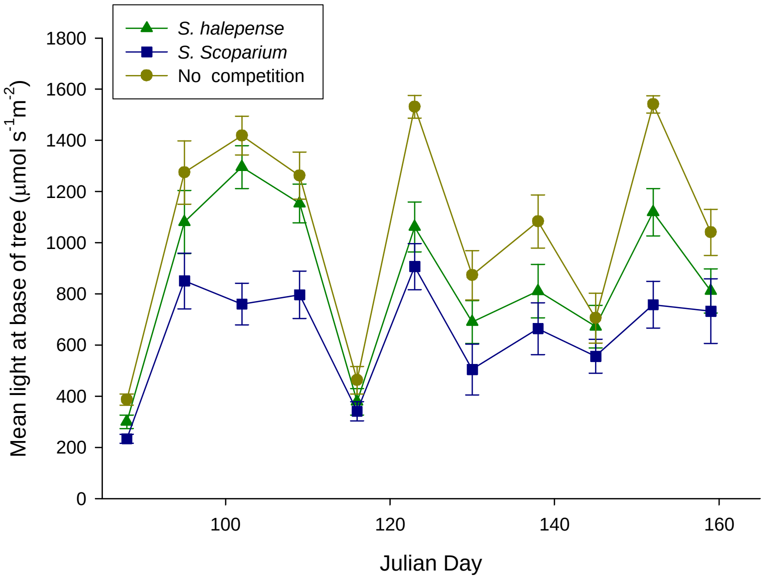

Fig 3.14: Light measurements taken at the base of each seedling. Means were pooled across soil treatments. Data points represent mean and bars standard error (n=8).

3.2.2 Growth and germination of P. glandulosa *and grass species*

3.2.2.1 Grass growth

Mean ramet/tiller height per pot of *S. scoparium* and *S. halepense* increased consistently over time until the eighth week (Fig 3.15). *S. halepense* ramets grew significantly taller (Table 3.7A) than *S. scoparium* tillers, yet *S. halepense* consistently allowed more light to reach the *P. glandulosa* seedlings (Fig 3.14). Initially, *S. scoparium* grew slightly taller in the invaded soil compared to *S. scoparium* in the native soil (Fig 3.15). After the eighth week, however, both *S. scoparium* and *S. halepense* planted in the native soil were slightly taller than grasses grown in invaded soil. Since both grasses grew differently over time, week was statistically significant (Table 3.7B).

Typical of a bunchgrass, *S. scoparium* grew numerous small tillers close together while *S. halepense* grew fewer larger ramets spaced 3-5 cm apart. Contrary to plant height, the average number of tillers/ramets per rhizome may have contributed (along with *S. scoparium's* standing dead biomass) to decreased light levels in these pots (Fig 3.16). The average number of tillers per *S. scoparium* rhizome was statistically larger than the number of *S. halepense* ramets (main effect of species: $F_{1,27}$= 457.49, P<0.0001). *S. scoparium* grew more tillers per rhizome in the invaded soil, and *S. halepense* grew slightly more ramets per rhizome in the native soil, causing a significant interaction between soil type and species ($F_{1,27}$= 6.07, P=0.02). Mean number of ramets/tillers also changed over time ($F_{10,18}$= 49.30, P<0.0001).

S. halepense started growing reproductive structures (inflorescences) earlier and produced more reproductive structures than *S. scoparium* (Fig. 3.17, $F_{3,31}$= 21.11, P<0.0001). Even though no overall significant soil effects were identified, both species produced slightly more reproductive structures in the invaded soil.

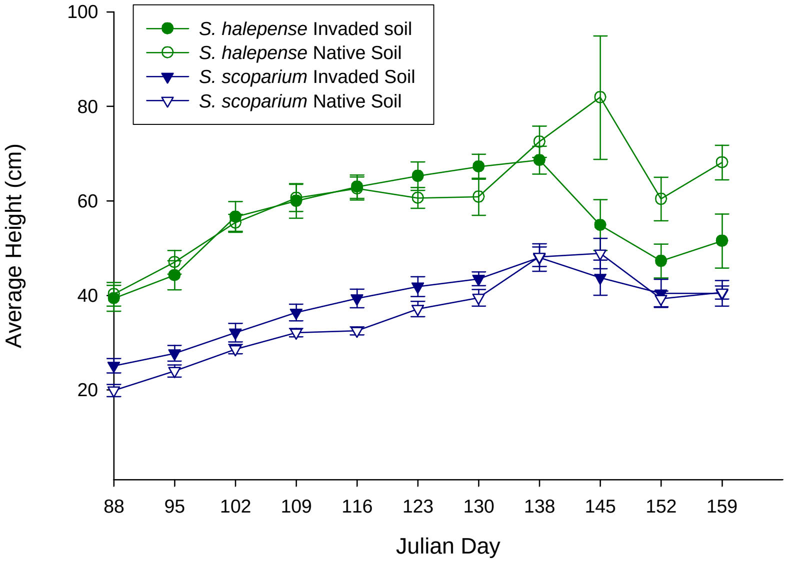

Fig 3.15: Average grass height per pot measured weekly for 11 weeks (n=8). Data points represent means and bars represent standard error.

Table 3.7: Multivariate repeated measures ANOVA for average growth of *S. scoparium* and *S. halepense*. A. Height of *S. scoparium* tillers B. Hieght of *S. halepense* ramets per pot planted in native and invaded prairie soils (n=8). Significant P-values are in bold italics.

Grass growth				
Source of variation	df	MS/Wilks' Lambda	F	P
A) Between-subjects				
Soil	1	63.74286	0.17	0.68
Species	1	39396.69364	104.08	***<.0001***
Soil*Species	1	1281.64286	3.39	0.08
B) Within-subjects				
Week	10,18	0.05468767	31.11	***<.0001***
Week*Soil	10,18	0.29755981	4.25	***0.004***
Week*Species	10,18	0.31040010	4.00	***0.005***
Week*Species*Soil	10,18	0.55599492	1.44	0.24

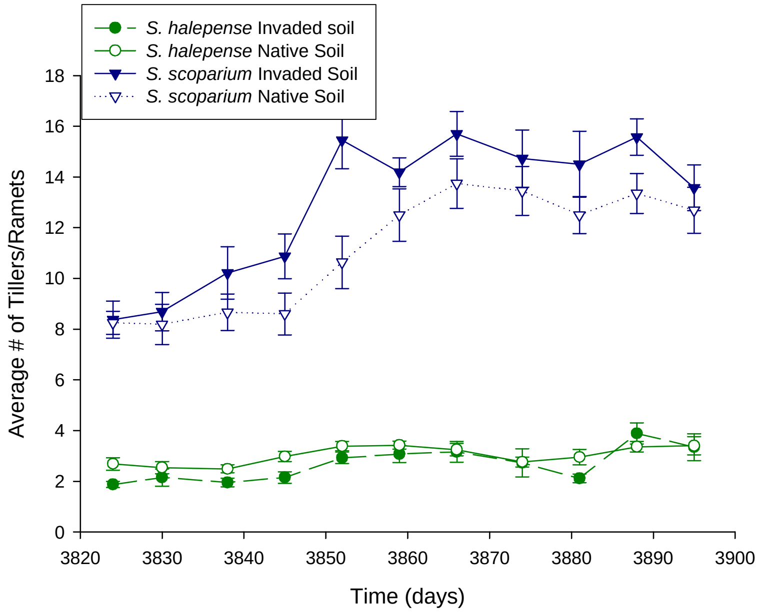

Fig 3.16: Average number of *S. scoparium* tillers or *S. halepense* ramets per pot. Counted weekly for 11 weeks. Data points represent means and bars represent standard error. (n=8).

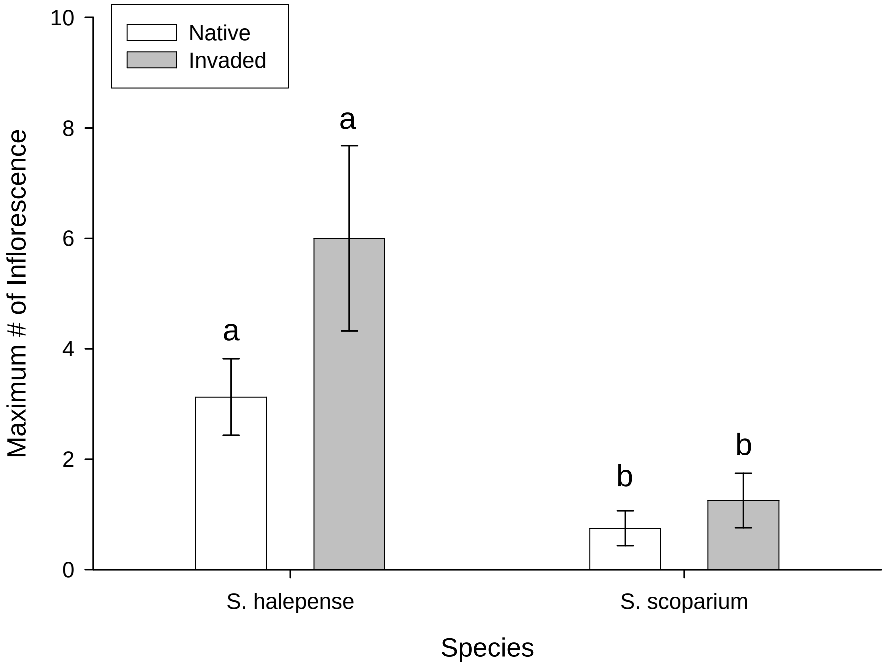

Fig 3.17: Mean maximum *S. scoparium* or *S. halepense* inflorescence counted for 11 weeks. Bars represent the mean and one standard error. Different lowercase letters refer to significant differences between soil & competition treatments. Means comparisons based on Tukey's HSD (n = 8).

3.2.2.2 P. glandulosa

3.2.2.2.1 Germination of P. glandulosa

Soil type did not affect *P. glandulosa* germination (Fig 3.18). More successful germination occurred when *P. glandulosa* was grown with *S. halepense* than when grown without competition (main effect of species: $F_{2,42} = 3.25$, $P = 0.05$). Germination of seeds planted with *S. scoparium* did not differ from those without competition or those planted with *S. halepense.*

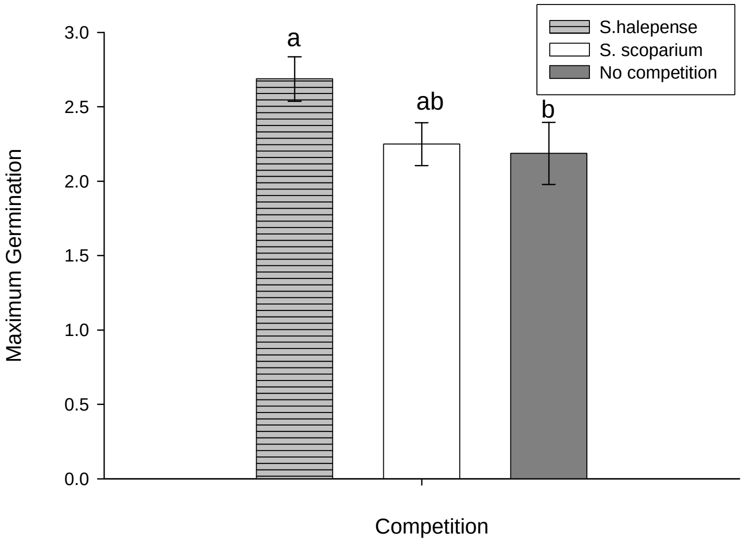

Fig 3.18: Mean number of *P. glandulosa* seeds that germinated. Pooled across soil types 15 days after sowing or date of maximum germination. Bars represent the mean and one standard error Different lowercase letters indicate significant pairwise differences between competition treatments. Means comparisons based on Tukey's HSD (n=8).

3.2.2.2.2 Growth of P. glandulosa

Seedlings grown without competition, in both native and invaded soils, grew significantly taller then those in pots with competition (main effect of competition: $F_{2,41}$=26.92, P<0.00010; Fig. 3.19). Seedlings grown in the invaded soil grew significantly taller than seedlings grown in native soil (main effect of soil: $F_{1,41}$=5.08, P=0.03). After the 43rd day of growth *P. glandulosa* seedlings were significantly taller when grown with *S. scoparium* compared to those grown with *S. halepense* (significant competition*week interaction: $F_{20,64}$=7.67, P<0.0001). *P. glandulosa* seedlings generally increased in height over time indicated by a significant week effect. ($F_{10,32}$=99.92, P<0.0001).

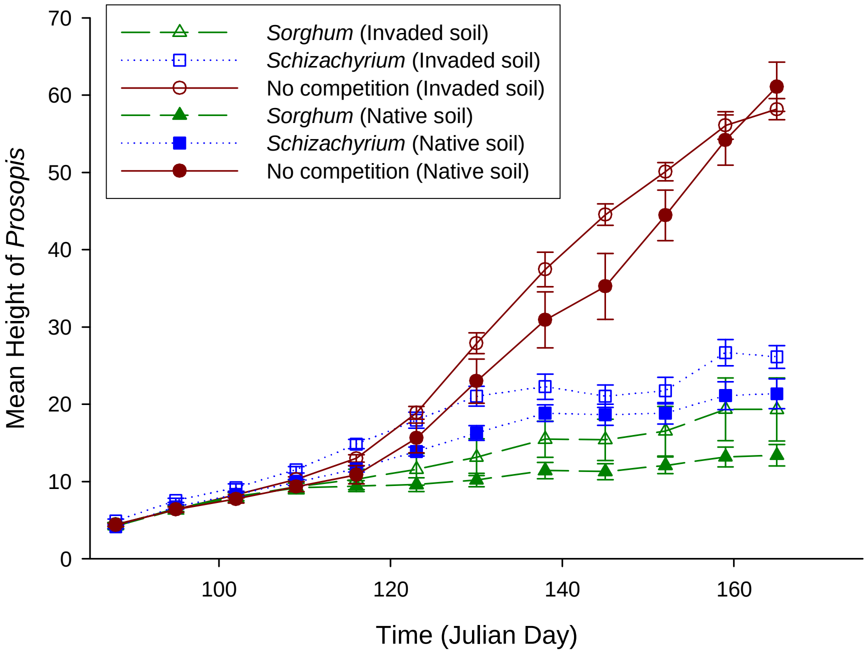

Fig 3.19: Average *P. glandulosa* height (n=8) measured weekly for 11 weeks (n=8). Data points represent means and bars represent standard error.

3.2.2.2.3 Biomass of P. glandulosa

Biomass data were similar to the height data for *P. glandulosa* seedlings (Fig 3.20AandB). Seedlings grown in pots without competition had significantly more above and below ground biomass then those grown with *S. scoparium* or *S. halepense* (main effect of competition: above: $F_{2,41} = 12.54$, $P < 0.000$, below: $F_{2,41} = 128.57$, $P < 0.0001$). Soil type also had the same impact on *P. glandulosa* biomass as it did on seedling height: seedlings grown in invaded soil produced significantly more above and below ground biomass then those planted in native soil pots (main effect of soil: above: $F_{1,41} = 4.03$, $P = 0.05$; below: $F_{1,41} = 6.04$, $P = 0.02$).

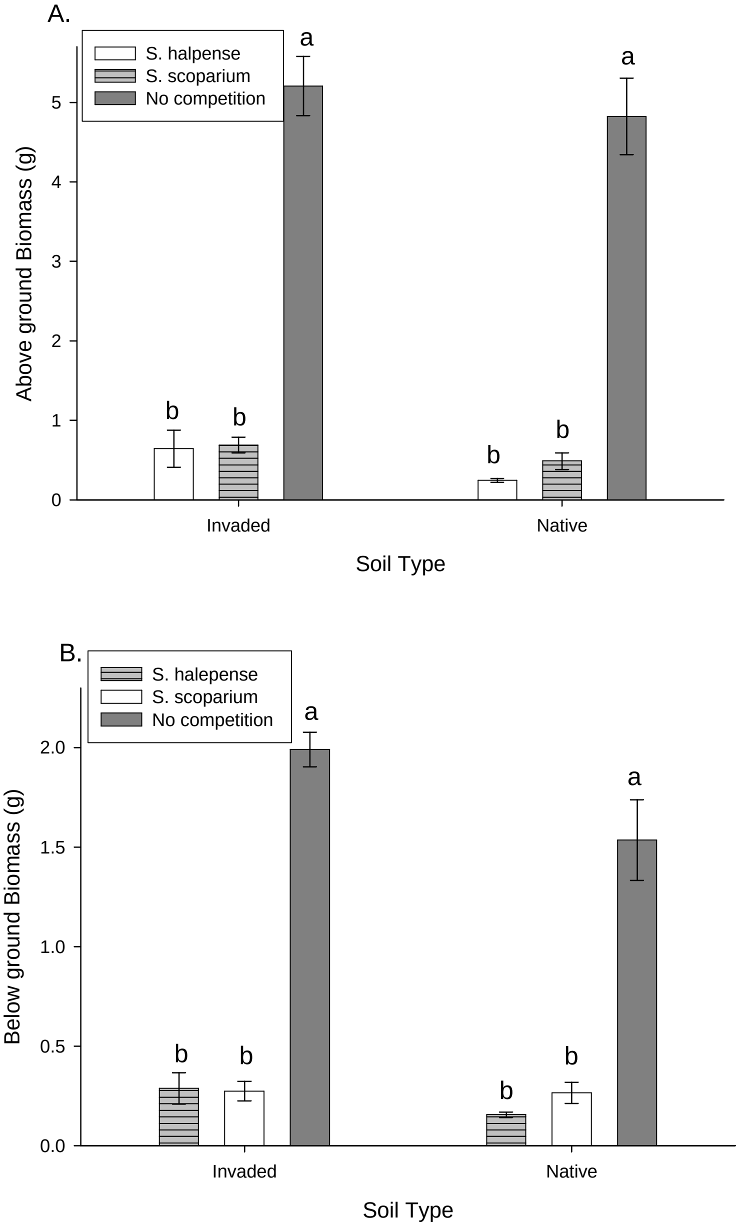

Fig 3.20: Biomass of *P. glandulosa* seedlings at harvest. A.Above ground biomass, B. Below ground biomass after 16 weeks of growth. Bars represent the mean and one standard error (n=8). Different lowercase letters refer to significant differences.

3.2.2.2.4 Nodule count P. glandulosa

The development of *Rhizobium* nodules on *P. glandulosa* roots did not exhibit a clear pattern (Fig 3.21). A Poisson regression revealed a significant soil and competition interaction effect on nodule development ($\chi^2 = 8.58$, P=0.01). In invaded soils, seedlings grown without competition developed significantly more nodules then those grown with either *S. scoparium* (pairwise comparison: P=0.03) or *S. halepense* (pairwise comparison: P=0.05). Native soils, however, had a different trend: slightly more nodules developed on seedlings in native soil pots with *S. halepense* then those without competition (pairwise comparison: P=0.08) or those grown with *S. scoparium* (pairwise comparison: P=0.07). Seedlings grown in native soil without competition developed significantly fewer nodules then those without competition in the invaded soil (P=0.2).

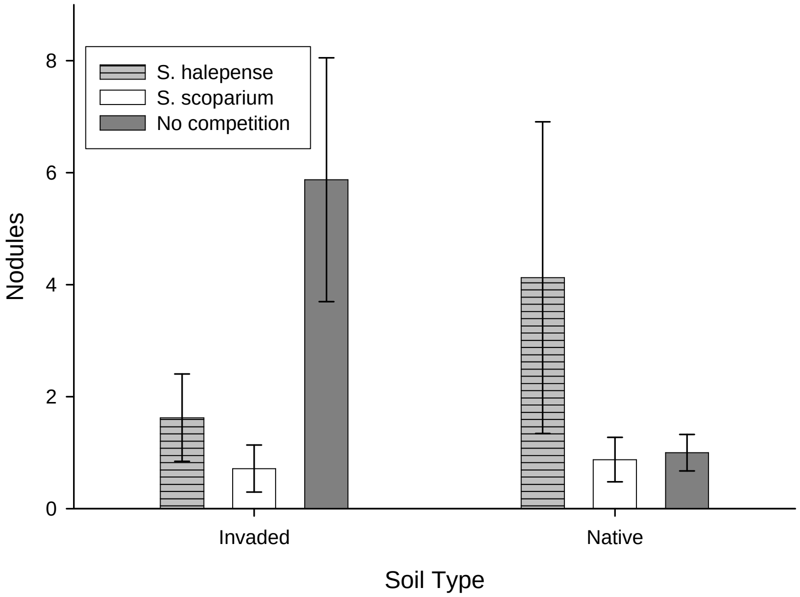

Fig 3.21: Mean number of nodules on *P. glandulosa* roots at harvest after 16 weeks of growth. Bars represent the mean and one standard error(n=8)..

3.2.3 Soil at harvest

3.2.3.1 Soil nutrient levels

Cores were taken both near *P. glandulosa's* rhizosphere and away from the rhizosphere (termed "location" for statistical analysis). Means were pooled across location in order to simplify the graphs (Fig 3.22ABandC). N was influenced by location of sample, competition and soil type. Overall, native soil pots had more N than invaded soil pots (main effect of soil: Table 3.8A). There was significantly more N in soil located outside the *P. glandulosa* rhizosphere compared to in the rhizosphere (main effect of location: Table 3.8A). In the "no competition" pots, native soils had more N than invaded soils, whereas there was no difference in N between the two soil types when grasses were also present (significant competition*soil interaction: Table 3.8A). Overall, pots without competition had more total N at harvest then those planted with either grass (main effect of competition: Table 3.8A).

Similarly, native soil had significantly more C than the invaded soil (Fig3.22B; main effect of soil: Table 3.8B). The native soil had similar amounts of carbon both inside and outside of *P. glandulosa* rhizosphere while the invaded soil had more C near the rhizosphere than outside of the rhizosphere (significant soil*location interaction: Table 3.8B). A significant interaction between competition and location was caused by greater C outside the rhizosphere than inside in the no competition treatments, but no similar differences in the presence of the grasses. This affect appeared to be driven by differences in the native soils (soil*location*competition also significant). Overall there was also more C in soils that had only *P. glandulosa* seedlings. (marginal effect of competition: Table3.8B: Fig3.22B).

Statistical analysis of the C:N molar ratio (Fig 3.22C) revealed a majority of the same effects as the analyses of total N and C. Pots with *S. scoparium* and *S. halepense* had individually higher C:N ratios near *P. glandulosa's* rhizosphere, while soil away from *P. glandulosa's* rhizosphere had a lower C:N ratio (significant location*competition interaction: Table 3.8C). The soil with the most N available for plant uptake was the invaded soil which had a significantly lower C:N ratio then the native soil (main effect of soil: Table3.8C). In contrast to total C and N, pots without competition had significantly lower C:N ratios then those growing both *P. glandulosa* and a grass species (main effect of competition, Table3.8C).

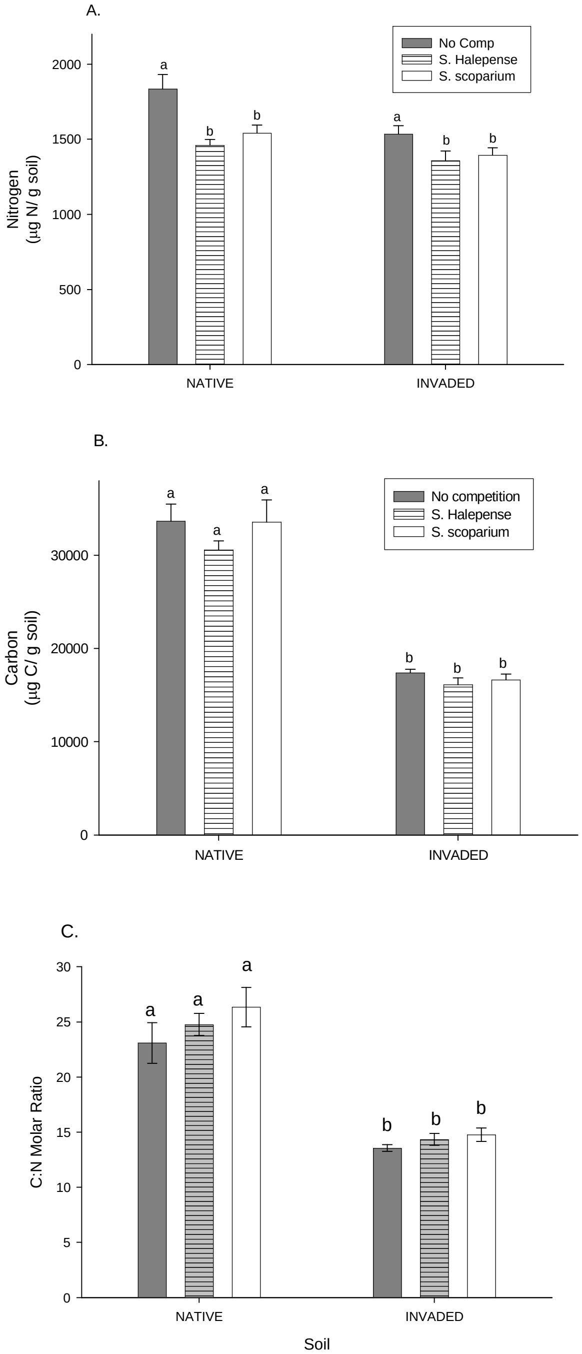

Fig 3.22: Mean soil nutrients levels at harvest. Total N (A), total C (B), and C:N Molar ratio of greenhouses soils sampled at harvest. Means were pooled across pot location (near *P. glandulosa* rhizosphere and away from rhizosphere) (n = 8). Bars represent the mean and one standard error. Different lowercase letters refer to significant differences.

Table3.8: Greenhouse soil nutrient ANOVA. A. total N, B. total carbon, and C. C:N molar ratio for all levels of competition, both soil treatments and pot locations. Significant P-values are in bold italics

A) Total N in Soil				
Source of variation	df	MS	F	P
Replicate(Pot)	28	66644.934	1.00	0.45
Pot	6	68479.101	1.02	0.41
Soil	1	1530949.011	22.87	***<.0001***
Location	1	640251.679	9.56	***0.002***
Soil*Location	1	33964.190	0.51	0.4773
Comp	2	1247298.343	18.63	***<.0001***
Soil*Comp	2	255141.073	3.81	***0.02***
Location*Comp	2	53833.440	0.80	0.45
Soil*Location*Comp	2	6592901.6	0.91	0.40
B) Total C in Soil				
Source of variation	df	MS	F	P
Replicate(Pot)	28	8148326	0.52	0.98
Pot	6	44840334	2.87	***0.01***
Soil	1	10968969276	701.71	***<.0001***
Location	1	9663736	0.62	0.43
Soil*Location	1	77770068	4.98	***0.03***
Comp	2	40015184	2.56	0.08
Soil*Comp	2	95963939	0.61	0.54
Location*Comp	2	118551814	7.58	***0.0007***
Soil*Location*Comp	2	111069832	7.11	***0.001***
C) C:N Molar Ratio				
Source of variation	df	MS	F	P
Replicate(Pot)	28	0.00494953	0.81	0.74
Pot	6	0.01416778	2.31	***0.04***
Soil	1	2.49016460	406.20	***<.0001***
Location	1	0.04506340	7.35	***0.01***
Soil*Location	1	0.00134683	0.22	0.64
Comp	2	0.05731325	9.35	***<.0001***
Soil*Comp	2	0.01039573	1.70	0.19
Location*Comp	2	0.02082395	3.40	***0.03***
Soil*Location*Comp	2	0.01390619	2.27	0.11

CHAPTER 4

DISCUSSION

4.1 Invaded communities differed from native in abiotic and biotic structure

My first objective was to determine if *S. halepense* was altering the abiotic and biotic structure of a prairie community. I predicted that *S. halepense's* annual dieback resulted in less standing dead and lower litter heights in the invaded zone compared to the standing dead biomass and litter heights of *S. scoparium* in the native zone. Light levels reaching the soil in the field would reflect this and be greater in the invaded zone than the native zone. The data did not support this prediction. The litter layer was thicker in the invaded zone, but the height of standing dead biomass was greater in the native zones. Differences between zones in light levels reaching soil were a result of already established neighboring plant species rather than differences in litter or standing dead. Mature *S. halepense* limited light penetration to the soil surface in the invaded zone more than *S. scoparium* limited light perturbation to the soil in the native zone. Unfortunately, light levels were only measured in spring and summer and the data may not have captured any seasonal differences in light among vegetation zone that occur in the fall or late winter. Other environmental variables may have contributed to lower light levels in the invaded zone such as shading from the nearby tree line and woody species in that zone. The greenhouse data appeared to tease out some of these confounding variables.

As expected, light reaching the soil surface in the greenhouse was reduced by the presence of either grass species. In comparison to the field data, light levels reflected the differences in growth habits between the two grass species. Since *S. scoparium's* standing dead was left intact, it consistently inhibited light from reaching seedlings. At the start of the experiment, however, seedlings planted with *S. halepense* received the same amount of light as those planted alone. After the first 4 weeks, as *S. halepense* grew taller and produced more ramets, the amount of light reaching the seedlings decreased, confirming that competition from neighboring plants is a greater inhibitor of light than either standing dead or litter in this case.

Due to the ability of *S. halepense* to create a monoculture through the production of a huge amount of biomass and a cyanide containing compound, I hypothesized that in the field soil N would be lower and C would be higher in the invaded zone when compared to the native zone. Soil nutrient levels did not follow this expected pattern: soil N levels were highest in the invaded zone and lowest in the native zone, total soil C was lowest in the invaded zone, and therefore C: N ratios were lower in the invaded zone compared to the native. As the height data indicated, *S. halepense* is a much taller plant than *S. scoparium,* suggesting more plant biomass was present in the invaded zone. This biomass, however, did not appear to require more N in the field. Major inputs of N in tallgrass prairies include deposition of atmospheric N, decomposition of litter and root biomass, and N fixation by microbes (Blair et al. 1998). Since the microbial ecology, decomposition rates and N mineralization were not included in this study, it is difficult to speculate as to what may be responsible for the larger amounts of N in this zone. However, the greater moisture and shading in the invaded zone suggest that plants in this zone may be decomposing faster then those in the native zone. More insects in the invaded zone, as suggested by the herbivory data, may also help to recycle nutrients into the soil.

The greenhouse experiment also tested the hypothesis that *S. halepense* would lower N levels when planted in both the invaded and native soils. While N fixation by *P. glandulosa* cannot be ruled out, the greenhouse soil nutrient data appears to solely reflect soil origin and the amount of plant biomass present in the soil at harvest. The low C and N content in the invaded soil pots may reflection the increased *P. glandulosa* biomass produced in that soil. It has been well documented that tallgrass prairies are typically low in N content so a high C: N ratio in the native soil is not surprising (Risser 1982). Competition for N is evident in the lower N levels in all pots with competition. Although *S. halepense* produced much larger plants than *S. scoparium,* both species reduced N levels equally when grown in pots regardless of soil type.

S. halepense's large amount of biomass also led me to predict that soil moisture would be lower in the invaded zone compared to the native. Similar to N, the gravimetric moisture data did not follow the predicted pattern but did indicate a shift in abiotic resources in the invaded zone: field soil moisture was greater in the invaded zone than the native. Changes in soil moisture content could be caused by the increased litter levels in the invaded area. Litter is known to act as natural "mulch" preventing soil moisture from evaporating (Dyksterhuis and Schmutch 1947, Foster 1999). The moisture and nitrogen data warrant a closer examination of soil-plant interactions of both *S. halepense* and the woody species in the invaded zone.

My results did not support the hypothesis that *S. halepense's* ability to create a monoculture would lower plant diversity in the invaded zone when compared to the native. Species richness and overall plant diversity was highest in the invaded zone, in contrast to a previous study in the same field (Rout 2005). A high percentage of diversity due to woody species was found in both the invaded (20%-40%) and mixed (-) litter (~30%) treatments. The fact that almost no woody species were found in the native zone plots may have been a reflection of small plots (0.25 m^2) and differences in growth forms among plants in all three zones. Even with sampling errors, the higher diversity in the invaded zone, mostly explained by woody species, suggests that this area is not a complete monoculture of *S. halepense,* and a conversion to woodland is taking place in this zone. Although evidence suggests that *S. halepense* may be driving this shift, it cannot be ruled out that the woody species themselves are responsible.

While none of my predictions were met, the *S. halepense* dominated community did differ from the *S. scoparium* community in both biotic and abiotic structure. Initially, I predicted that *P. glandulosa* seedlings would receive more light in the invaded zone compared to the native zone. However, less light was able to reach the soil surface in the invaded zone than the native zone. Litter and standing dead biomass did not impede light as much as competition from live plant neighbors. A study that looks at light available in fall and late winter might better explain the effects of litter and standing dead on light penetration. The invaded zone soil had significantly more N in the field compared to the native zone soil. However, at the end of the greenhouse study native zone soil had more N than invaded. The greenhouse results may be a reflection of the uptake of more N by larger *P. glandulosa* trees in that soil. This may also support the idea that decomposition rates in the invaded zone are greater compared to the native zone and when in pots the soil is not receiving the same recycling of nutrients that occurs in the field. Invaded zone soil had significantly less C than the native zone soil in both the field and greenhouse. This difference in C may be reflecting differences in microbial activity or just a greater biomass of plant matter in the invaded soil. Since *S. halepense* is the dominant species in the invaded prairie it is obviously affecting the abiotic structure of the community. Not so obvious, however, are the effects woody species have on nutrient availability within the invaded zone.

4.2 Both native and exotic grasses inhibit growth of P. glandulosa *seedlings*

My second objective was to determine if *S. halepense* facilitates the invasion of *P. glandulosa* and in doing so is changing the community structure from herbaceous prairie to woodland. I predicted that in an *S. halepense* altered environment, *P. glandulosa* would be a better competitor in the invaded zone compared to a native zone dominated by *S. scoparium*. The results of the growth data did not support this hypothesis, but germination data suggest seedling emergence was facilitated in the invaded zone.

P. glandulosa more successfully germinated in the field when sowed in the *S. halepense* dominated invaded zone. Increased soil moisture and higher soil N levels in the invaded zone soil may have been responsible for the increased germination. Wilsey and Polley (2003) found soil nutrient content and water availability more important to seedling establishment then light in moisture limited Texas prairies. The light data further supports these findings since litter removal stimulated the growth of *P. glandulosa* in the invaded zone yet there were no significant light differences between litter treatments.

A trend, although not significant, for inhibition of germination by litter in the other two zones suggests that litter, regardless of type or height, may prevent *P. glandulosa* seedling recruitment in native grasslands. Litter may indirectly inhibit *P. glandulosa* establishment by increasing the productivity of native grasses since *S. scoparium* was taller in plots where ambient litter was left in place. This trend was not seen with *S. halepense* or *S. nutans.* The increased productivity of neighbors in the native zone may have led to increased competition for already limited resources (water and N) further inhibiting seedling establishment and survival (Wilsey and Polley 2003).

In greenhouse experiments, germination of *P. glandulosa* was highest when planted with *S. halepense,* regardless of soil type. This conflicted with previous studies indicating decreased germination of *P. glandulosa* when planted with herbaceous species (Bush and Van Auken 1989, Glendlening and Paulsen 1955), but supported my field results that found higher levels of germination in the invaded zone regardless of competition. There was no effect of soil type on germination in the greenhouse, and *P.*

glandulosa seeds were able to germinate successfully in both native and invaded soils. Since all pots were watered evenly this supports the idea that water may be more important to germination of *P. glandulosa* then either light or nutrient levels.

In contrast to the results of the germination data, *P. glandulosa* grew tallest in the native zone when competition by neighboring grasses was removed compared with all other field treatments. Similar to research on herbaceous seedlings (Foster 1999), litter did not have an effect on the height of *P. glandulosa* transplant seedlings. This suggests that a reduction in native plant cover either by grazing or human disturbance in native prairies may be facilitating the success of *P. glandulosa*. A majority of other competition experiments involving *P. glandulosa* found that a reduction in biomass of native grasses favors *P. glandulosa* growth, disturbance is important in seedling establishment, and most of the competition from grasses occurs belowground (Archer 1988, Bush and Van Auken 1989, Van Auken and Bush 1997, Bush and Van Auken, 1990). Due to *P. glandulosa*'s association with N fixing bacteria, lower levels of soil N and higher C:N ratios in the native soils may have led to its increased height in this zone. In greenhouse studies Bush and Van Auken (1989) noticed that *P. glandulosa* grew better in soils with lower N levels.

The reduced height of *P. glandulosa* was not due to the seedlings inability to grow in the invaded zone. My measure of seedling success is biased by the severe herbivory that occurred within that zone. Prior to the onset of severe herbivory in the field, *P. glandulosa* grew taller in the invaded zone when compared to seedlings in the native zone. The taller height of *S. halepense* compared to the native grasses may have provided cover for more insects. Also, the dhurrin content of *S. halepense* may have caused the herbivores to selectively forage for *P. glandulosa* seedlings in that zone. However, the ability of *S. halepense* to alter the insect population has not been explored and deserves further study.

The greenhouse experiment excluded the impact of herbivores and may therefore be a better measure of *P. glandulosa*'s competitive abilities. Biomass and height of *P. glandulosa* seedlings responded similarly to treatments. Seedling growth was equally inhibited by the presence of neighbors, regardless of species, compared to the no neighbors treatments. This supports field results and previous research indicating *P. glandulosa* is inhibited by native grasses and requires disturbance to invade any grassland (Archer 1988, Bush and Van Auken 1989, Van Auken and Bush 1997, Bush and Van Auken 1990). While higher light levels in the native zone may have contributed to *P. glandulosa's* increased height and biomass, in earlier field and greenhouse studies belowground competition interfered more with seedling establishment and growth than aboveground competition (Van Auken and Bush 1997). The increased N and perhaps water in the invaded soil may explain the pattern of increased seedling height in the invaded soil pots, regardless of competition.

While the nodule count at harvest suggested the presence of *Rhizobium,* there was not sufficient evidence to indicate that the seedlings were fixing N. While the number of nodules in the invaded soil was correlated with high biomass and N content, this pattern did not occur in the native soil. Jenkins et al. (1987) has shown that *P. glandulosa* seedlings fail to form nodules in soil with high nutrient levels. Because of this and inconsistencies in the nodule count, I believe that the increased nodules on seedlings grown without competition in the invaded soil may simply be a function of the increased biomass, and not necessarily a direct response to soil N levels.

4.3 Invasions of both native and exotic species into remnant prairies is multivariate in origin and may alter both diversity and community structure

My research found complex interactions among interspecific competition, soil resource levels and disturbance allow for the establishment of *P. glandulosa,* and perhaps other woody species, in grasslands (Archer 1999, Bush and Van Auken 1997). These experiments underline the importance of native grasses and their growth habits in preventing woody establishment in remnant prairies. Litter accumulation and standing dead biomass of a prairie bunchgrass like *S. scoparium* not only inhibits the germination of other species but also acts as a mulch layer that retains necessary water in arid climates (Dyksterhuis 1947, Wilsey 2003). While the role of litter as fuel for fire was not examined in my study, the need for periodic burning to release stores of nutrients into the soil and promote the growth of native forbs is supported by the extremely low N content and diversity in the native zone (Hobbs et al. 1991, Rogers and Hartnett 2001). The success of *P. glandulosa* seedlings in the low N native zone, once competition was removed, underscores the need to understand multivariate anthropogenic drivers (disturbance, abiotic resources, and seedling dispersal) of community change.

The diversity and species richness findings in the native zone contradict research that cites tallgrass prairies as relatively diverse communities (Dyksterhuis 1946, Diamond and Smeins 1985, Polley et al. 2005). Seed dispersal and drought have both been cited as causing low community diversity (Haddad et al. 2002, Tilman 1997). A year long drought, fragmentation and the invasive species cover may have limited wind dispersal of native seeds into this remnant prairie further exacerbating the low diversity (Rout 2005). Nonetheless, the low diversity and species richness of the native zone and its role in promoting or inhibiting the spread of *S. halepense* and woody species deserves further examination.

Woody species were present in high numbers in both the invaded and mixed zones but not in the native zone suggesting that the conversion from grassland to woodland is already happening in this field. However, MacDougall and Turkington's (2005) "driver" or "passenger" model may not explore enough community interactions to adequately explain the shift in community structure. What is not clear from my results and the application "driver" and "passenger" hypotheses is the role that *S. halepense* and *P. glandulosa* may be playing in this conversion. The idea that the woody species, such as *P. glandulosa,* invaded the area prior to *S. halepense* arrival cannot be discounted. Unlike wind dispersed seeds, *P. glandulosa* and other woody species in this field are typically dispersed long distances by large browse animals such as deer and may have been present in the seed bank prior to the *S. halepense* invasion. It is possible that the arrival of woody species such as *P. glandulosa* and *Rubus* sp., increased forage activity by browse species, thereby increasing disturbance and facilitating the invasion of *S. halepense*. Since it is difficult to determine the complete history of a remnant prairie, it may be better to view the invasion from Tilman's (2004) stochastic theory of invasibility and focus on current interactions found in this remnant prairie. Low diversity in the native system combined with *S. halepense* indirect effects on soil moisture, light, and N availability may be interacting to drive community level changes in this remnant prairie.

In support of MacDougall and Turkington's (2005) findings, these results suggest that anthropogenic influences such as fragmentation, low diversity in the native system, disturbance, and land management practices may be partially responsible for changes in this remnant prairie community. However, MacDougall and Turkington failed to examine any impacts invasive species have on other trophic levels or the effect they have on nutrient cycling. While current ecological theory is attempting to define the roles diversity and resource competition play in determining community structure and invasibility (reviewed in Shea and Chesson 2002), the results of this study highlight the difficulty in pinpointing any single mechanism that contributes to the success of invasive species. Understanding interactions between both exotic and native invasive requires a comprehensive investigation of both positive and negative community interactions and structure. The need to understand invasive species is not only important to conserve the remaining 10% of north American prairies, but may also help to slow the rapid loss of global biodiversity occurring in all ecosystems.

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BIOGRAPHICAL INFORMATION

Amie Treuer received a B.S. in Biology from the University of Texas at Arlington in 2004 where she met Dr. Laura Gough. She encouraged Amie to enroll in the Master's of Biology program at UTA. Her research interests include; studying invasive species in a wide variety of ecosystems and determining their modes of invasion, the effects of climate change on the plant community, and determining human impacts on both the plant and microbial community. Amie has always enjoyed the outdoors and she feels privileged to be allowed to make a career spending time enjoying nature.