PROXIMATE MECHANISMS OF CONTEMPORARY *JUNIPERUS VIRGINIANA* EXPANSION

By

AMY CHRISTINE GANGULI

Bachelor of Science
University of Rhode Island
Kingston, Rhode Island
1997

Master of Science
Texas Tech University
Lubbock, Texas
1999

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
July, 2005

PROXIMATE MECHANISMS OF CONTEMPORARY JUNIPERUS VIRGINIANA EXPANSION

Thesis Approved:

Thesis Advisor

Dean of the Graduate College

DEDICATION

I dedicate this dissertation to my family and friends. Your endless support gave me the strength to persist and accomplish my academic goals.

PREFACE

All of the chapters of this dissertation were written as manuscripts that will be submitted to peer-reviewed journals. Chapter one, "Influence of plant community traits on *Juniperus virginiana* invasion", will be submitted to *Applied Vegetation Science*. Chapter two, "Influence of resource availability on *Juniperus virginiana* expansion in a forest–prairie ecotone", will be submitted to *Ecological Applications*. Chapter three, "When are native species inappropriate for conservation plantings?" will be submitted to the *Wildlife Society Bulletin*. Each chapter follows the style and guidelines of the respective journal in which it was intended to be submitted.

ACKNOWLEDGEMENTS

Many people provided support throughout my graduate program at Oklahoma State University (OSU) that made the completion of my dissertation possible. I would like to extend sincere gratitude to my major advisor Dr. David Engle and to the members of my graduate committee, Dr. Samuel Fuhlendorf, Dr. Eric Hellgren, and Dr. Michael Palmer. Individually and collectively you have pushed me to become a better ecologist and you have made valuable contributions to this project. Special thanks to Dr. David Engle for your patience and guidance throughout my program.

Funding for this project was provided by the United States Environmental Protection Agency (US EPA) through an interagency agreement with the Biological Resources Division of the United States Geological Survey (USGS) and was administered by the Oklahoma Cooperative Fish and Wildlife Research Unit. Dr. David Leslie administered the funding for this research and Dr. Paul Mayer had a critical role in overall project development and has made valuable contributions to many aspects of this research. I received additional funding in the form of a research assistantship from the Oklahoma Agricultural Experiment Station, a teaching assistantship from Dr. Jeffory Hattey, and through several academic scholarships.

A project of this magnitude required considerable field assistance. I would like to thank Chris Leibbrandt and Valerie Horncastle for helping me set up the research grids utilized in this research. Larry Levesque, Chris O'Melia, Jay Kerby, the Stansberry family, Jack Eckroat, Tim Tunnell, and Ken Nelson

assisted with the seedling transplant. Chris Stansberry, Chad Cummings, and Ken Nelson provided crucial support with vegetation sampling. I sincerely appreciate the assistance with soil and vegetation sampling that Matt Franklin, Claudia Rosas, Matt Stacey, Kate Hellgren and Chris Leibbrandt provided. John Weir provided critical logistical support associated with my field sites.

Several people at OSU made my experience more memorable. I would like to especially thank Roshini Nambiar and Dr. Susan Tunnell for being so supportive throughout my program and Dr. Karen Hickman for providing support and friendship at a crucial time. I appreciate the experiences I have had with students at OSU, especially those shared with the range club, the rangeland ecology graduate students, and the great office mates I have had. Sincere thanks to faculty and to support staff members of the Plant and Soil Science Department, you made my daily experiences at OSU pleasurable.

I wholeheartedly appreciate the support family and friends have given me throughout my academic endeavors. Even when times were tough and the light at the end of the tunnel was difficult to see you constantly encouraged me to reach for the golden ring. I am extremely grateful for the support my parents, Fran and Prabhash, and my brother Greg have offered. Dr. Karen Launchbaugh and the Wild Women of Range were extremely supportive and helped me keep things in perspective throughout my graduate program. Finally, I would like to thank Chris Leibbrandt for unselfishly helping me with various aspects of this project, but more importantly I thank you for your constant love and the unwavering support you have given me throughout this endeavor.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

Chapter I

Chapter II

Chapter III

LIST OF FIGURES

Figure Page

Chapter I

Chapter II

Chapter III

NOMENCLATURE

Plant nomenclature follows the National Plants Database published by the United States Department of Agriculture, Natural Resource Conservation Service (USDA, NRCS 2004).

United States Department of Agriculture, Natural Resources Conservation Service. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA, USA.

CHAPTER I

INFLUENCE OF PLANT COMMUNITY TRAITS ON *JUNIPERUS VIRGINIANA* INVASION

Questions: Does invasion by *Juniperus virginiana* decrease with increasing species diversity (plant species richness and Shannon's H′) and what role, if any does plant species composition play in invasion by *J. virginiana*?

Location: Central Oklahoma, United States

Methods: We established a transplant experiment to evaluate the relationship between *J. virginiana* seedling survival and growth and plant community traits in 3 distinct albeit contiguous plant communities: 1) tallgrass prairie; 2) old-field; and upland oak forest. In each plant community we transplanted 900 two-year-old *J. virginiana* seedlings in a systematic grid design. *J. virginiana* seedling survival and growth were monitored 6, 18, and 30 months following transplant and canopy cover by species, species richness, and Shannon's H′ were collected in 1 x 1-m plots surrounding each transplanted seedling.

Results: Species diversity was either positively associated or was not related with *J. virginiana* seedling survival and seedling growth. *J. virginiana* seedling invasion was associated with plant species composition, but was most strongly associated with plant species composition in the disturbed old-field.

Conclusion: Greater levels of plant species diversity provide little safeguard to plant communities threatened by *J. virginiana* invasion. However, *J. virginiana* invasion may be limited in areas where plant species composition reflects the presence of abiotic stressors such as limited resource environments. All of the plant communities we investigated are susceptible to *J. virginiana* invasion, differing only in the probable rates of conversion to *J. virginiana* woodland.

Nomenclature: National PLANTS Database (USDA, NRCS 2004).

Keywords: eastern redcedar, invasion, seedlings, H′, species richness, woody plant expansion

Abbreviations: DCA = Detrended Correspondance Analysis; USDA = United States Department of Agriculture; NRCS = Natural Resource Conservation Service.

Introduction

Concern regarding invasion of non-indigenous plant species and invasion of native plants (encroachment) into natural and semi-natural plant communities has stimulated interest in, and need for, identifying attributes of plant communities that make them more susceptible to invasion by either non-indigenous or native species. Although there has been considerable success in identifying biological attributes of successful invasive species (Rejmánek & Richardson 1996; Williamson & Fitter 1996), and identifying biotic (e.g. plant community traits, soil microbes) and abiotic attributes (e.g. resource availability, disturbance) of plant communities that make them more susceptible to invasion (Hobbs & Huenneke 1992; Tilman 1997; Davis et al. 2000; Callaway et al. 2004), the complex relationship between a species and its environment has made it difficult to generate consistent predictions of invasion success.

Among the potential mechanisms postulated for community invasibility, investigation of plant community traits has received a great deal of attention and criticism. Plant community traits hypothesized to influence non-indigenous species invasion include plant species pool (Smith & Knapp 2001), community composition (Planty-Tabacchi 1996; Larson, et al. 2001; Dukes 2002; Stohlgren et al. 2002), and community diversity (Tilman 1997; Levine & D'Antonio 1999; Stohlgren 1999; Kennedy et al. 2002). In C_4-dominated grasslands, sites that had greater ratios of non-indigenous species to native species in the local species pool were more susceptible to invasion by non-indigenous species (Smith & Knapp 2001). Investigations regarding plant community composition and invasibility have focused on identifying communities or species assemblages (Planty-Tabacchi 1996; Lonsdale 1999; Symsted 2000; Larson et al. 2001; Stohlgren et al. 2002), and successional stages (Planty-Tabacchi 1996) that are more susceptible to invasion by non-indigenous species.

The most extensively studied plant community trait with regard to community invasibility is plant species diversity. The dominant hypothesized relationship between diversity and invasion is inverse, that is, as plant species diversity increases, the success of an invasive species decreases. Plant species diversity is suspected to reduce invasion success because as native species diversity increases, niche occupation increases, which may present a form of resistance to invasion (Elton 1958, Tilman 1997). However, many different relationships between plant species diversity and invasibility have been reported in the literature, which may be a result of spatial scale at which the study was conducted (Tilman 1997; Lonsdale 1999; Kennedy et al. 2002; Stohlgren 2002), or the lack of control for extrinsic factors (Robinson et al. 1995, Levine & D'Antonio 1999). Despite conflicting results, the relationship between plant community traits and invasibility remains an extensively studied topic in invasion ecology, partly because the discovery of mechanisms driving such relationships might be used to develop approaches for invasive species management and control.

Although plant community traits have been the focus of research on cause of non-indigenous species invasions, the focus of research on the cause of native woody plant expansion has been on livestock introduction, fire suppression, and climate change (Archer 1989; Van Auken 2000). Regardless of the mechanism, woody plant expansion, by native and non-indigenous species, is a global phenomenon in grassland and savanna ecosystems (Archer 1994; Binggeli 1996). Over the past 200 years, several *Juniperus* species have rapidly expanded their distribution in North America (Archer 1994). One such example of a rapidly expanding native woody species in the Great Plains is *Juniperus virginiana* (Schmidt & Leatherberry 1995; Coppedge et al. 2001a; Hoch et al. 2002). *J. virginiana* is indigenous to the eastern United States (east of the 100th meridian), but in the prairies of the Great Plains it was historically excluded by fire except on isolated sites too rough or too shallow to produce sufficient fuel to carry fire (Arend 1950; Bragg & Hurlbert 1976; Guyette & McGinnes 1982).

Grassland invasion by *J. virginiana* is an ecological concern because it changes plant and animal community composition (Gehring & Bragg 1992; Coppedge et al. 2001b; Hoch et al. 2002; Chapman et al. 2004a, Horncastle et al. 2005), reduces grassland productivity (Engle et al. 1987; Smith & Stubbendieck 1990; Hoch et al. 2002), and alters biogeochemistry (Norris et al. 2001a; b, Smith and Johnson 2003; 2004). Human health also has been compromised by *J. virginiana* through pollen related allergies and asthma (Levetin & Buck 1980).

Our overall goal was to test the effects of plant community traits on invasion by a native woody plant after keystone processes that previously limited its distribution have been altered. Therefore, we transplanted *J. virginiana* seedlings in plant communities at risk of invasion by *J. virginiana*. We compared *J. virginiana* seedling survival and growth, two phases of the invasion process, in these plant communities and evaluated *J. virginiana* survival and growth relative to plant species richness, diversity, and community composition. Our specific objectives were to 1) test the hypothesis that invasion by *J. virginiana* decreases with increasing plant species diversity, and 2) determine the role that plant species composition as a community trait plays in invasion by *J. virginiana*.

Study Area

Our study was conducted from 2001 to 2003 in north-central Oklahoma at the Oklahoma State University, Research Range (36°03′N, 97°12′W). We selected a study area of contiguous albeit distinct plant communities susceptible to invasion by *J. virginiana*. One site in each of 3 plant communities—tallgrass prairie, old-field, and upland oak forest—was used to evaluate the relationship between *J. virginiana* seedling survival and growth and plant community traits. Before initiating this study, domestic livestock lightly grazed the research sites. We excluded domestic herbivory upon initiation of this study. Average annual precipitation in this area is 831 mm, mostly falling from April through October, and the average frost-free growing period is 203 days (National Oceanic and Atmospheric Administration 1999).

The tallgrass prairie and old-field sites were comprised of fine to fine-loamy soils (Renfrow-Coyle-Grainola Association) derived from weathered shale and sandstone under prairie vegetation (Henley et al. 1987). The dominant herbaceous species on the tallgrass prairie site were *Schizachyrium scoparium*, *Andropogon gerardii*, *Sorghastrum nutans*, *Ambrosia psilostachya, and Symphyotrichum ericoides*. The tallgrass prairie site also contained isolated mottes of *Rhus* spp., *Symphoricarpos occidentalis*, *Prunus angustifolia*, and *J. virginiana*. The old-field was abandoned farmland that was terraced and subjected to soil erosion during cultivation. Vegetation naturally reestablished after cultivation ceased and *J. virginiana* invaded southern and eastern portions of this site. The dominant vegetation on the old-field was *Schizachyrium scoparium*, *Aristida purpurascens, Sorghastrum nutans*, *Ambrosia psilostachya*, and *Lespedeza virginica*. The upland oak forest site had loamy to fine-loamy soils (Stephenville-Darnelli Association) derived from weathered sandstone under oak (Henley et al. 1987). Dominant overstory vegetation on this site was *Quercus stellata* and *Q. marilandica.* The understory vegetation was dominated by *Symphoricarpos occidentalis*, *Dichanthelium oligosanthes*, *Toxicodendron radicans*, *Celtis occidentalis* and *Q. stellata*.

Methods

We investigated *J. virginiana* invasion through a transplant experiment in which 2-year-old *J. virginiana* seedlings were transplanted in a systematic grid design (180 x 180-m) within each plant community. By systematically planting established seedlings, we intended to control for germination effects and the clumped dispersal of *J. virginiana* by birds and mammals (Holthuijzen & Sharik 1985). In each grid, we transplanted 900 seedlings so that each seedling was 6 m away from its neighbors. We established 1 x 1-m permanent plots around each seedling for subsequent vegetation measurements.

We obtained two-year-old, bare-root *J. virginiana* seedlings from the Oklahoma Department of Forestry, Forest Regeneration Center (Goldsby, Oklahoma) and planted the seedlings from during 20-27 March 2001. Our seedling planting protocol included 1) using tree planting bars (Jim-Gem®) to make holes in the soil; 2) placing seedlings in the holes so that their root collars were approximately 2 cm below the soil surface; 3) using tree planting bars to subsequently close the holes; and 4) compacting the ground by foot to eliminate air pockets. We measured seedling height and diameter following the transplant and seedling height, diameter, and survival were measured 6, 18, and 30 months following the transplant. Height of each seedling was measured by recording the standing height of the tallest leader and diameter was measured with digital calipers approximately 1 cm above the soil surface in 2 opposing directions. Seedlings were counted as dead if they did not appear to have chlorophyll or if seedlings were removed from the location where they were transplanted. The average seedling height and diameter at the time of transplant were 255 mm and 4.5 mm, respectively. We combined seedling height and diameter into an index of seedling growth (seedling height x seedling stem area) from which we calculated percentage growth {[(final seedling size - initial seedling size) / initial seedling size]*100}.

We estimated understory canopy cover by species on 1 x 1-m plots centered on each transplanted seedling. We identified canopy cover as occupying 0.25%, 0.5%, 1.0%, >1-5%, >5-10%, >10-25%, >25-50%, >50-75%, >75-95%, or >95-100% of the plot and used cover values or cover-class midpoints in subsequent analysis. We sampled the tallgrass prairie and upland oak sites during the 2002 growing season and the old-field site was sampled during the 2003 growing season. Using the cover data from each plot, we calculated plant species richness and diversity (Shannons H′; Ludwig & Reynolds 1988).

Data Analysis

To determine if species composition varied among and within our plant communities we performed Detrended Correspondance Analysis (DCA) on square-root transformed data using CANOCO version 4.5 (ter Braak & Šmilauer 2002). In the analysis, we down-weighted rare species, detrended by segments, and used non-linear rescaling. Because DCA axis scores are scaled in units of species standard deviations or beta diversity (Hill & Gauch 1980) and most of the variation in species composition is along axis 1, we used axis 1 sample scores as an index of sample species composition in subsequent analyses within each plant community. Results from a DCA analysis of the 3 plant communities confirmed that these communities were distinct in ordination space (Table 1).

We used logistic regression to model the probability of survival of *J. virginana* seedlings 30 months following seedling transplant in relation to plant species richness, species diversity, and species composition (DCA axis 1 sample scores). Seedling survival is a binomial variable (1 = alive, 0 = dead) and was our dependent variable. We evaluated significance of logistic regression parameters using the Wald χ^2 statistic (Hosmer & Lemeshow 2000). We evaluated plant community differences in *J. virginiana* seedling survival using chi-square analysis.

To determine if plant community traits were related to *J. virginiana* seedling growth we used regression analysis (PROC REG; SAS Institute 2000). We created separate models for each plant community trait with seedling growth index (30 months following seedling transplant) as the dependent variable and plant species richness, species diversity, and species composition (DCA axis 1 sample scores) as independent variables.

Results

J. virginiana invasion differed remarkably among plant communities. *J. virginiana* invasion was more probable and was more rapid in the tallgrass prairie over a 30-month period than in the other two plant communities (Fig. 1a; b). In contrast, *J. virginiana* invasion in the upland oak forest was limited by low growth of surviving seedlings, whereas *J. virginiana* invasion in the old-field was limited by both low survival and low growth of surviving seedlings (Fig. 1a; b).

Our data did not support the hypothesis that invasion was reduced with greater plant diversity in the 3 communities we investigated. In no instance did *J. virginiana* survival (Table 2; Fig. 2a; b; Fig. 3a; b; c; d; e; f) or growth (Fig. 4a; b; c; d; Fig. 5a; b; c; d) decline with greater species diversity. In some instances, *J. virginiana* seedling survival and growth increased with increasing species diversity. Seedling growth varied widely regardless of species diversity and this was true across plant communities (Fig. 4a; b; c; d; Fig. 5a; b; c; d). However, high variance in seedling growth in the tallgrass prairie translated into high growth potential among a small but ecologically significant proportion of the seedling population. Again, this high variance was spread equally across the gradient in diversity.

Invasion success of *Juniperus virginiana* was in several respects related to species composition. First, seedling growth and survival differed among the three plant communities (Fig. 1a; b). Invasion, assessed by both seedling survival and growth, was greatest in tallgrass prairie followed by upland oak forest and old-field (Fig. 1a; b). Secondly, *J. virginiana* seedling survival (Fig. 6b;

c; d) and growth (Fig. 7b; c; d) also differed with plant species composition within each plant community, and survival was more sensitive to change in species composition than to change in species richness or diversity. This result was especially true for survival in the old field, where probability of survival varied from 25 to 75%. Lowest survival occurred in plant assemblages that are typically associated with disturbance on fine-textured soil, including species such as *Bothriochloa laguroides* (DCA axis 1 species score = -0.12) and *Amphiachyris dracunculoides* (DCA axis 1 species score = 0.40;Table 2; Table 3; Fig. 6c). Increasing seedling survival in the upland oak forest (Table 2; Fig. 6d) was associated with species normally found in glades (Table 3). Change in seedling survival across the three plant communities (Fig. 6a) and within the tallgrass prairie (Fig. 6b) was not obviously associated with a meaningful change in species composition. The relationship of seedling growth to plant species composition (Fig. 7a; b; c; d), although significant, was slight.

Discussion

Species diversity was either not related or was positively associated with *J. virginiana* invasion. Our results contrast with other invasion studies in which greater species diversity was negatively related to invasion (Tilman 1997; Dukes 2002; Kennedy et al. 2002). Most of the relationships we observed between invasion and plant species diversity were not strong, a result that is consistent with findings from studies using similar plot size (i.e., 1-m^2) in naturally occurring populations of invasive species (Stohlgren et al. 2003). However, our findings support a growing body of literature demonstrating a positive relationship between diversity and invasion (Levine and D’Antonio 1999; Lonsdale 1999; Stohlgren et al. 1999; Thompson et al. 2001; Huston 2004). Factors that relate positively to diversity and to invasion often covary in that factors that facilitate greater species coexistence may be responsible for the greater susceptibility of a community to invasion (Levine and D’Antonio 1999; Thompson et al. 2001; Huston 2004).

That species diversity and invasibility are inconsistently correlated may reflect differences in the nature and design of experiments more than the relationship itself (Zavaleta & Hulvey 2004). Spatial extent of the study, experimental control of factors possibly influencing invasion (i.e., controlled studies), and the response variable measured differ markedly among studies and might influence outcomes. For example, diversity and invasion were negatively correlated in controlled studies conducted at small spatial scales (Tilman 1997; Dukes 2002; Kennedy et al. 2002), were poorly correlated in studies conducted in a natural setting at small spatial scales (Stohlgren et al. 2003), were positively correlated in studies conducted at large spatial scales (Lonsdale 1999; Stohlgren et al. 1999; 2002; 2003), and were positively correlated in studies conducted in a natural setting (Robinson et al. 1995; Planty-Tabacchi et al. 1996; Wiser et al. 1998; Levine and D’Antonio 1999). Our results support those of similar studies (i.e., those conducted in an uncontrolled environment on small plots representing the spatial scale associated with plant neighborhood) (Stohlgren et al. 2003). Utilizing different response variables (e.g., germination, survival, growth, reproduction) in invasion studies potentially influences outcomes because factors such as establishment and impact of invasion vary independently over environmental gradients (Huston 2004; Levine et al. 2004).

J. virginiana seedling success was associated with plant species composition, but was most strongly associated with plant species composition in the disturbed old-field. This result may indicate that *J. virginiana* seedling survival, which we found to be greatest in association with plants typically found on disturbed sites, may be a function of soil resource availability (Davis et al. 2000; Huston 2004). Soil resources and vegetation in old-fields are typically heterogeneous as a result of historical cultivation (Sietman et al. 1994; Tunnell 2002). The tallgrass prairie and upland oak forest sites likely do not display comparable levels of heterogeneity in soil resource availability, even though species composition within the oak forest is more diverse than in the old field. Light, the factor likely limiting *J. virginana* seedling survival and seedling growth (Lassoie et al. 1983), may exert less influence in the upland oak forest than soil resources exert in the old field.

Although our results did not establish a strong relationship between invasion and plant community composition (i.e., proportional representation of species within the community), plant community composition has long been viewed as influencing community invasibility (Elton 1958). Research in tallgrass prairie has recently demonstrated that dominance, measured as the relative proportion of C_4 perennial grasses, was strongly related to invasion by an exotic legume, and dominance was more strongly related to invasion than species richness (Smith et al. 2004). Because acquisition of resources is species-specific, interspecific competition also may dictate invasion success (Grime 1977). Indeed, Levine et al. (2004) concluded from a recent meta-analysis that competition from resident plants is an important contributor to biotic resistance.

The abiotic environment, which we did not address in this paper, undoubtedly influences *J. virginiana* seedling survival and seedling growth (Chapter II). Availability of resources, in particular, has been linked recently to seedling survival and growth of invasive plants (Davis et al. 2000; Davis & Pelsor 2001). Resource availability can alter competition intensity within the resident plant community such that intensity decreases as unused resources increase (Davis et al. 1998; Davis et al. 2000). Thus, opportunistic woody species such as *J. virginiana* might invade more successfully if resource availability reduces the competition intensity of resident vegetation (Davis et al. 2000). Resource availability can change within a plant community as a result of disturbance that alters the use of resources by resident vegetation and biogeochemical processes that increase resource availability (Tilman 1985; Davis et al. 2000). Resources commonly limiting to seedling survival and growth include water (Davis et al. 1998; Davis et al. 1999), light (Nicotra et al. 1999; Lin et al. 2002), and soil nutrient availability (Kaelke et al. 2001). Controlled study would elucidate the relationship between resource availability and *J. virginiana* invasion.

Perhaps the most enlightening aspect of our results is that a few rapidly growing *J. virginiana* individuals distributed across the plant species diversity and species composition gradient hold greatest potential for altering ecosystems.

This was especially the case in the tallgrass prairie where a few *J. virginiana* seedlings grew much more rapidly than the average. As was the case with mean growth rate, these rapidly growing individuals were equally spread across the diversity gradient. This result is ecologically significant because these few individuals are more likely to represent effective transformers than slower-growing seedlings in the seedling pool. Transformation occurs when these seedlings continue to rapidly grow (Engle and Kulbeth 1992) and subsequently influence plant and animal community structure (Gehring & Bragg 1992; Coppedge et al. 2001b; Chapman et al. 2004b) and ecosystem function (Norris et al. 2001a; b; Hoch et al. 2002). Moreover, because of their height and area of influence, seedlings that rapidly reach large size are most likely to survive the natural control process of fire (Buehring et al. 1971), and further reduce their exposure to fire by reducing fine fuel loading (Engle et al. 1987; Smith & Stubbendieck 1990).

In the absence of fire, a few rapidly growing *J. virginiana* individuals within a plant community may present the catalyst for accelerated invasion and an eventual irreversible plant community shift to *J. virginiana* woodland (Fuhlendorf et al. 1996, Hoch et al. 2002). Accelerated invasion might occur through a series of positive feedback mechanisms because *J. virginiana* trees in grassland attract frugivorous birds that favor vertical structure (McDonnell 1986; Holthuijzen et al. 1987). Frugivorous birds feeding on *J. virginiana* seed also disperse *J. virginiana* seed into favorable microsites, which often surround trees (Joy & Young 2002) and other perch points (Livingston 1972) utilized by avian dispersers. The strength of positive feedback likely differs among the three plant communities we studied because growth and survival of *J. virginiana* differ. Thus, the rate of conversion to *J. virginiana* woodlands would also vary among the three plant communities we studied.

Implications

All habitats studied here are susceptible to invasion, differing only in the probable rates of conversion to *J. virginiana* woodland. These data suggest that management to preempt *J. virginiana* invasion or to remove established invaders initially should target tallgrass prairie areas given the rapid growth of *J. virginiana* in tallgrass prairie. Eliminating isolated, fruit-bearing *J. virginiana* trees in tallgrass prairie and old-fields may reduce seed dispersal and circumvent establishment of *J. virginiana* clusters within grasslands. Upland oak forest may succumb to *J. virginiana* invasion at slower rates than tallgrass, perhaps allowing more time for management intervention. However, high survival in upland oak forest suggests that invasion and conversion will be inevitable albeit gradual. *J. virginiana* that eventually reach crown height in oak forest may outcompete deciduous trees, shade new recruits, and increase the risk of fire damage to oak forest. Exhaustive efforts to remove invading *J. virginiana* appear justified especially in tallgrass prairie but also in old-growth oak forest and old-growth juniper stands because conservation of these rare ecosystems is a priority (Clark 2003).

References

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *Am. Nat.* 134: 545-561.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. Pages 13-68 in Vavra, M., Laycock, W. & Pieper, R. eds. Ecological Implications of Livestock Herbivory in the West. Denver (CO): Society for Range Management.

Arend, J. L. 1950. Influence of fire and soil on distribution of eastern redcedar in the Ozarks. *J. For.* 48: 129-130.

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. *J. Veg. Sci.* 7: 121-124.

Bragg, T. B. & Hurlbert, L. C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.* 29: 19-24.

Buehring, N., Santelmann, P. W. & Elwell, H. M. 1971. Responses of eastern redcedar to control procedures. *J. Range Manage.* 24: 378-382.

Callaway, R. W., Thelen, G. C., Rodriguez, A. & Holben W. E. 2004 Soil biota and exotic plant invasion. *Nature* 427:731-733.

Chapman, R. N., Engle, D. M., Masters, R. E. & Leslie, D. M. Jr. 2004a. Tree invasion constrains the influence of herbaceous structure in grassland bird habitats. *Écoscience* 11: 55-63.

Chapman, R. N., Engle, D. M., Masters, R. E. & Leslie, D. M. Jr. 2004b. Grassland vegetation and bird communities in the southern Great Plains of North America. *Ag. Ecosystems Environ.* 104: 577-585.

Clark, S. L. 2003. Stand dynamics of an old-growth forest in the Cross Timbres of Oklahoma. Ph.D. Dissertation, Oklahoma State Univ., Stillwater, Oklahoma.

Coppedge, B. R., Engle, D. M., Fuhlendorf, S. D., Masters, R. E. & Gregory, M. S. 2001a. Urban sprawl and juniper encroachment effects on abundance of wintering passerines in Oklahoma. In: Bowman R and Marzluff J (eds) Avian Ecology in an Urbanizing World, pp 225-242. Kluwer Academic Publishers, Boston, MA.

Coppedge, B. R., Engle, D. M., Masters, R. E. & Gregory, M. S. 2001b. Avian responses to landscape change in fragmented southern Great Plains grasslands. *Ecol. Appl.* 11: 47-59.

Davis, M. A., Grime, J. P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88: 528-534.

Davis, M. A. & Pelsor, M. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecol. Lett.* 4: 421-428.

Davis, M. A., Wrage, K. J. & Reich, P. B. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *J. Ecol.* 86: 652-661.

Davis, M. A., Wrage, K. J., Reich, P. B., Tjoelker, M. G., Schaeffer, T. & Muermann, C. 1999. Survival, growth, photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. *Plant Ecol.* 145:341-350.

Dukes, J. S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. *Ecol. Appl.* 12:602-617.

Elton, C. S. 1958. The ecology of invasions by animals and plants. The University of Chicago, London, UK.

Engle, D. M., Stritzke, J. F. & Claypool, P. L. 1987. Herbage standing crop around eastern redcedar trees. *J. Range Manage.* 40: 237-239.

Engle, D. M. & Kulbeth, J. D. 1992. Growth dynamics of crowns of eastern redcedar at three locations in Oklahoma. *J. Range Manage.* 45: 301-305.

Fuhlendorf, S. D., Smeins, F. E. & Grant, W. E. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. *Ecol. Model.* 90: 245-255.

Gehring, J. L. & Bragg, T. B. 1992. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. *Am. Midl. Nat.* 128: 209-217.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat*. 111: 1169-1194.

Guyette, R. & McGinnes, E. A. Jr. 1982. Fire history of an Ozark glade in Missouri. *Trans. Mo. Academy Sci.* 16: 85-93.

Henley, J., Gelnar, R. D. & Mayhugh, R. E. 1987. Soil survey of Payne County, Oklahoma. USDA, Soil Conserv. Serv. Washington, DC, US.

Hill, M. O. & Gauch, H. G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.

Hobbs, R. J. & Huenneke, L. F. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* 6: 324-337.

Hoch, G. A., Briggs, J. M. & Johnson, L. C. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5: 578-586.

Holthuijzen, A. M. A. & Sharik, T. L. 1985. The red cedar (*Juniperus Virginiana* L) seed shadow along a fenceline. *Am. Midl. Nat.* 113: 200-202.

Holthuijzen, A. M. A., Sharik, T. L. & Fraser, J. D. 1987. Dispersal of eastern red cedar (*Juniperus virginiana*) into pastures - an overview. *Can. J. Bot.* 65: 1092-1095.

Horncastle, V. J., Hellgren, E. C., Mayer, P. M., Ganguli, A. C., Engle, D. M. & Leslie, D. M. Jr. 2005. Implications of invasion by eastern redcedar (*Juniperus virginiana*) on community structure of small mammals in the southern Great Plains. *J. Mammal*: (*in press*).

Hosmer, D. W. & Lemeshow, S. 2000. Applied Logistic Regression. Wiley, New York, NY, US.

Huston, M. A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity Distrib.* 10: 167-178.

Joy, D. A. & Young D. R. 2002. Promotion of mid-successional seedling recruitment and establishment by *Juniperus virginiana* in a coastal environment. *Plant Ecol.* 160: 125-135.

Kaelke, C. M., Kruger, E. L. & Reich, P. B. 2001. Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light availability gradient. *Can. J. For. Res.* 31: 1602-1616.

Kennedy, T. A., Naeem, S., Howe, K. M., Knops, J. M. H., Tilman, D. & Reich, P. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417: 636-638.

Larson, D. L., Anderson, P. J. & Newton, W. 2001. Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecol. Appl.* 11: 128-141.

Lassoie, J. P., Dougherty, P. M., Reich, P. B., Hinckley, T. M., Metcalf, C. M. & Dina, S. J. 1983. Ecophysiological investigations of understory eastern redcedar in central Missouri. *Ecol.* 64: 1355-1366.

Levine, J. M. & D'Antonio, C. M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15-26.

Levine, J. M., Adler, P. B. & Yelenik, S. G. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Letters* 7: 975-989.

Levetin, E. & Buck, P. 1980. Hay fever plants in Oklahoma. *Ann. Allergy* 45: 26-32.

Lin, J., Harcombe P. A,, Fulton, M. R. & Hall, R. W. 2002. Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. *Oecologia* 132: 428-435.

Livingston, R. B. 1972. Influence of birds, stones and soil on the establishment of pasture Juniper, *Juniperus communis*, and red cedar, *J. virginiana* in New England pastures. *Ecol.* 53: 1141-1147.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522-1536.

Ludwig, J. A. & Reynolds, J. F. 1988. Statistical ecology. Wiley, New York, NY, US.

McDonnell, M. J. 1986. Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bull. Torrey Bot. Club* 113: 6-11.

National Oceanic and Atmospheric Administration. 1999. Climatological data annual summary, Okla. Vol. 107, Num. 13.

Nicotra, A. B., Chazdon, R. L. & Iriatre, S. V. B. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80: 1908-1926.

Norris, M. D., Blair, J. M. & Johnson, L. C. 2001a. Land cover change in eastern Kansas: litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. *Can. J. Bot.* 79: 214-222.

Norris, M. D., Blair, J. M., Johnson, L. C. & McKane, R. B. 2001b. Assessing changes in biomass, productivity, and C and N stores following *Juniperus* *virginiana* forest expansion into tallgrass prairie. *Can. J. For. Res.* 31: 1940-1946.

Planty-Tabacchi, A. M., Tabacchi, E., Naiman, R. J., DeFerriari, C. & Decamps, H. 1996. Invasibility of species rich communities in riparian zones. *Conserv. Biol.* 10: 598-607.

Rejmánek, M. & Richardson, D. M. 1996. What attributes make some plant species more invasive? *Ecology* 77:1655-1661.

Robinson, G. R., Quinn, J. F. & Stanton, M. L. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76: 786-794.

SAS Institute. 2000. SAS/STAT user's guide. Release 8.1. SAS Institute, Cary, North Carolina.

Schmidt, T. L. & Leatherberry E. C. 1995. Expansion of eastern redcedar in the lower Midwest. *North. J. Appl. For.* 12: 180-183.

Sietman, B. E., Fothergill, W. B. & Finck, E. J. 1994. Effects of haying and old-field succession on small mammals in tallgrass prairie. *Am. Midl. Nat.* 131: 1-8.

Smith, D. L. & Johnson, L. C. 2003. Expansion of *Juniperus* in the Great Plains: changes in soil organic carbon dynamics. *Global Biogeochem. Cy*. 17: 1-12.

Smith, D. L. & Johnson, L. C. 2004. Vegetation-mediated changes in microclimate reduce soil respiration as woodlands expand into grasslands. *Ecology* 85: 3348-3361.

Smith, M. D. & Knapp, A. K. 2001. Size of the local species pool determines invasibility of a C4-dominated grassland. *Oikos* 92: 55-61.

Smith, M. D., Wilcox, J. C., Kelly, T. & Knapp, A. K. 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106: 253-262.

Smith, S. D. & Stubbendieck, J. 1990. Production of tallgrass prairie herbs below eastern redcedar. *Prairie Nat.* 22: 13-18

Stohlgren T. J., Barnett, D. T. & Kartesz, J.T. 2003. The rich get richer: patterns of plant invasions in the United States. *Front. Ecol.* 1: 11-14.

Stohlgren, T. J., Binkley, D., Chong, G. W., Kalkhan, M. A., Schell, L. D., Bull, K. A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* 69: 25-46.

Stohlgren, T. J., Chong, G. W., Schell, L. D., Rimar, K. A., Otsuki, Y., Lee, M., Kalkhan, M. A. & Villa, C. A. 2002. Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. *Environ. Manage.* 29: 566-577.

Symsted, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81: 99-109.

ter Braak, C. J. F. & Šmilauer, P. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY.

Thompson, K., Hodgson, J. G., Grime J. P. & Burke, M. J. W. 2001. Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *J. Ecol*. 89: 1054-1060.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat*. 125: 827-852.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81-92.

Tunnell, S. J. 2002. The importance of topographic gradients in an Oklahoma old field. In: Vegetation dynamics following cessation of severe disturbance in an old field. Ph.D. Dissertation, Oklahoma State Univ., Stillwater, Oklahoma.

USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA US.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annu. Rev. Ecol. Syst.* 31: 197-215.

Williamson, M. H. & Fitter, A. 1996. The characters of successful invaders. *Biol. Conserv.* 78: 163-170.

Wiser, S. K., Allen, R. B., Clinton, P. W. & Platt, K. H. 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79: 2071-2081.

Zavaleta, E.S. & Hulvey. K. B. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306: 1175-1177.

Table 1. Mean ($\bar{x}$) and standard error (SE) of plant community traits sampled on 1 x 1-m quadrats in tallgrass prairie, old field, and upland oak forest vegetation in the southern Great Plains.

Plant Community	Species Richness	Shannon's H'	DCA Axis 1 Sample Scores
Tallgrass Prairie	16 ± 0.1	1.7 ± 0.01	2.0 ± 0.01
Old-field	12 ± 0.1	1.3 ± 0.10	1.0 ± 0.02
Upland Oak Forest	6 ± 0.1	1.1 ± 0.02	3.8 ± 0.03

Table 2. Logistic regression models of seedling survival (dependant variable) using species richness, species diversity (Shannon's H′), and DCA axis one sample scores as independent variables.

Site/Variable	Parameter Estimate	Standard Error	Wald χ^2	P
Across Plant Communities				
Species Richness	0.01	0.01	3.21	0.073
Shannons H′	0.15	0.08	3.46	0.063
DCA Axis 1	0.05	0.03	2.34	0.126
Tallgrass Prairie				
Species Richness	0.08	0.02	16.46	<0.001
Shannons H′	0.49	0.21	5.22	0.022
DCA Axis 1	-0.29	0.16	3.50	0.062
Old-field				
Species Richness	0.04	0.02	2.85	0.091
Shannons H′	-0.11	0.17	0.40	0.527
DCA Axis 1	0.74	0.13	34.97	<0.001
Upland Oak Forest				
Species Richness	0.02	0.03	0.76	0.383
Shannons H′	0.05	0.14	0.13	0.724
DCA Axis 1	-0.22	0.08	6.77	0.009

Table 3. Detrended correspondence analysis axis 1 species scores for an inclusive list of the 10 most frequently occurring plant species within the tallgrass prairie, old-field, and upland oak forest plant communities.

	Separate DCA of each plant community			
Species	Tallgrass prairie	Old-field	Upland oak forest	Combined DCA (All three sites)
	---------------- DCA axis 1 sample scores ----------------			
Ambrosia psilostachya	0.16[†]	0.65[†]	0.95	1.65[†]
Andropogon gerardii	1.73[†]	3.24	0.17[†]	2.43[†]
Aristida purpurascens	-2.10	3.95[†]	—*	-0.56
Bromus japonicus	2.14[†]	-1.35	0.95	2.41
Carex sp.	1.26[†]	2.84[†]	1.50[†]	2.45[†]
Celtis occidentalis	3.20	2.73	3.30[†]	4.79
Coelorachis cylindrica	-0.16[†]	3.05	0.16	1.72
Dichanthelium oligosanthes	1.66[†]	1.37[†]	1.57[†]	3.18[†]
Dichanthelium scoparium	0.26	4.17[†]	1.38	0.49
Digitaria cognatum	0.91	2.38[†]	0.45	0.88[†]
Lespedeza virginica	0.49	2.80[†]	0.37	0.12
Parthenocissus quinquefolia	4.44	2.64	3.54[†]	4.93
Quercus stellata	3.68	4.18	4.26[†]	6.07
Schizachyrium scoparium	0.61[†]	2.20[†]	-0.29	1.00[†]
Smilax bona-nox	3.70	—*	3.08[†]	4.47
Sorghastrum nutans	0.62[†]	2.39[†]	-0.60	0.82[†]
Sporobolus compositus	0.43[†]	-0.34	0.90	2.33[†]
Symphoricarpos occidentalis	3.18	0.77	2.62[†]	3.72[†]
Symphyotrichum ericoides	1.24[†]	1.01[†]	0.16	1.48[†]
Tridens flavus	2.57	2.57	1.22[†]	3.43
Ulmus americana	4.26	-0.38	2.40[†]	4.33

* not present in this plant community

[†] most frequently occurring species within a plant community

Figure Legends

Figure 1 (a, b). Growth and survival of *J. virginiana* seedlings 8, 20, and 30 months following transplant within the tallgrass prairie, old-field, and upland oak forest plant communities in the southern Great Plains. (A) Mean *J. virginiana* seedling growth index ± standard error of established seedlings in the tallgrass prairie (SD = 1691; %CV = 75), old-field (SD = 689; %CV = 160), and upland oak forest (SD = 370; %CV = 115). (B) *J. virginiana* seedling survival in each plant community. *J. virginiana* seedling survival did not differ between the tallgrass prairie and the upland oak forest. Seedling survival was lower in the old-field than in the other two communities (χ^2=42.9, d.f.=2, P<0.001).

Figure 2 (a, b). Logistic regression relationship of *J. virginiana* seedling survival as a function of plant community traits (with 95% confidence intervals for predicted values) for each of 3 plant communities. (A) Logistic regression relationship of *J. virginiana* seedling survival as a function of species richness for each of 3 plant communities. (B) Logistic regression relationship of *J. virginiana* seedling survival as a function of Shannon's H' for each of 3 plant communities.

Figure 3 (a, b, c, d, e, f). Logistic regression relationship of *J. virginiana* seedling survival as a function of plant community diversity traits (with 95% confidence intervals for predicted values). (A) Logistic regression relationship of *J. virginiana* seedling survival as a function of plant species richness in the tallgrass prairie. (B) Logistic regression relationship of *J. virginiana* seedling survival as a function of Shannon’s H' in the tallgrass prairie. (C) Logistic regression relationship of *J. virginiana* seedling survival as a function of plant species richness in the old-field. (D) Logistic regression relationship of *J. virginiana* seedling survival as a function of Shannon’s H' in the old-field. (E) Logistic regression relationship of *J. virginiana* seedling survival as a function of plant species richness in the upland oak forest. (F) Logistic regression relationship of *J. virginiana* seedling survival as a function of Shannon’s H' in the upland oak forest.

Figure 4 (a, b, c, d). Regression analysis results of *J. virginiana* seedling growth index as a function of plant species richness. (A) Regression analysis of *J. virginiana* seedling growth index as a function of plant species richness for each of 3 plant communities ($y = 166.0 – 13.8x + 6.5x^2$). (B) Regression analysis of *J. virginiana* seedling growth index as a function of plant species richness in the tallgrass prairie ($y = 844.0 + 87.1x$). (C) Regression analysis of *J. virginiana* seedling growth index as a function of plant species richness in the old-field ($y = -162.2 + 47.2x$). (D) Regression analysis of *J. virginiana* seedling growth index as a function of plant species richness in the upland oak forest ($y = 250.6 – 12.7x + 3.5x^2$).

Figure 5 (a, b, c, d). Regression analysis results of *J. virginiana* seedling growth index as a function of Shannon’s H′. (A) Regression analysis of *J. virginiana* seedling growth index as a function of Shannon’s H′ for each of 3 plant communities ($y = 37.0 + 183.9x + 338.3x^2$). (B) Regression analysis of *J.*

virginiana seedling growth index as a function of Shannon's H′ in tallgrass prairie. (C) Regression analysis of *J. virginiana* seedling growth index as a function of Shannon's H′ in the old-field ($y = -103.3 + 412.7x$). (D) Regression analysis of *J. virginiana* seedling growth index as a function of Shannon's H′ in the upland oak forest ($y = 332.6 – 180.7x + 122.9x^2$).

Figure 6 (a, b, c, d). Logistic regression relationship of *J. virginiana* seedling survival as a function of plant species composition (DCA axis 1 sample scores) (with 95% confidence intervals for predicted values). (A) Logistic regression relationship of *J. virginiana* seedling survival as a function of axis 1 sample scores from a DCA of the 3 plant communities. (B) Logistic regression relationship of *J. virginiana* seedling survival as a function of axis 1 sample scores from a DCA of the tallgrass prairie. (C) Logistic regression relationship of *J. virginiana* seedling survival as a function of axis 1 sample scores from a DCA of the old-field. (D) Logistic regression relationship of *J. virginiana* seedling survival as a function of axis 1 sample scores from a DCA of the upland oak forest.

Figure 7 (a, b, c, d). Regression analysis results of *J. virginiana* seedling growth index as a function of plant species composition (DCA Axis 1 sample scores). (A) Regression analysis of *J. virginiana* seedling growth index as a function of axis 1 sample scores from a DCA of the 3 plant communities ($y = -124.7 + 1389x – 288.5x^2$). (B) Regression analysis of *J. virginiana* seedling growth index as a function of axis 1 sample scores from a DCA of the tallgrass prairie ($y = 1087.8 + 1911.9x – 658.0\ x^2$). (C) Regression analysis of *J. virginiana* seedling growth index as a function of axis 1 sample scores from a DCA of the old-field ($y = 1016.0 - 239.83x$). (D) Regression analysis of *J. virginiana* seedling growth index as a function of axis 1 sample scores from a DCA of the upland oak forest ($y = 717.7 – 247.3x + 31.0x^2$).

Figure 1.

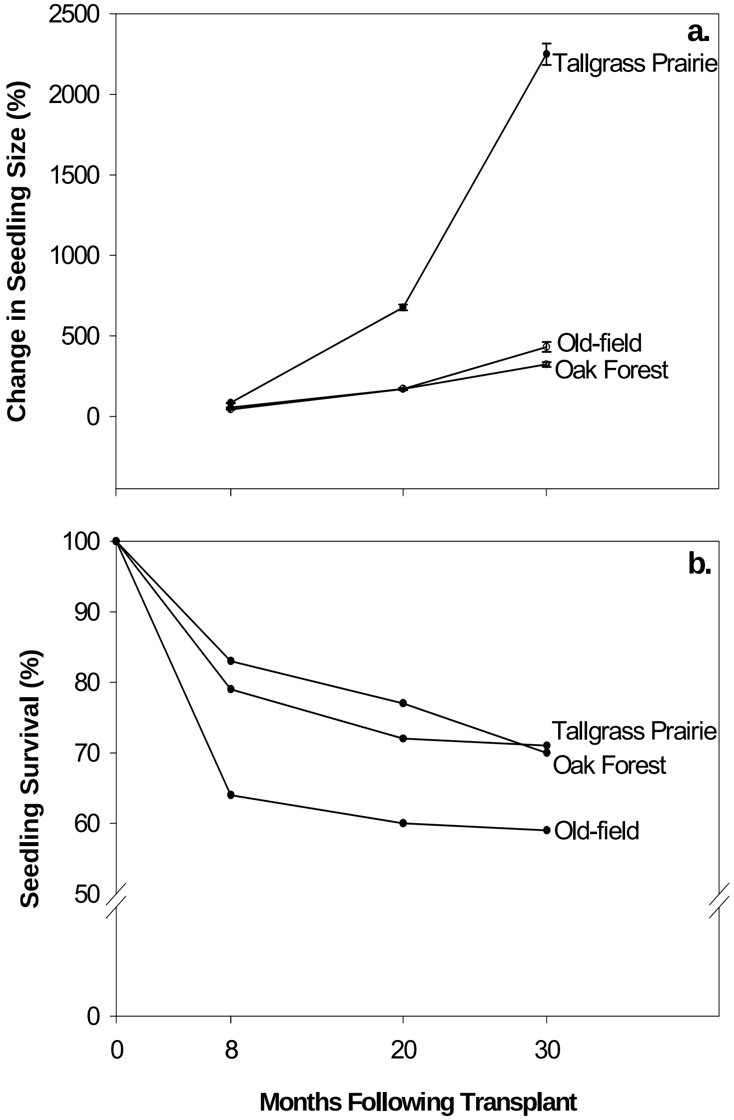

a.
Change in Seedling Size (%)
2500
2000
1500
1000
500
0
Tallgrass Prairie
Old-field
Oak Forest
b.
Seedling Survival (%)
100
90
80
70
60
50
0
Tallgrass Prairie
Oak Forest
Old-field
0
8
20
30
Months Following Transplant

Figure 2.

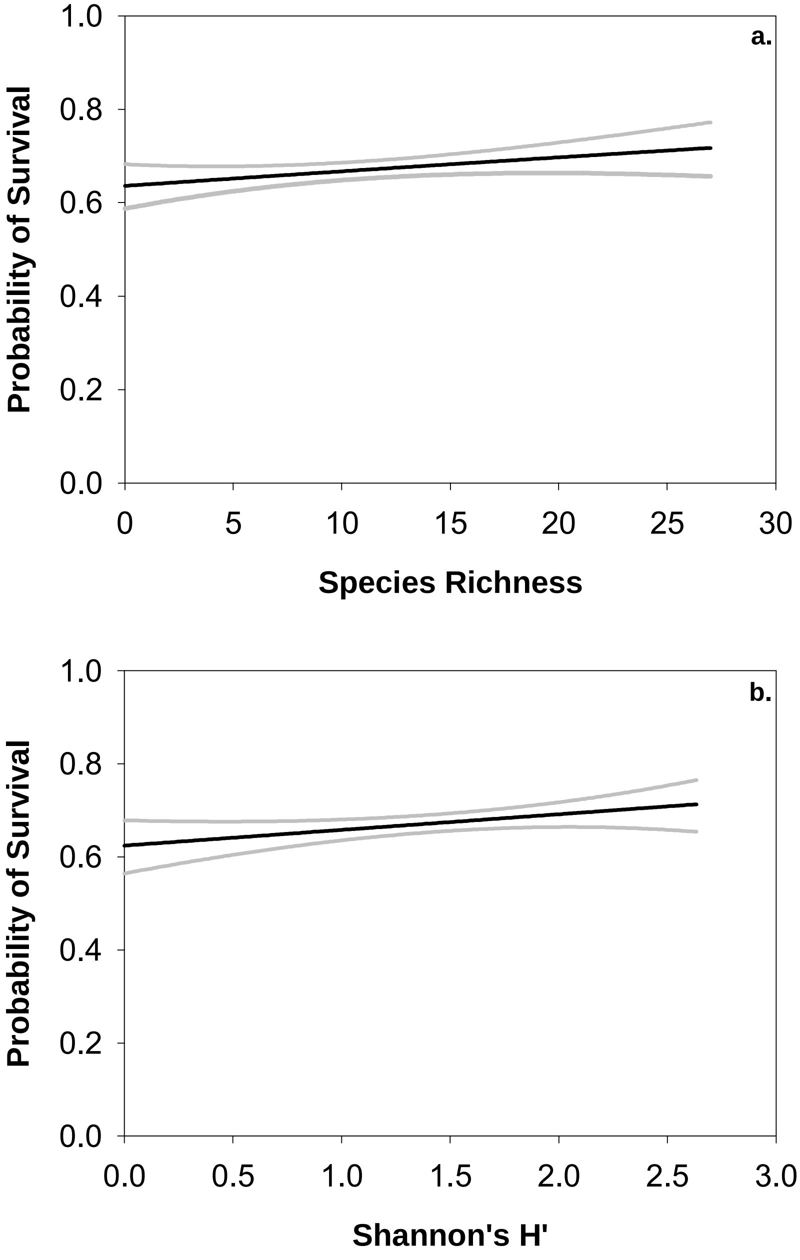

a.
Probability of Survival
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
Species Richness
b.
Probability of Survival
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Shannon's H'

Figure 3

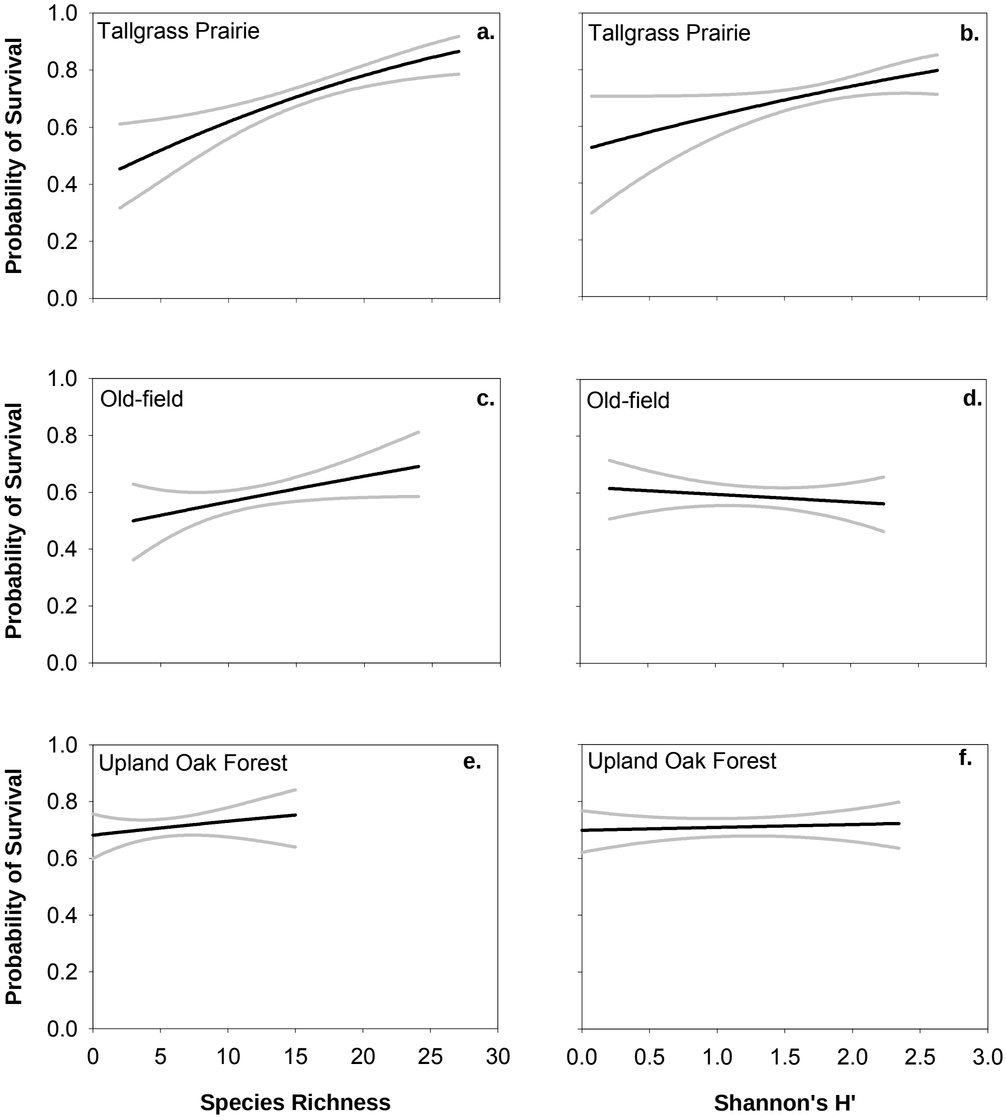
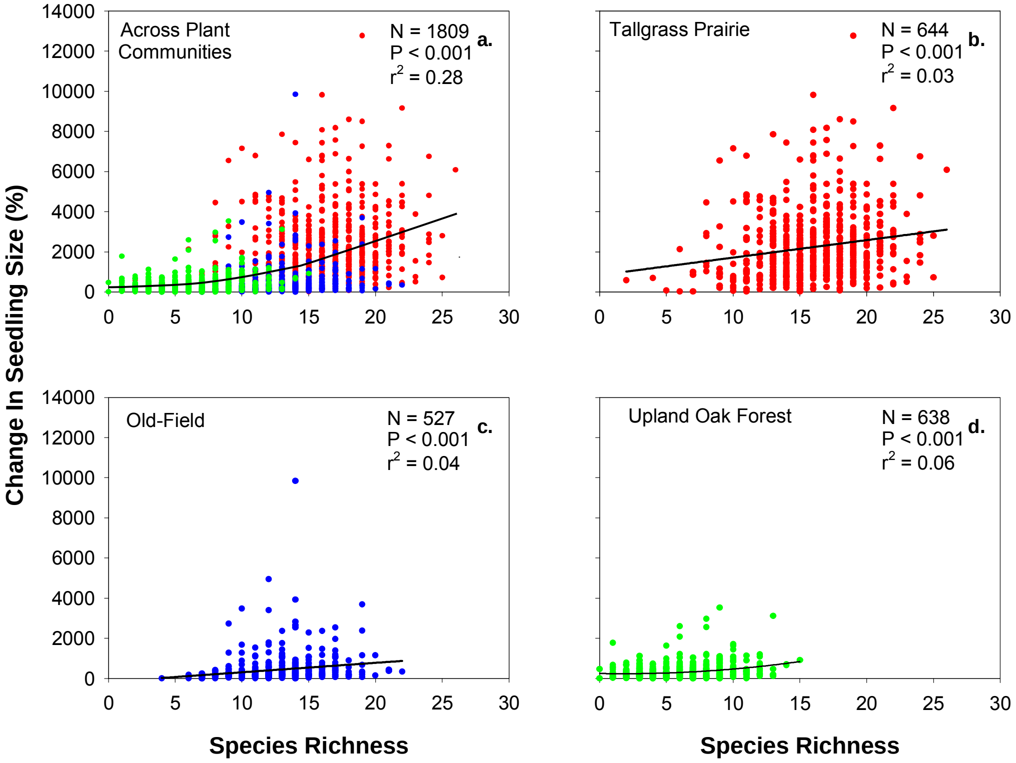

Probability of Survival
1.0
0.8
0.6
0.4
0.2
0.0
Tallgrass Prairie
a.
Tallgrass Prairie
b.
Old-field
c.
Old-field
d.
Upland Oak Forest
e.
Upland Oak Forest
f.
0
5
10
15
20
25
30
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Species Richness
Shannon's H'

Figure 4.



Change In Seedling Size (%)
Across Plant Communities
N = 1809
P < 0.001
r² = 0.28
a.
Tallgrass Prairie
N = 644
P < 0.001
r² = 0.03
b.
Old-Field
N = 527
P < 0.001
r² = 0.04
c.
Upland Oak Forest
N = 638
P < 0.001
r² = 0.06
d.
14000
12000
10000
8000
6000
4000
2000
0
0
5
10
15
20
25
30
Species Richness
Species Richness

Figure 5.

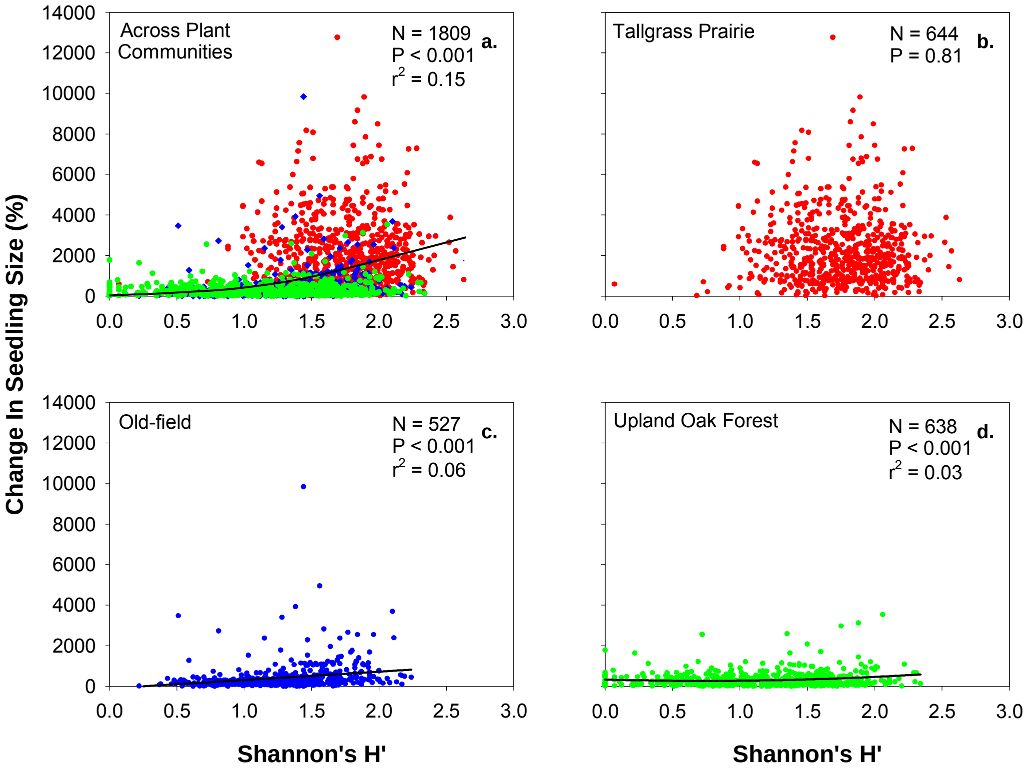

Across Plant Communities
N = 1809
P < 0.001
r² = 0.15
a.
Tallgrass Prairie
N = 644
P = 0.81
b.
Old-field
N = 527
P < 0.001
r² = 0.06
c.
Upland Oak Forest
N = 638
P < 0.001
r² = 0.03
d.
Change In Seedling Size (%)
Shannon's H'
Shannon's H'
0
2000
4000
6000
8000
10000
12000
14000
0.0
0.5
1.0
1.5
2.0
2.5
3.0

Figure 6.

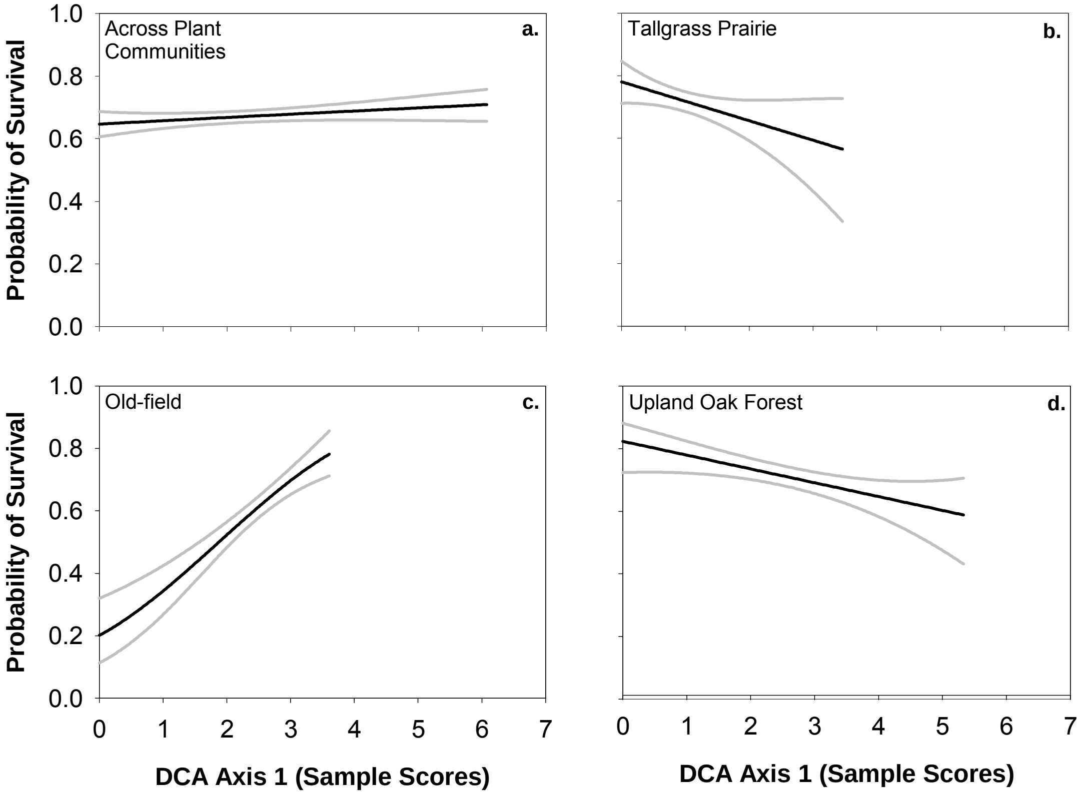
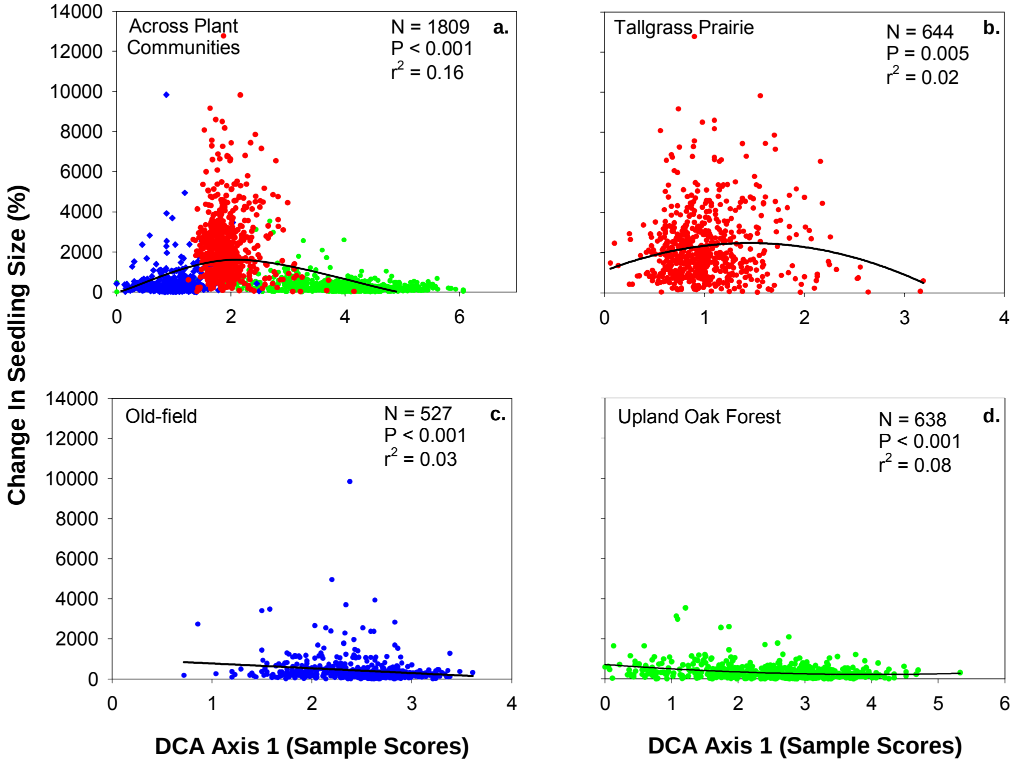

Probability of Survival
1.0
0.8
0.6
0.4
0.2
0.0
Across Plant Communities
a.
Tallgrass Prairie
b.
Old-field
c.
Upland Oak Forest
d.
0
1
2
3
4
5
6
7
DCA Axis 1 (Sample Scores)

Figure 7.


Change In Seedling Size (%)
14000
12000
10000
8000
6000
4000
2000
0
Across Plant Communities
N = 1809
P < 0.001
r2 = 0.16
a.
0
2
4
6
Tallgrass Prairie
N = 644
P = 0.005
r2 = 0.02
b.
0
1
2
3
4
Old-field
N = 527
P < 0.001
r2 = 0.03
c.
0
1
2
3
4
Upland Oak Forest
N = 638
P < 0.001
r2 = 0.08
d.
0
1
2
3
4
5
6
DCA Axis 1 (Sample Scores)
DCA Axis 1 (Sample Scores)

Chapter II

INFLUENCE OF RESOURCE AVAILABILITY ON *JUNIPERUS VIRGINIANA* EXPANSION IN A FOREST–PRAIRIE ECOTONE

Abstract: Widespread expansion of the fire-intolerant species, *Juniperus virginiana*, in North America where fire has largely been removed has prompted the need to identify mechanisms driving *J. virginiana* expansion. We transplanted *J. virginiana* seedlings in three plant communities within an oak forest–tallgrass prairie ecotone. We evaluated *J. virginiana* seedling survival and seedling growth, two important phases in woody plant expansion, relative to two belowground resource factors, soil texture (clay content, as an index to available soil water) and plant available nitrogen (PAN) and an aboveground factor, photosynthetic active radiation (PAR). In each plant community we transplanted 900 two-year-old *J. virginiana* seedlings in a systematic grid design and monitored *J. virginiana* seedling survival and growth 6, 18, and 30 months following transplant. Seedling survival and seedling growth were related to soil and PAR data collected on 1-m^2 quadrats centered on each transplanted seedling using path analysis at two spatial scales (144 m^2 and 2916 m^2). *J. virginiana* seedling survival and seedling growth were inconsistently related to a single resource factor as a direct influence across plant communities and spatial scales in this ecotone. However, indirect and direct influence of a single belowground resource factor, soil clay content, emerged as an integrating resource factor that drives *J. virginiana* seedling survival and seedling growth. The direct and indirect effects of soil texture together provide insight into the rate of *J. virginiana* expansion within the oak forest-tallgrass prairie ecotone.

Key words: crosstimbers forest, eastern redcedar, limiting factors, seedlings, soil texture, tallgrass prairie, woody plant expansion

INTRODUCTION

Woody plant expansion is a global phenomenon in grassland and savanna ecosystems (Archer 1994, Binggeli 1996). Factors often attributed as drivers of woody plant expansion include livestock introduction, fire suppression, and climate change (Archer 1989, Van Auken 2000). A recent synthesis of over two decades of research on woody plant expansion in the tallgrass prairie of central North America illustrates the widespread expansion of woody plants in the absence of fire (Briggs et al. 2005). This synthesis revealed that re-introduction of historic fire regimes may not reverse woody plant expansion in tallgrass prairie (Briggs et al. 2005), furthermore, infrequent fire can accelerate woody plant expansion in tallgrass prairie (Briggs et al. 2005).

Models of plant community dynamics based on plant-soil interactions characterized by limiting resources (Lauenroth and Coffin 1992, Seastedt and Knapp 1993, Burke et al. 1998) might be useful in understanding successional pathways of plant communities or the resources of greatest importance in woody plant expansion in the absence of fire. Limiting resources driving plant-soil interactions can change along an increasing precipitation gradient and are associated with a shift from belowground-driven plant community dynamics to aboveground-driven plant community dynamics (Lauenroth and Coffin 1992, Burke et al. 1998). Arid grassland communities, for example, are thought to be primarily driven by water limitation (Noy-Meir 1973, Lauenroth et al. 1978). In contrast, forest-dominated plant communities are generally found at upper portions of the precipitation gradient and are driven primarily by light limitation (Burke et al. 1998). At intermediate locations along the annual precipitation gradient (approximately 700 to 1200mm) plant community dynamics can be indeterminate, that is, plant community dynamics can be driven by either belowground or aboveground plant-soil interactions (Lauenroth and Coffin 1992). For example, sub-humid to humid grassland communities that span this precipitation region are thought to be driven by spatial and temporal limitations of water, nitrogen, and light (Seastedt and Knapp 1993). Although plant-soil interactions are thought to change along an increasing precipitation gradient, soil texture can modify plant-soil interactions because of the influence of soil texture on water infiltration and water availability (McBride and Strahan 1984, Burke et al. 1998). Thus, in forest–grassland ecotones, like the upland oak forest–tallgrass prairie ecotone of central North America, soil texture or other topoedaphic factors can modify plant community dynamics (Knapp et al. 1993, Tunnell 2002).

For some plant communities, resource-mediated plant-soil interactions are overshadowed by historic disturbance regimes like fire. Several *Juniperus* species in North America were historically limited in distribution by natural and man-made fire (Bragg and Hurlbert 1976, Guyette and McGinnes 1982, Miller and Rose 1995). *Juniperus virginiana* is one such example of a species that has expanded in grasslands following anthropogenic alteration of historic fire regimes (Schmidt and Leatherberry 1995, Coppedge et al. 2001a, Hoch et al. 2002). Expansion of *J. virginiana* is an ecological concern because it changes plant and animal community composition (Gehring and Bragg 1992, Coppedge et al. 2001b, Horncastle et al. 2005), reduces grassland productivity (Engle et al. 1987, Smith and Stubbendieck 1990), and alters biogeochemistry (Norris et al. 2001a, b, Smith and Johnson 2004). In the absence of fire, other factors such as resource availability might drive plant community dynamics to include woody plant expansion. Resource availability, for example, has been recently linked to the success of invasive plants establishing in grasslands (Davis et al. 2000, Davis and Pelsor 2001).

Resources commonly limiting to woody seedling survival and seedling growth include water (Davis et al. 1998, Davis et al. 1999), light (Nicotra et al. 1999, Lin et al. 2002), and soil nutrient availability (Kaelke et al. 2001). The availability of limiting resources can alter competition intensity within the resident plant community such that competition intensity decreases as unused resources increase (Davis et al. 1998, Davis et al. 2000). Resource availability can change within a plant community as a result of disturbance that alters the use of resources by resident vegetation, and by biogeochemical processes that increase resource availability (Tilman 1985, Davis et al. 2000).

Our objective was to determine if a single belowground resource constrains *J. virginiana* expansion across plant communities within a common precipitation zone in an oak forest-tallgrass prairie ecotone as opposed to a mixture of belowground and aboveground factors that vary with plant community. The oak forest–tallgrass prairie ecotone is located in a geologic transition zone with upland oak forest sites occurring on sandstone-derived soils and tallgrass prairie sites occurring on shale- and limestone-derived soils (Dyksterhuis 1948, Hoagland et al. 1999). We transplanted *J. virginiana* seedlings in three plant communities within an oak forest–tallgrass prairie ecotone to evaluate *J. virginiana* seedling survival and seedling growth, two important phases in woody plant expansion, relative to two belowground factors, soil texture (percent clay) and plant available nitrogen (PAN) and an aboveground factor, photosynthetic active radiation (PAR).

STUDY AREA

Our study was conducted from 2001 to 2003 in north-central Oklahoma at the Oklahoma State University, Research Range (36°03′N, 97°12′W). We selected a study area of contiguous albeit distinct plant communities within an oak forest-tallgrass prairie ecotone. Upland oak (*Quercus* spp.) forests of Oklahoma, commonly referred to as the cross timbers, are considered to be the western extent of the eastern deciduous forest (Hoagland et al. 1999). The cross timbers ecosystem consists of a mosaic of upland oak forest, savanna, and prairie habitat currently encompassing approximately 4.8 million hectares from southeastern Kansas to north-central Texas (Hoagland et al. 1999).

One site in each of 3 plant communities—old-field, tallgrass prairie, and upland oak forest—was used to evaluate the relationship between *J. virginiana* seedling survival and growth and resource availability. Before initiating this study, domestic livestock lightly grazed the research sites. We excluded domestic herbivory upon initiation of this study. Average annual precipitation in this area is 831 mm, mostly falling from April through October, and the average frost-free growing period is 203 days (National Oceanic and Atmospheric Administration 1999).

The tallgrass prairie and old-field sites were comprised of fine to fine-loamy soils (Renfrow-Coyle-Grainola Association) derived from weathered shale, limestone, and sandstone under prairie vegetation (Henley et al. 1987). The dominant herbaceous species on the tallgrass prairie site were *Schizachyrium scoparium*, *Andropogon gerardii*, *Sorghastrum nutans*, *Ambrosia psilostachya, and Symphyotrichum ericoides*. The tallgrass prairie site also contained isolated mottes of *Rhus* spp., *Symphoricarpos occidentalis*, *Prunus angustifolia*, and *J. virginiana*. The old-field was abandoned farmland that was terraced and subjected to soil erosion during cultivation. Vegetation naturally reestablished after cultivation ceased and *J. virginiana* invaded southern and eastern portions of this site. The dominant vegetation on the old-field was *Schizachyrium scoparium*, *Aristida purpurascens, Sorghastrum nutans*, *Ambrosia psilostachya*, and *Lespedeza virginica*. The upland oak forest site had loamy to fine-loamy soils (Stephenville-Darnelli Association) derived from weathered sandstone under oak (Henley et al. 1987). Dominant overstory vegetation on this site was *Quercus stellata* and *Q. marilandica.* The understory vegetation was dominated by *Symphoricarpos occidentalis*, *Dichanthelium oligosanthes*, *Toxicodendron radicans*, *Celtis occidentalis* and *Q. stellata*.

METHODS

We investigated *J. virginiana* expansion through a transplant experiment in which 2-year-old *J. virginiana* seedlings were transplanted in a systematic grid design (180 x 180-m) within each plant community (Figure 1). By systematically planting established seedlings, we intended to control for germination effects and the clumped dispersal of *J. virginiana* by birds and mammals (Holthuijzen and Sharik 1985). In each grid we transplanted 900 seedlings so that each seedling was 6 m away from its neighbors. We established 1 x 1-m permanent plots around each seedling for subsequent soil and vegetation measurements.

We utilized this spatial design to investigate the effects of scale (i.e., increasing grain size) on the relationship between resource availability and *J. virginiana* seedling survival and seedling growth. Spatial dependence of ecological processes has been found in large landscape-scale investigations (Godfray and Lawton 2001, Fuhlendorf et al. 2002) as well as small-scale plot investigations (Purves and Law 2002). Therefore we selected two spatial scales to investigate the effects of scale on the relationship between resource availability and *J. virginiana* seedling survival and seedling growth. We used

ArcView GIS software v.3.3 with the Moving Windows Statistics v.1.1a extension to aggregate groups of 4 and 81 adjacent samples into single data units (Isaaks and Srivastava 1989) which correspond to areas of 144-m^2 and 2916-m^2 respectively (Table 1.). We allowed moving windows to overlap and calculated the mean for each window.

We obtained two-year-old, bare-root *J. virginiana* seedlings from the Oklahoma Department of Forestry, Forest Regeneration Center (Goldsby, Oklahoma) and planted the seedlings during 20-27 March 2001. Our seedling planting protocol included 1) using tree planting bars (Jim-Gem®) to make holes in the soil; 2) placing seedlings in the holes so that their root collars were approximately 2 cm below the soil surface; 3) using tree planting bars to subsequently close the holes; and 4) compacting the ground by foot to eliminate air pockets. We measured seedling height and diameter following the transplant and seedling height, diameter, and survival were measured 6, 18, and 30 months following the transplant. Height of each seedling was measured by recording the standing height of the tallest leader and diameter was measured with digital calipers approximately 1 cm above the soil surface in 2 opposing directions. Seedlings were counted as dead if they did not appear to have chlorophyll or if seedlings were removed from the location where they were transplanted. The average seedling height and diameter at the time of transplant was 255 mm and 4.5 mm respectively. We combined seedling height and diameter into an index of seedling growth (seedling height x seedling stem area) from which we calculated percentage growth {[(final seedling size - initial seedling size) / initial seedling size]*100}.

We sampled soil chemical and physical properties throughout each grid during May – June 2001. Around each eastern redcedar seedling, 4 soil cores (15cm deep) were collected and combined to form a composite sample, dried in a forced-air oven at 60 °C, and ground to pass a 2mm sieve. Soils were analyzed for texture, nitrate-nitrogen (NO_3-N), ammonium-nitrogen (NH_4-N), pH, phosphorus, and potassium. We focus on plant available nitrogen (PAN) because nitrogen is often recognized as the most limiting nutrient to plant growth (Blair et al. 1998) and percent clay because the clay fraction of soil is important indicator of soil water infiltration rates and water retention (Harlan 1957). In using percent clay as an indicator of plant available water, we assume that as the clay fraction of soil increases the amount of water available to plants decreases. Soil nitrate and ammonium were extracted with 1 molar potassium chloride solution. Both were analyzed by flow injection utilizing the cadmium reduction method for nitrate and the salicylate method for ammonium. We used the sum of our nitrate and ammonium values to estimate total plant available nitrogen (Schlesinger et al. 1996). Soil texture was determined through the hydrometer method (Gee and Bauder 1986). Photosynthetic Active Radiation (PAR) was measured above each seedling with a LI-190SA Quantum Sensor (LI-COR, Inc., Lincoln, NE, USA) on cloudless days within 75 minutes of solar noon May - July 2002.

DATA ANALYSIS

We used path analysis, a general form of multiple regression (Dewey and Lu 1959, Sokal and Rohlf 1995), to assess effect of resource availability traits on *J. virginiana* seedling survival and seedling growth. Path analysis allowed us to assess the direct and indirect effects of the resource availability traits (predictor variables) on *J. virginiana* seedling survival and seedling growth (criterion variables) (Figure 2). Direct effects between the predictor variables and *J. virginiana* seedling survival and seedling growth were shown with standardized partial regression coefficients and can be greater than one because a standard deviation change in the predictor variable may potentially effect more than one standard deviation change in the criterion variable (Sokal and Rohlf 1995). Indirect effects of the predictor variables (i.e., indirectly influencing *J. virginiana* seedling survival or seedling growth) were shown as Pearson's correlation coefficients. We performed the path analysis using SAS (ver.8 SAS, Inc), and we used $P < 0.05$ to determine significance of path models and direct and indirect effects within path models.

RESULTS

J. virginiana seedling survival and seedling growth, two phases of expansion process, differed across the three plant communities we investigated (Figure 3) as did the three resource factors (Table 1). *J. virginiana* seedling survival was 72% in the tallgrass prairie, 71% in the upland oak forest, and 59% in the old-field grassland. Seedlings in the tallgrass prairie grew more over 30 months than did seedlings in the old-field grassland and upland oak forest (Figure 3).

Path analysis confirmed that resource availability factors that limit *J. virginiana* seedling survival and seedling growth differ among the three sites we investigated (Fig. 4; 5). In fact, resource variables that limit *J. virginiana* seedling survival differ from the resource variables that limit *J. virginiana* seedling growth within a plant community (Fig. 4; 5). Furthermore, the relative importance of resource factors influence on *J. virginiana* seedling survival and seedling growth changes at different spatial scales and overall path model predictability of seedling survival and seedling growth improved with increasing spatial scale (Fig. 4; 5).

J. virginiana seedling survival and seedling growth increased with increasing levels of PAR and PAN. In contrast, *J. virginiana* seedling survival and seedling growth increased with decreasing soil clay content across communities and spatial scales. PAR generally had the strongest direct effect on seedling growth and seedling survival (Figures 4-5). However, there are a few instances where clay had the strongest direct effect on seedling survival and growth (Figure 5 a, d) and seedling survival was poorly related to all of the resource factors in the oak forest (Figure 4c; 5c) suggesting the resource factors that constrain *J. virginiana* expansion vary across plant communities and spatial scale in this ecotone. This supports our hypothesis that multiple resource factors control *J. virginiana* expansion in the ecotone.

However, even stronger evidence supports the alternative hypothesis that soil clay content is the primary resource factor influencing seedling survival and seedling growth. Consistently across communities and spatial scales, clay either directly influenced or indirectly influenced seedling survival and seedling growth (Figures 4-6). Thus, our results provide compelling evidence that factors controlling *J. virginiana* expansion are determinate (i.e., one factor) rather than indeterminant as we had hypothesized. Clay was consistently negatively related to *J. virginiana* seedling survival and seedling growth and positively correlated to PAR, which in turn was consistently positively related to seedling survival and seedling growth (Figure 4-6). PAN had direct influence on seedling survival and seedling growth in a few relationships, but clay was correlated to PAN in most of these. Therefore, these results indicate that soil texture (i.e., clay content) is an integrating factor controlling *J. virginiana* expansion in this ecotone.

DISCUSSION

Plant-soil interactions and resulting plant community dynamics are hypothesized to be driven by limiting resources that vary along a precipitation gradient (Lauenroth and Coffin 1992, Burke et al. 1998). Areas of low precipitation characterized by arid to semi-arid grassland plant communities are postulated to be dominated by belowground constraints, and water is the most limiting resource (Noy Meir 1973, Lauenroth et al. 1978). In contrast, areas of high precipitation characterized by mesic forests are postulated to be dominated by aboveground constraints, and light is the most limiting resource (Kaelke et al.

2001, Lin et al. 2002, Green et al. 2004). In areas of intermediate precipitation, such as sub-humid to humid grasslands, this hypothesis suggests that plant community dynamics are characterized by indeterminate limiting resource factors, commonly water, nitrogen, and light that are spatially and temporarily variable (Lauenroth and Coffin 1992, Seastedt and Knapp 1993, Burke et al. 1998). We applied this hypothesis to the expansion of *J. virginiana* in an oak forest–tallgrass prairie ecotone located within an intermediate precipitation zone by hypothesizing that several factors would control expansion.

When direct effects of resource factors are considered only, our results support the hypothesis that within an intermediate precipitation zone, resource factors influencing success of a single expanding species are indeterminate. That is, *J. virginiana* seedling survival and seedling growth were inconsistently directly related to a single resource factor. Perhaps the most enlightening aspect of our results is that even when soil texture (i.e., percent clay) was not directly related to *J. virginiana* seedling survival and seedling growth, percent clay was consistently indirectly related to seedling survival and seedling growth through its influence on either PAR or PAN. This consistent relationship of clay with *J. virginiana* seedling survival and seedling growth supports the alternative hypothesis that *J. virginiana* expansion in this ecotone is determinant, insomuch that *J. virginiana* expansion can be predicted largely by inherent site characteristics driven directly or indirectly by one single resource variable, soil clay. Our results support the concept that multiple resource factors have the potential to interact to create an integrated limiting condition important to plant community dynamics, or in the case of this study, the survival and growth of a single expanding species (Chapin 1980, Seastedt and Knapp 1993).

Resource factors influencing *J. virginiana* expansion in this ecotone might be expected to not vary because a single belowground factor, soil texture, generally defines plant community composition (i.e. forest versus prairie) in the oak forest–tallgrass prairie ecotone (Dyksterhuis 1948, Bell and Hulbert 1974, Hoagland et al. 1999) and often globally (Walter 1971). Thus, coarse textured soil permits rapid infiltration so that hardwood trees are community dominants, and light, not water or nitrogen, is generally the most limiting resource to plant community dynamics, and as we found, light directly limits expansion of *J. virginiana*. In contrast, when fine-soil texture limits water infiltration, grasses dominate, and water, not light, is the dominant factor controlling plant community dynamics, and as we found, water directly and indirectly limits expansion of *J. virginiana*.

More broadly considered, however, limiting resource factors are considered indeterminant. Water, nitrogen, and light vary in the importance of their role in constraining plant community dynamics within grasslands in this geographic region of intermediate resource dominance because these resources vary spatially and temporally (Seastedt and Knapp 1993, Burke et al. 1998). For example, grazing and fire directly alter resource availability as well as aboveground biomass, plant community structure, and plant species composition in tallgrass prairie (Seastedt and Knapp 1993, Blair et al. 1997, Fuhlendorf and Engle 2001). By altering plant biomass, litter quality, and litter quantity, fire and grazing change the spatial and temporal availability of water, nitrogen, and light, and therefore indirectly modify plant community characteristics (Seastedt and Knapp 1993). Therefore, limiting resource factors are more likely determinate where the influence of fire or grazing has been removed.

Even within the old field, which is an anthropogenically altered plant community where soil nitrogen might be expected to dominate as a limiting resource factor, soil texture was the overriding resource factor associated with seedling survival and growth. Degraded soil quality of the old field adds further to the complexity inherent in high spatial and temporal variability of limiting resources in this ecotonal region. For example, secondary succession processes differ on nutrient-rich soils compared to nutrient-poor soils (Gleeson and Tilman 1990), and nitrogen is the most limiting nutrient in tallgrass prairie and old-fields (Wedin 1995, Blair et al. 1998, Knops and Tilman 2000). Thus, degraded soil quality in old-fields might result in nitrogen playing a relatively more important role in the ecotone. However, clay was consistently a more important resource factor than was PAN in the old field. Others also have found soil nitrogen to be relatively unimportant in expansion of native woody plants in intact tallgrass prairie as compared to light availability (Heisler et al. 2004, Briggs et al. 2005).

Coupled with its indirect effect on the two other resource factors, soil texture is uniformly the dominant resource factor constraining eastern redcedar establishment in the oak forest-tallgrass prairie ecotone. This provides critical insight into expansion rate, and therefore, insight into conservation priorities and mitigation strategies. Indeed, time to reach a threshold of plant community state change to juniper woodland likely would vary among the three plant communities we investigated within the oak forest-tallgrass prairie ecotone. Furthermore, rapidly growing *J. virginiana* seedlings in tallgrass prairie might rapidly reach a point that fire, if re-introduced, would no longer carry through the stand or fire intensity would be insufficient to kill the trees (Buehring et al. 1971, Engle et al. 1987, Smith and Stubbendieck 1990). In contrast, slower growth of even the most rapidly growing seedlings in both the old-field and oak forest plant communities delays passage to juniper woodland. Therefore, these data suggest that conservation efforts to prevent *J. virginiana* expansion or to remove established individuals should target tallgrass prairie communities first given the high survival and rapid growth potential of *J. virginiana* in tallgrass prairie.

Our results provide substantial evidence that resource factors constraining expansion of *J. virginiana* are strongly determinant in an oak forest-tallgrass prairie ecotone that lies within an intermediate precipitation zone. Moreover, this was uniformly true across considerable spatial variability in availability of resources known to be important to plant growth and community dynamics within this ecotonal region. On the other hand, the dominant resource factor, soil texture, is strongly coupled in many instances to the other two resource factors we investigated. Coupling of resource factors and resource-factor interactions commonly occur in plant community dynamics (Palmer 1993). In this sense, the relationship is not truly determinant in the ecotone we studied, and we suggest that this is likely the rule rather than the exception, as has been noted for North

American grassland plant communities at both extremes of the precipitation gradient (Burke et al. 1998).

LITERATURE CITED

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? American Naturalist **134**:545-561.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. Pages 13-68 *in* M. Vavra, W. Laycock, and R. Pieper, editors. Ecological Implications of Livestock Herbivory in the West. Society for Range Management, Denver, Colorado, USA.

Bell, E. L., and L. C. Hulbert. 1974. Effect of soil on occurrence of cross timbers and prairie in southern Kansas. Transactions of the Kansas Academy of Science **77**:203-209.

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. Journal of Vegetation Science **7**:121-124.

Blair, J. M. 1997. Fire, N availability and plant response in grasslands: a test of the transient maxima hypothesis. Ecology **78**: 2359-2368.

Blair, J. M., T. R. Seastedt, C. W. Rice, and R. A. Ramundo. 1998. Terrestrial nutrient cycling in tallgrass prairie. Pages 222-243 *in* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. C. Collins, editors. Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, New York, New York, USA..

Bragg, T. B., and L. C. Hurlbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management **29**:19-24.

Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. Bioscience **55**:243-254.

Buehring, N., P. W. Santelmann, and H. M. Elwell. 1971 Responses of eastern redcedar to control procedures. Journal of Range Management **24**:378-382.

Burke, I. C., W. K. Lauenroth, M. A. Vinton, P. B. Hook, R. H. Kelly, H. E. Epstein, M. R. Aguiar, M. D. Robles, M. O. Aguilera, K. L. Murphy, and R. A. Gill. 1998. Plant-soil interactions in temperate grasslands. Biogeochemistry **42**:121-143.

Chapin, F. S. III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics **11**:233-60.

Coppedge, B. R., D. M. Engle, S. D. Fuhlendorf, R. E. Masters, and M. S. Gregory. 2001a. Urban sprawl and juniper encroachment effects on abundance of wintering passerines in Oklahoma. Pages 225-242 *in* R. Bowman, and J. Marzluff editors. Avian ecology in an urbanizing world. Kluwer Academic Publishers, Boston, Massachusetts, USA

Coppedge, B. R., D. M. Engle, R. E. Masters, M. S. Gregory. 2001b. Avian responses to landscape change in fragmented southern Great Plains grasslands. Ecological Applications **11**:47-59.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters **4**:421-428.

Davis, M. A., K. J. Wrage, and P. B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. Journal of Ecology **86**:652-661.

Davis, M. A., K. J. Wrage, P. B. Reich, M. G. Tjoelker, T. Schaeffer, and C. Muermann. 1999. Survival, growth, photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. Plant Ecology **145**:341-350.

Dewey, D. R., and K. H. Lu. 1959. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agronomy Journal **51**:515-518.

Dyksterhuis, E. J. 1948. The vegetation of the western cross timbers. Ecological Monographs **18**:325-376.

Engle, D. M., J. F. Stritzke, and P. L. Claypool. 1987. Herbage standing crop around eastern redcedar trees. Journal of Range Management **40**:237-239.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. Bioscience **51**:625-632.

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie, and J. S. Shackford. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landscape Ecology **17**:617-628.

Gee, G. W., and J. W. Bauder. 1986. Particle-size analysis. Pages 383-411 *in* A. Klute, editor. Methods of Soil Analysis, Part 1: Physical and Mineralogical Methods. American Society of Agronomy, Madison, Wisconsin, USA.

Gehring, J. L., and T. B. Bragg. 1992. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. American Midland Naturalist **128**:209-217.

Gleeson, S. K., and D. Tilman. 1990. Allocation and the transient dynamics of succession on poor soils. Ecology **71**:1144-1155.

Godfray, H. C. J., and J. H. Lawton. 2001. Scale and species numbers. TRENDS in Ecology and Evolution **16**:400-404.

Green, P. T., P. S. Lake, and D. J. O'Dowd. 2004 Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. Biological Invasions **6**:1-9.

Guyette, R., and E. A. McGinnes Jr. 1982. Fire history of an Ozark glade in Missouri. Transactions of the Missouri Academy of Science **16**:85-93.

Harlan, J. R. 1957. Grasslands of Oklahoma. Oklahoma State University, Stillwater, Oklahoma, USA.

Heisler, J. L., J. M. Briggs, A. K. Knapp, J. M. Blair, A. Seery. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. Ecology **85**:2245-2257.

Henley, J., R. D. Gelnar, and R. E. Mayhugh. 1987. Soil survey of Payne County, Oklahoma. USDA, Soil Conserv. Serv. Washington, DC, USA.

Hoagland, B. W., I. H. Butler, and F. L. Johnson. 1999. Pages 231-245 *in* R. C. Anderson, J. Fralish, and J. Baskin editors.. The savanna, barren, and rock outcrop communities of North America. Cambridge University Press, USA.

Hoch, G. A., J. M. Briggs, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems **5**:578-586.

Horncastle, V. J., Hellgren, E. C., Mayer, P. M., Ganguli, A. C., Engle, D. M. & Leslie, D. M. Jr. 2005. Implications of invasion by eastern redcedar (*Juniperus virginiana*) on community structure of small mammals in the southern Great Plains. Journal of Mammalogy: (*in press*).

Isaaks, E. H., and R. M. Srivastava. 1989. An introduction to applied geostatistics. Oxford University Press, New York, New York, USA.

Kaelke, C. M., E. L. Kruger, and P. B. Reich. 2001. Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light availability gradient. Canadian Journal of Forest Research **31**:1602-1616.

Knapp, A. K., J. T. Fahnestock, S. P. Hamburg, L. B. Statland, T. R. Seastedt, D. S. Schimel. 1993. Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. Ecology **74**:549-560.

Knops, J. M. H., and D. Tilman. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. Ecology **81**:88-98.

Lauenroth, W. K., and D. P. Coffin. 1992. Belowground process and the recovery of semiarid grasslands from disturbance. Pages 131-150 *in* M. K. Wali editor. Ecosystem rehabilitation: Vol 2. Ecosystem analysis and synthesis. SPB Academic Publishing, The Hague, The Netherlands.

Lauenroth, W. K., J. L. Dodd, and P. L. Simms. 1978. The effects of water- and nitrogen induced stresses on plant community structure in semiarid grassland. Oecologia **36**:211-222.

Lin, J., P. A. Harcombe, M. R. Fulton, and R. W. Hall. 2002. Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. Oecologia **132**:428-435.

McBride, J. R., and J. Strahan. 1984. Establishment and survival of woody riparian species on gravel bars of an intermittent stream. American Midland Naturalist **112**:235-245.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management **52**:550-559.

National Oceanic and Atmospheric Administration. 1999. Climatological data annual summary, Oklahoma Vol. 107, Num. 13.

Nicotra, A. B., R. L. Chazdon, and S. V. B. Iriatre. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecology **80**:1908-1926.

Norris, M. D., J. M. Blair, and L. C. Johnson. 2001a. Land cover change in eastern Kansas: litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. Canadian Journal Botany **79**:214-222.

Norris, M. D., J. M. Blair, L. C. Johnson, and R. B. McKane. 2001b. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Canadian Journal of Forest Research **31**:1940-1946.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics **4**:25-41.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology **74**:2215-2230.

Purves, D. W., and R. Law. 2002. Fine-scale spatial structure in a grassland community: quantifying the plant's-eye view. Journal of Ecology **90**:121-129.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology **77**:364-374.

Schmidt, T. L., and E. C. Leatherberry. 1995. Expansion of eastern redcedar in the lower Midwest. Northern Journal of Applied Forestry **12**:180-183.

Seastedt, T. R., and A. K. Knapp. 1993. Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. The American Naturalist **141**:621-633.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statics in biological research. W. H. Freeman and Company, New York, New York, USA.

Smith, D. L., and L. C. Johnson. 2004. Vegetation-mediated changes in microclimate reduce soil respiration as woodlands expand into grasslands. Ecology **85**:3348-3361.

Smith, S. D., and J. Stubbendieck. 1990. Production of tallgrass prairie herbs below eastern redcedar. Prairie Naturalist **22**:13-18

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. **125**:827-852.

Tunnell, S. J. 2002. The importance of topographic gradients in an Oklahoma old field. In: Vegetation dynamics following cessation of severe disturbance in an old field. Ph.D. Dissertation, Oklahoma State University, Stillwater, Oklahoma, USA.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecological Systematics **31**:197-215.

Walter, H. 1971. Natural savannahs as a transition to the arid zone. Pages 238-265 *in* J. H Burnett editor. Ecology of tropical and subtropical vegetation. Van Nostrand Reinhold Company, New York., New York, USA.

Wedin, D. A. 1995. Species, nitrogen, and grassland dynamics: the constraints of stuff. Pages 253-262 *in* C. G. Jones, and J. H. Lawton editors. Linking Species and Ecosystems. Chapman and Hall, New York, New York, USA.

Table 1. Mean ($\overline{x}$), standard deviation (SD), and the % coefficient of variation (CV) of clay, plant available nitrogen (PAN), and photosynthetic active radiation (PAR) in three plant communities in the southern Great Plains at the 1 x 1-m spatial scale (n = 900 for each plant community).

	Tallgrass prairie		Old-field grassland		Upland oak forest	
Variable	($\overline{x}$) ± SD	CV	($\overline{x}$) ± SD	CV	($\overline{x}$) ± SD	CV
Clay (%)	19 ± 5	13	24 ± 8	33	13 ± 5	22
PAN (ppm)	14.5 ± 3.4	24	12.0 ± 3.4	29	11.3 ± 3.3	30
PAR (μmol s^{-1} m^{-2})	1600 ± 490	30	1630 ± 620	38	340 ± 520	152

Figure Legends

Figure 1. Systematic grid sampling design utilized in each plant community. Soil, photosynthetic active radiation, and *J. virginiana* seedling measurements were made on 1 x 1-m quadrats centered on each transplanted seedling (n = 900 per study location). Adjacent samples were aggregated to investigate the effect of increasing scale on the relationship between resource availability and *J. virginiana* seedling survival and seedling growth.

Figure 2. A priori hypothesized relationships between resource availability traits photosynthetic active radiation (PAR), plant available nitrogen (PAN), clay, and *J. virginiana* seedling survival and seedling growth. One-way arrows represent path coefficients that are standardized partial regression coefficients. Path coefficients measure the direct influence of a predictor variable on a criterion variable. Two-way arrows between predictor variables are Pearson's correlation coefficients and represent the indirect effects of predictor variables on a criterion variable.

Figure 3. Percent change in seedling size 30 months after *J. virginiana* seedlings were transplanted into (a) tallgrass prairie, (b) old-field grassland, and (c) upland oak forest.

Figure 4 (a, b, c, d, e, f). Path analysis of *J. virginiana* seedling survival and seedling growth at a fine spatial scale (grain = 144-m^2) in tallgrass prairie (a, d), old-field grassland (b, e) and upland oak forest (c, f). Direct arrows to seedling survival (a, b, c) or seedling growth (d, e, f) from prediction variables photosynthetic active radiation (PAR), plant available nitrogen (PAN), and clay include standardized partial regression coefficients, and arrows between prediction variables are Pearson's correlation coefficients. Solid lines indicate positive relationships between variables, whereas dashed lines indicate negative relationships in the path analysis. Standardized partial regression coefficients and correlation coefficients are only shown when significant $P \leq 0.05$.

Figure 5 (a, b, c, d, e, f). Path analysis of *J. virginiana* seedling survival and seedling growth at a coarse spatial scale (grain = 2916-m^2) in tallgrass prairie (a, d), old-field grassland (b, e) and upland oak forest (c, f). Direct arrows to seedling survival (a, b, c) or seedling growth (d, e, f) from prediction variables photosynthetic active radiation (PAR), plant available nitrogen (PAN), and clay include standardized partial regression coefficients, and arrows between prediction variables are Pearson's correlation coefficients. Solid lines indicate positive relationships between variables, whereas dashed lines indicate negative relationships in the path analysis. Standardized partial regression coefficients and correlation coefficients are only shown when significant $P \leq 0.05$.

Figure 6. Path analysis of *J. virginiana* seedling survival and seedling growth across plant communities at a fine spatial scale (grain = 144-m^2) and coarse spatial scale (grain = 2916-m^2). Direct arrows to seedling survival (a, b) or

seedling growth (c, d) from prediction variables photosynthetic active radiation (PAR), plant available nitrogen (PAN), and clay include standardized partial regression coefficients, and arrows between prediction variables are Pearson's correlation coefficients. Solid lines indicate positive relationships between variables, whereas dashed lines indicate negative relationships in the path analysis. Standardized partial regression coefficients and correlation coefficients are only shown when significant $P \leq 0.05$.

Figure 1.

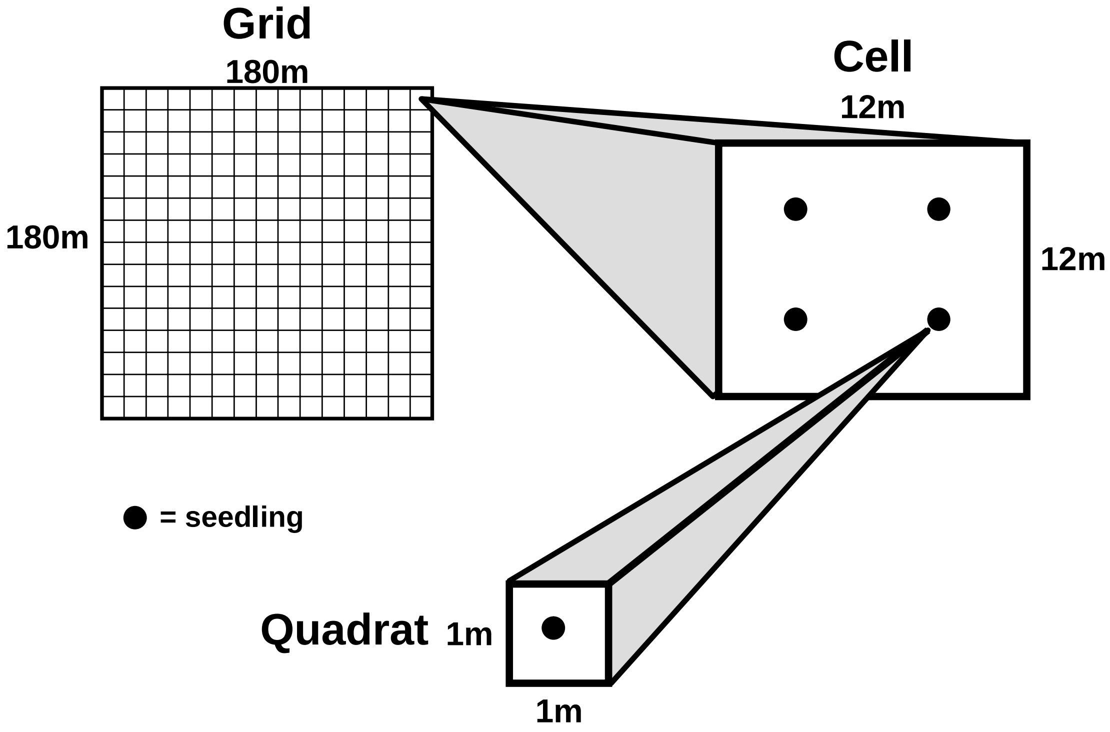


Figure 2

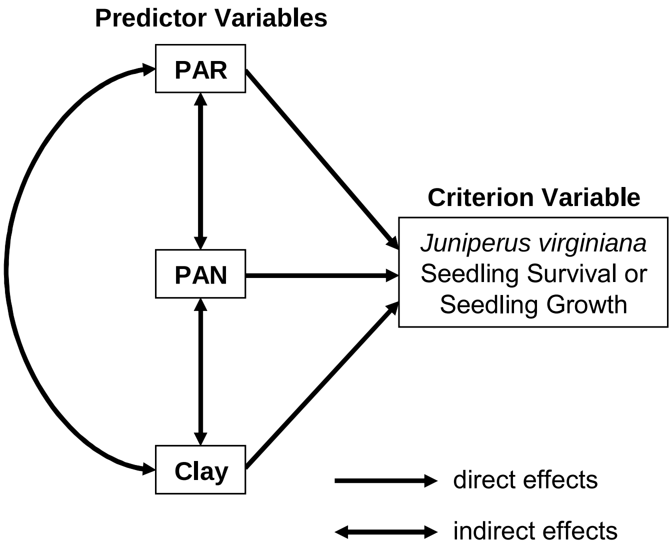
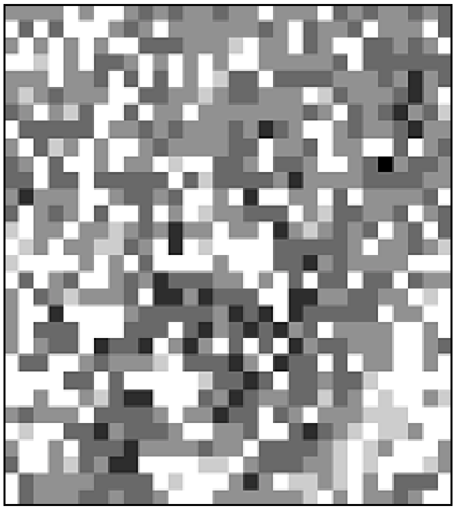
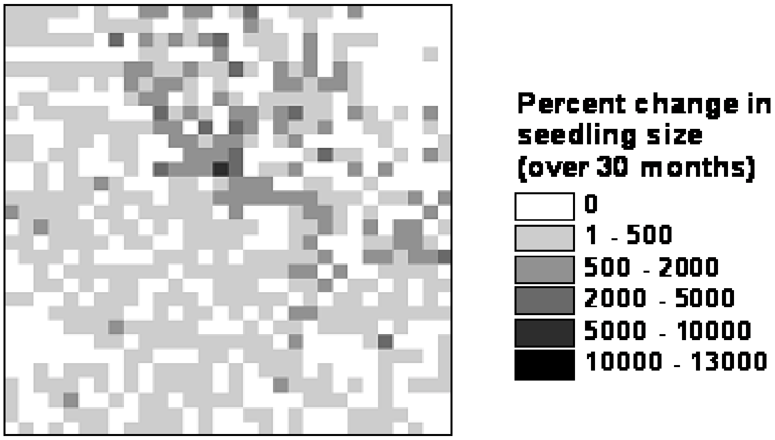

Predictor Variables
PAR
PAN
Clay
Criterion Variable
Juniperus virginiana
Seedling Survival or
Seedling Growth
direct effects
indirect effects

Figure 3.



b. Old-field



c. Upland oak forest

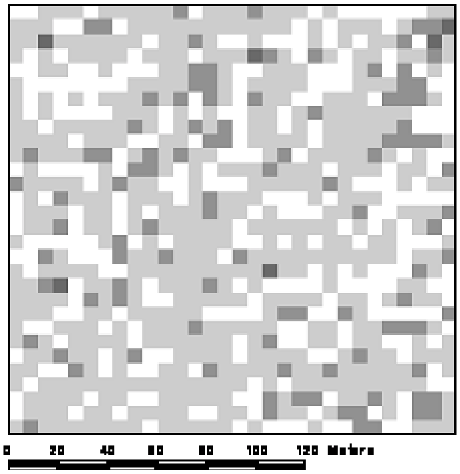
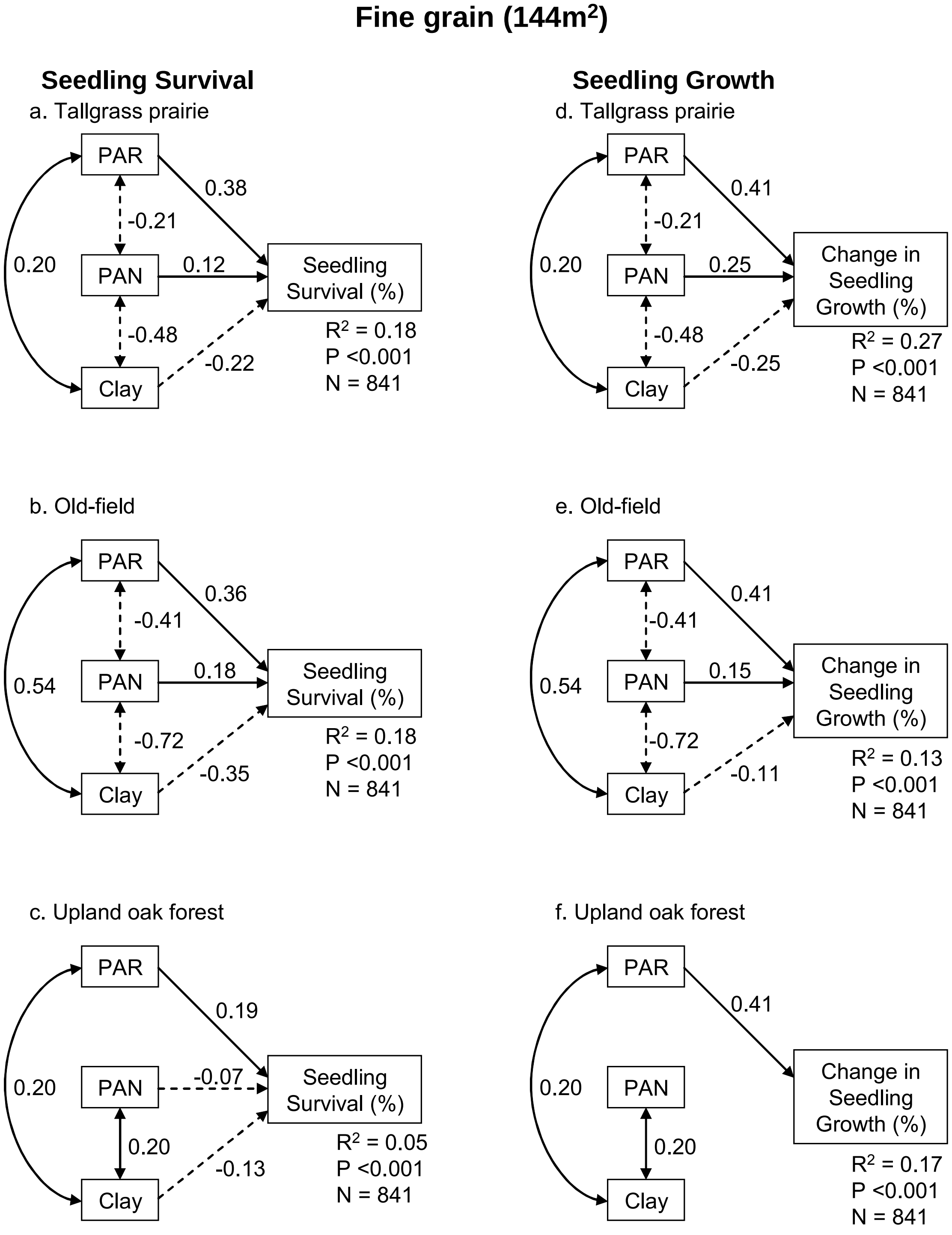


Figure 4.



Fine grain (144m²)
Seedling Survival
Seedling Growth
a. Tallgrass prairie
PAR
PAN
Clay
Seedling Survival (%)
0.38
-0.21
0.20
0.12
-0.48
-0.22
R² = 0.18
P <0.001
N = 841
d. Tallgrass prairie
PAR
PAN
Clay
Change in Seedling Growth (%)
0.41
-0.21
0.20
0.25
-0.48
-0.25
R² = 0.27
P <0.001
N = 841
b. Old-field
PAR
PAN
Clay
Seedling Survival (%)
0.36
-0.41
0.54
0.18
-0.72
-0.35
R² = 0.18
P <0.001
N = 841
e. Old-field
PAR
PAN
Clay
Change in Seedling Growth (%)
0.41
-0.41
0.54
0.15
-0.72
-0.11
R² = 0.13
P <0.001
N = 841
c. Upland oak forest
PAR
PAN
Clay
Seedling Survival (%)
0.19
0.20
-0.07
0.20
-0.13
R² = 0.05
P <0.001
N = 841
f. Upland oak forest
PAR
PAN
Clay
Change in Seedling Growth (%)
0.41
0.20
0.20
R² = 0.17
P <0.001
N = 841

Figure 5.

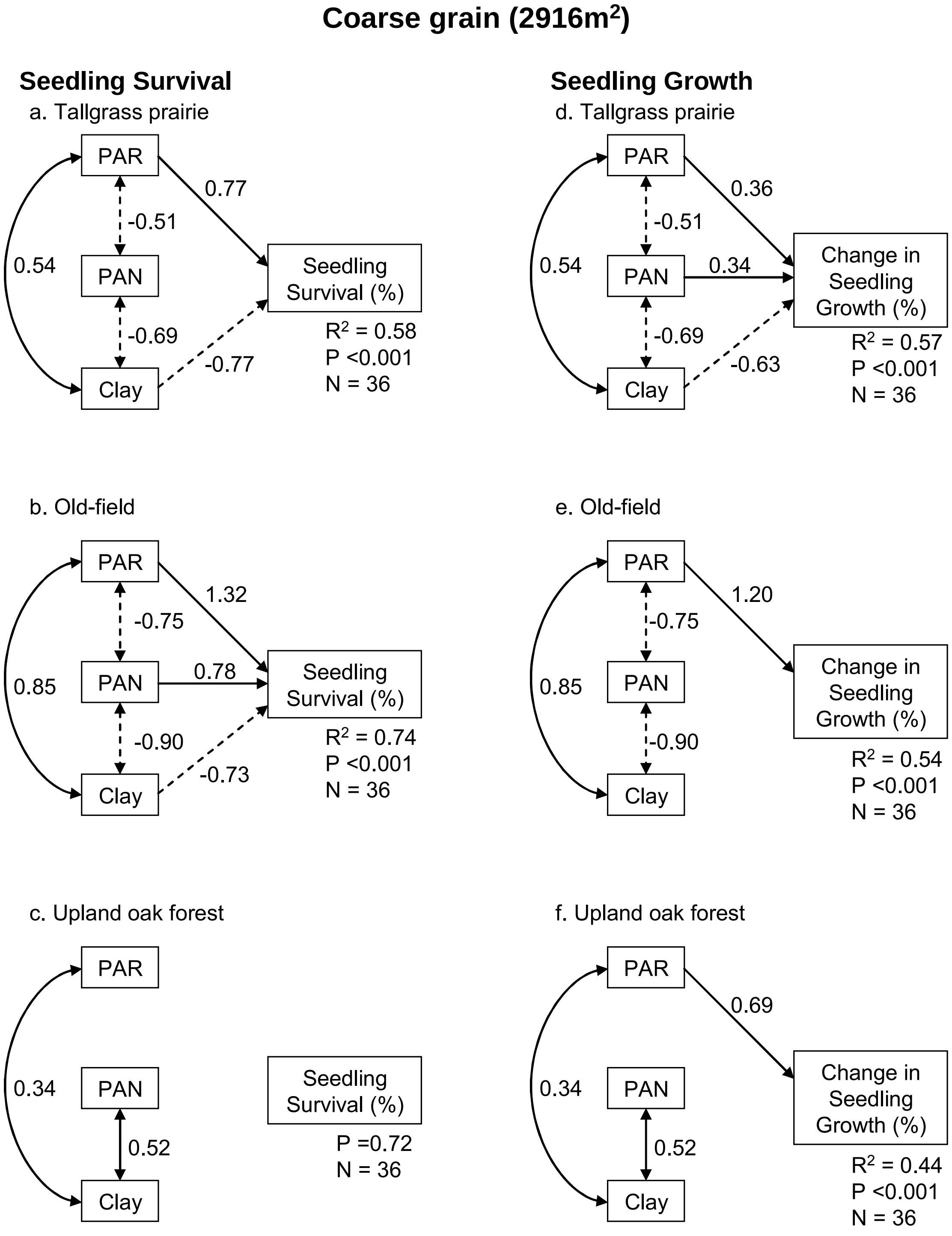
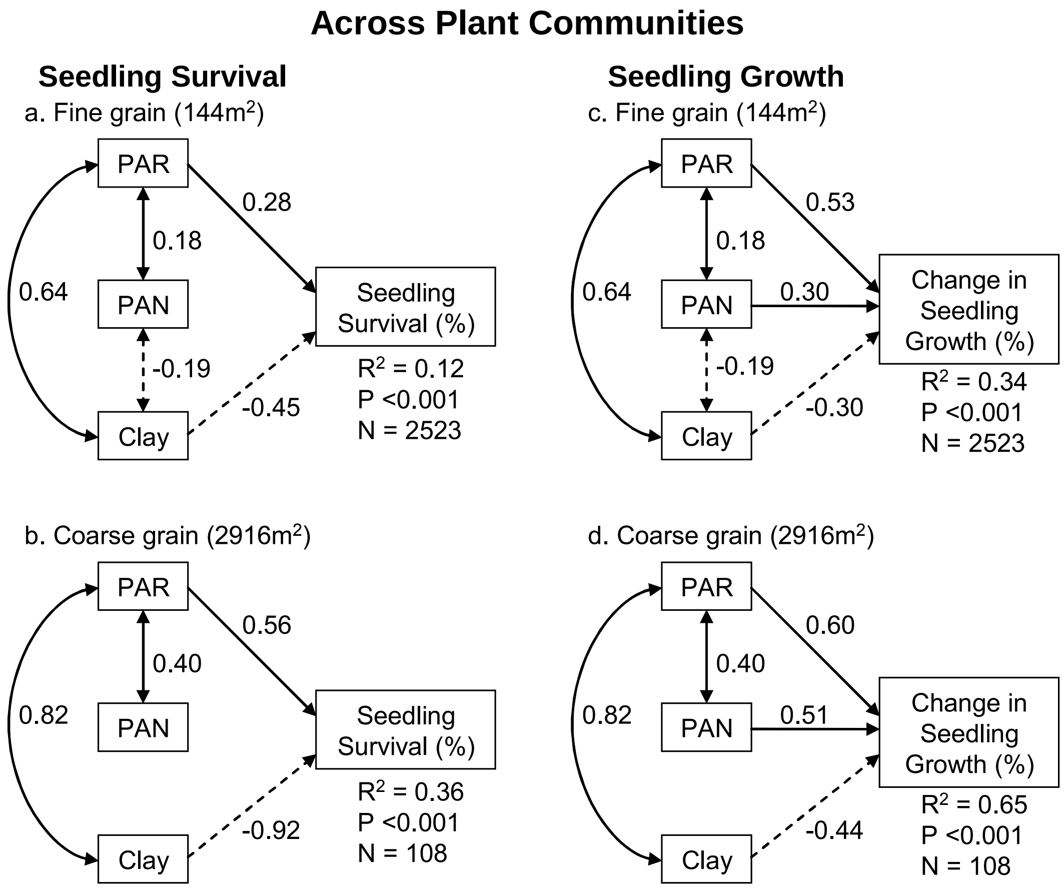

Coarse grain (2916m²)
Seedling Survival
a. Tallgrass prairie
PAR
PAN
Clay
0.77
-0.51
0.54
-0.69
-0.77
Seedling Survival (%)
R² = 0.58
P <0.001
N = 36
b. Old-field
PAR
PAN
Clay
1.32
-0.75
0.85
0.78
-0.90
-0.73
Seedling Survival (%)
R² = 0.74
P <0.001
N = 36
c. Upland oak forest
PAR
PAN
Clay
0.34
0.52
Seedling Survival (%)
P =0.72
N = 36
Seedling Growth
d. Tallgrass prairie
PAR
PAN
Clay
0.36
-0.51
0.54
0.34
-0.69
-0.63
Change in Seedling Growth (%)
R² = 0.57
P <0.001
N = 36
e. Old-field
PAR
PAN
Clay
1.20
-0.75
0.85
-0.90
Change in Seedling Growth (%)
R² = 0.54
P <0.001
N = 36
f. Upland oak forest
PAR
PAN
Clay
0.69
0.34
0.52
Change in Seedling Growth (%)
R² = 0.44
P <0.001
N = 36

Figure 6.


Across Plant Communities
Seedling Survival
a. Fine grain (144m²)
PAR
PAN
Clay
Seedling Survival (%)
0.28
0.18
0.64
-0.19
-0.45
R² = 0.12
P <0.001
N = 2523
Seedling Growth
c. Fine grain (144m²)
PAR
PAN
Clay
Change in Seedling Growth (%)
0.53
0.18
0.64
0.30
-0.19
-0.30
R² = 0.34
P <0.001
N = 2523
b. Coarse grain (2916m²)
PAR
PAN
Clay
Seedling Survival (%)
0.56
0.40
0.82
-0.92
R² = 0.36
P <0.001
N = 108
d. Coarse grain (2916m²)
PAR
PAN
Clay
Change in Seedling Growth (%)
0.60
0.40
0.82
0.51
-0.44
R² = 0.65
P <0.001
N = 108

CHAPTER III

WHEN ARE NATIVE SPECIES INAPPROPRIATE FOR CONSERVATION PLANTINGS?

Abstract: Conservation agencies and organizations are generally reluctant to encourage the use of invasive plant species in conservation programs. Harsh lessons learned in the past have resulted in tougher screening protocols for non-indigenous species introductions and removal of many non-indigenous invaders from planting programs worldwide. Although the focus of screening and risk assessment programs has traditionally been on non-indigenous species, we present an example of a rapidly expanding native tree, eastern redcedar (*Juniperus virginiana),* widely used in planting programs throughout the United States. Intentional planting of eastern redcedar and fire suppression have converted many native grasslands to eastern redcedar woodlands. We contacted state nurseries to evaluate the extent of eastern redcedar distribution programs throughout the United States, identified major uses for the seedlings, and determined the duration of the distribution programs. In 2001, 22 state nurseries distributed over 2.3 million seedlings, mostly used for windbreaks and wildlife habitat improvement. The oldest distribution programs and greatest number of seedlings were distributed within the prairie biogeographic province. Planting and subsequent expansion of eastern redcedar threatens remaining prairie fragments and other vegetation types in many areas of North America. Programs that encourage planting of eastern redcedar in prairie ecosystems are likely accelerating the decline of grassland endemic species through displacement and fragmentation. We recommend evaluating the invasive potential of all species proposed for use in conservation programs and we present a conceptual framework for the assessment of native and non-indigenous species used in conservation programs.

Key words: conservation programs, eastern redcedar, *Juniperus virginiana*, prairie, woody encroachment

Introduction

Woody plants have rapidly invaded grasslands and savannas worldwide presenting an ecological and economic threat to many natural and managed ecosystems (Archer 1994, Binggeli 1996, Pimentel 2002). A global investigation of 1,060 woody plant invasions revealed that accidental introductions represented a small proportion of the total invasions (0.2%) whereas human-mediated introductions for amenity purposes (30.9%), forestry (12.3%), and agriculture (11.3%) represented over half of the total invasive events (Binggeli 1996). Many factors have been implicated in the spread of woody plants including livestock introduction, fire suppression, and climate change (Archer 1989, Van Auken 2000). Factors that present a barrier to woody plant expansion include lack of dispersal (Johnstone 1986), life-history traits (Rejmánek and

Richardson 1996), edaphic properties (Archer 1994), removal of herbivory (Weltzin et al. 1997), and fire (Bragg and Hurlbert 1976).

Conservation seedling programs have come under scrutiny for using woody species that subsequently invade natural grasslands. Most of the attention has been placed on non-indigenous species such as Russian olive (*Elaeagnus angustifolia*), a species native to Eurasia that was introduced into the United States (Olson and Knopf 1986, Lesica and Miles 1999) and black wattle (*Acacia mearnsii*), a species native to Australia that was introduced to South Africa (de Wit et al. 2001). In response to criticism from environmental and natural resource conservation communities (Olson and Knopf 1986), many United States agencies and non-government organizations switched from promoting non-indigenous species to promoting species native to North America. Many successes resulted, but indiscriminant use of native species may pose comparable risk to conservation because similar potential exists for invasion and subsequently altering ecosystem structure and function. We use eastern redcedar (*Juniperus virginiana*), a tree native to eastern North America and a plant we suspected was used widely in conservation planting programs throughout the United States, as a study of arbitrary planting of native species for conservation purposes. The objectives of this paper are to (i) examine the origin of tree invasion and consequences to grasslands and (ii) offer a screening framework to assess the invasion risk of native species used in planting programs.

Origin of tree encroachment and consequences to grasslands

History of tree planting in North American grasslands

Grasslands are among the most endangered ecosystems in North American (Samson and Knopf 1994, Samson et al. 2004). From the time of European settlement, the native flora and fauna of the North American grasslands have declined under an altered fire regime and landscape fragmentation resulting from conversion to cropland agriculture and human settlement. Tree invasion and tree planting projects are less obvious sources of fragmentation that followed settlement (Henzlick 1965, Droze 1977, Engle et al. 2003).

Tree planting in North American grasslands was initiated at settlement when pioneers from eastern states, who longed for the trees they left behind in the east, and desperately needed timber for fuel and building materials (Droze 1977). The United States government promoted tree planting through a number of programs including the Timber Culture Act of 1873, which granted homesteads of 160 acres provided trees were planted to 40 of those acres (Droze 1977). In an effort to cope with the decline of soil and wildlife resources associated with unsustainable farming practices and drought of the 1930’s and 1950’s, tree planting was promoted by federal action agencies (e.g., Soil Conservation Service), which culminated in modern state and federal tree planting programs for conservation (Glanz 1994).

Survey of agency-sponsored tree planting programs

Since the evaluation by Olson and Knopf (1986) of agency-sponsored planting of the invasive Russian olive, no systematic evaluation of agency-sponsored tree planting programs has been conducted despite continued agency operated tree planting programs. Therefore, we conducted a telephone survey of state-operated seedling nurseries in autumn of 2001. We focused on eastern redcedar, a plant we suspected was used widely in conservation planting programs, and on state-operated seedling nurseries in the contiguous United States. State nurseries, in contrast to private nurseries, function as a low-cost source of plant materials for conservation purposes rather than for urban landscaping. Three states did not operate state nurseries, and data from nine states were either inaccessible or not compiled. From the remaining 36 forest and conservation tree nurseries in the United States (USDA/FS 1994), we determined the following information: (1) the number of eastern redcedar seedlings sold in 2001, (2) the average number of seedlings sold annually, (3) seedling price, (4) seedling use, (5) program duration, and (6) if seedlings were distributed solely through conservation districts. Missing responses were a result of incomplete records kept by some nurseries (Table 1). Larger nurseries sell their seedlings in large quantities (bundles of 100 or 1,000), therefore their seedling estimates were rounded accordingly.

Twenty-two state nurseries sold eastern redcedar to public and private entities, and conservation districts in four states (Montana, Wyoming, Michigan, and Massachusetts) purchased eastern redcedar seedlings from other state nurseries to distribute within their respective districts in 2001. The average number of seedlings distributed by states during 2001 was less than 128,000, but some states sold markedly more (Table 1). In 2001, a year of below-average seedling production in most states and seedling crop failure in Ohio and Indiana, 80% of the seedlings (1,842,000) were distributed in the Great Plains states. Nebraska, with a distribution program dating from 1926, distributed more than 1.2 million eastern redcedar and 350,000 Rocky Mountain juniper (*J. scopulorum*) seedlings from the 1980s to the early 1990s.

Seedling purchase from each of the 22 state nurseries has been open to any person or agency and for any use. The most common conservation uses for the seedlings were windbreaks and wildlife habitat plantings. Seedlings were used to a lesser extent for soil stabilization, living snow fences, shelterbelts, Conservation Reserve Program plantings, and mine reclamation. Non-conservation uses of seedlings included privacy fencing, Christmas trees, and duck blinds. Seedling prices varied (Table 1), and purchases of seedlings in bundles of 100 or 1,000 were common and typically resulted in bulk discounts. The duration of the eastern redcedar seedling distribution programs ranged from 5 to 76 years, with the older programs located in the prairie biogeographic province.

Conservation implications of tree-planting programs

By contributing to tree invasion and fragmentation of prairie caused by tree invasion (Holthuijzen and Sharik 1985, Holthuijzen et al. 1987, Coppedge et al. 2001a), tree planting in the historically treeless North American prairies contradicts conservation. Grassland invasion by eastern redcedar alters plant and animal community composition (Henzlick 1965, Gehring and Bragg 1992, Coppedge et al. 2001a, Chapman et al. 2004, Horncastle et al. 2005), reduces wildlife and livestock forage production (Engle et al. 1987, Smith and Stubbendieck 1990, Hoch et al. 2002), and alters biogeochemistry (Norris et al. 2001a, 2001b). Our survey indicated that eastern redcedar is planted extensively in the United States and that the oldest distribution programs and greatest number of seedlings are distributed within the prairie biogeographic province, a particularly alarming finding given the threatened status of prairies (Samson and Knopf 1994, Samson et al. 2004).

As first noted by Olson and Knopf (1986), conservation programs have notoriously promoted planting non-indigenous invasive woody plants to benefit wildlife habitat. Notable examples of invasive woody plants used in the United States include Russian olive, autumn olive (*E. umbellata)*, multiflora rose (*Rosa multiflora)*, and Japanese honeysuckle (*Lonicera japonica)*. Perhaps because of this history that has included criticism by scientists (Olson and Knopf 1986), many conservation programs have switched from promoting non-indigenous species to promoting species native to a particular region.

Although a form of wildlife habitat enhancement is indeed accomplished by tree planting in prairie, many birds and mammals that use eastern redcedar for food and cover (Van Dersal 1938) are habitat generalists that thrive at the expense of native prairie habitat specialists (Henzlick 1965, Coppedge et al.

2001a, 2001b). Eastern redcedar is planted in some states specifically to support non-indigenous game species such as ring-necked pheasants (*Phasianus colchicus*) despite negative effects of eastern redcedar on sensitive sympatric native species such as the lesser prairie chicken (*Tympanuchus pallidicinctus*) (Fuhlendorf et al. 2002). In fact, tree planting and woody plant expansion are associated with loss of grassland biodiversity including the recent decline of grassland birds (O'Leary and Nyberg 2000, Woodward et al. 2001, Coppedge et al. 2001a, Fuhlendorf et al. 2002), the fastest declining bird guild in North America (Knopf 1994, Herkert 1995).

Conservation enigmas associated with tree planting using native species

Tree-planting programs supported by conservation agencies are perhaps the most enigmatic element of tree invasion in North American grasslands. The enigma is all the more troubling when tree planting is operated within an agency that administers programs to remove trees from grasslands. For example, the Natural Resource Conservation Service in Oklahoma has in the recent past administered conservation programs encouraging tree planting while also administering federal cost-share conservation programs that remove eastern redcedar from grassland. This apparent contradiction in conservation practices sends the public a mixed message and otherwise detracts from conservation efforts.

Another troubling enigma is the current dispute and confusion within the scientific community that excludes native species from classification of potentially invasive simply because native species are indigenous to the continent (Richardson et al. 2000). This position ignores the fact that endemic species with wide amplitude of environmental tolerance are potentially invasive when barriers to their expansion are removed (Johnstone 1986, Myster 1993, de la Cretaz and Kelty 1999). Invasion by native and non-indigenous species, distinguished only because of semantic arguments based on geographic origin (Elton 1958, Richardson et al. 2000), operate through identical ecological processes (Thompson et al. 1995, Davis et al. 2000). Ignoring functional similarity between non-indigenous and native invaders leads ultimately to the perception that any native plant species is benign if not beneficial, regardless of regional and site endemism.

The enigma of failure to consider the invasive potential of eastern redcedar in particular has resulted in a long history of liberal transportation of eastern redcedar seeds and seedlings throughout the United States (Figure 1). Many states we surveyed trade or sell eastern redcedar seedlings to other states, with the farthest exchange being from North Carolina to California. In general, transportation of nursery stock of any species across state borders is poorly restricted (Reichard and White 2001) although several nurseries have voluntarily discontinued growing and selling non-native and native plants such as eastern redcedar that pose an invasive threat (Baskin 2002).

The exceptionally wide range of environmental tolerance of eastern redcedar founds these enigmas. Eastern redcedar thrives in the absence of fire in an environment normally hostile to trees, and it shares other traits common to woody invasive species of plants introduced for horticultural or conservation purposes. Ease of propagation, rapid growth, and high rates of survival (Richardson 1998, Reichard and White 2001) are traits preferred for trees planted in prairies. Traits that render eastern redcedar attractive to land owners and managers for establishing trees in prairies also enable eastern redcedar to effectively invade prairie.

Acknowledging the role of keystone processes

When evaluating the potential invasiveness of a native species for use in conservation planting programs, we recommend that agencies insure that keystone processes are functional components of ecosystem dynamics. Expansion of many native woody species in North America can be attributed to anthropogenic alteration of keystone processes that presented barriers to species distribution and abundance (see review by Archer 1994). Keystone processes such as fire, herbivory, or climate maintain ecosystem function and structure. Altering, adding, or removing any of these processes may alter properties of ecosystems to include increasing susceptibility to invasion even by native species historically absent from the site.

In the Great Plains prairies, eastern redcedar has been directly influenced by keystone process modification (i.e., fire and grazing). Eastern redcedar was historically excluded throughout the Great Plains by natural and anthropogenic fire except on isolated sites too rough or too shallow to produce sufficient fuel to carry fire (Arend 1950, Bragg and Hurlbert 1976, Guyette and McGinnes 1982).

Fire suppression throughout the Great Plains is a major factor contributing to the substantial encroachment by eastern redcedar in this region (Guyette and McGinnes 1982, Schmidt and Leatherberry 1995, Coppedge et al. 2001b). Because fire no longer operates through most Great Plains grasslands, planting eastern redcedar is likely to result in invasion of the remaining native grasslands in the region (Coppedge et al. 2001, Hoch et al. 2002).

Expansion of honey mesquite (*Prosopis glandulosa*) into grasslands of the American Southwest represents yet another consequence of altered keystone processes with respect to the expansion of native woody plants in grasslands. Honey mesquite, a woody plant native to the southwestern United States, has increased in distribution and abundance in grasslands and savannas following the addition of one keystone process (dispersal through livestock grazing) and the removal of another keystone process (herbivory by black-tailed prairie dog [*Cynomys ludovicianus*]). Encroachment of honey mesquite into grasslands and savannas was historically suppressed through black-tailed prairie dog herbivory (Weltzin et al. 1997). Perceived conflicts of prairie dogs with livestock production resulted in the large-scale extirpation of black-tailed prairie dog throughout North America (Miller et al. 1994, Vermeire et al. 2004). Ironically, livestock have been the primary agent augmenting honey mesquite seed dispersal in grasslands and savannas (Brown and Archer 1987). Removal of prairie dog, a species that suppressed honey mesquite expansion, to benefit livestock production, an activity that increased dispersal of honey mesquite, illustrates the unintended consequences of altering keystone processes (Weltzin et al. 1997). Livestock dispersal of seed also has been suggested to be a primary factor aiding the spread of velvet raisen (*Grewia flava*), a native shrub expanding in African savannas (Tews et al. 2004).

The impact of removing keystone processes has long been appreciated with native animals but not plants. For example, an ecological equivalence to planting eastern redcedar in areas where the keystone process (i.e., fire) has been removed would be introducing an ungulate (e.g., white-tailed deer [*Odocoileus virginianus*]) in areas where the keystone process of predation including human hunting has been removed. Predation was the keystone process that limited population size, consequently the removal of predation ultimately leads to rapid population growth until resources become limiting. In general, risks associated with introducing a native herbivore are often taken into consideration as compared to the poorly understood and often-ignored risks associated with native plants.

Assessing the risk of native species used in conservation programs

Native plants with wide environmental tolerances sometimes expand into formerly unoccupied sites and regions when ecological barriers are removed through the loss of keystone processes such as fire and herbivory. Risk assessment is a potential solution for evaluating native species considered for conservation use in ecosystems where ecological barriers have been removed. A process in which invasive characteristics of species are used to construct screening protocols for potentially invasive species, risk assessment could minimize the hazard of using potentially invasive native plants in conservation programs. Risk assessment protocols have been recommended (National Research Council 2002) and used successfully to screen non-indigenous species (Pheloung et al. 1999, Rouget et al. 2002, Hughes and Madden 2003, Daehler et al. 2004). We argue that screening protocols also should be constructed for potentially invasive native woody plants, and furthermore, these protocols should include the status of keystone processes acting on ecosystems. Developed for non-indigenous species, risk assessment has been rarely used to assess the invasive potential of native species (for an exception see Martyn et al. 2003).

Existing weed risk assessment protocols would have little value in predicting invasion by native species because current protocols fail to incorporate the presence of keystone processes that historically limited the distribution of native species. Weed risk assessments are limited generally to questions regarding history and biogeography, undesirable characteristics, and biology and ecology of the species under evaluation (Pheloung et al. 1999). Weed risk assessment protocols are fast, objective, cost-efficient, and adaptable for any number of invasive species of any region (Pheloung et al. 1999, Daehler et al. 2004), so elements of the risk assessment framework should be considered for incorporation into risk assessments for potentially invasive native species.

When considering planting any plant species, either non-indigenous or native, for conservation purposes, a risk assessment is advisable (Figure 2). Within this framework we recommend using established risk assessment protocols (Figure 2, right pathway) (e.g., Daehler et al. 2004) to assess the invasive potential of non-indigenous species. We propose an additional screening framework (Figure 2, left pathway) for evaluating the invasion risk of native species proposed for use in conservation programs. In this framework, native species are assessed by evaluating extrinsic (edaphic properties and keystone processes) limiting factors and intrinsic species traits. A species poses little risk of invasion if the species is limited by species traits such as low growth rate, shade intolerance, low seed viability, or absence of seedling establishment. If edaphic properties (e.g., soil texture, soil depth, resource availability, topography) limit the distribution and abundance of a species, the risk of invasion will be low in areas where the limiting edaphic properties exist, but high in areas where the limiting edaphic properties do not exist. For example, cottonwood (*Populus deltoides*) is a native tree limited to moist soils (Fowells 1965) in much of the western Great Plains, thus risk of invasion of cottonwood is low on upland sites. In contrast, eastern redcedar is a native species with a wide tolerance to a variety of edaphic properties thus risk of invasion is high on most sites. Species limited by a keystone process that has been removed (e.g., eastern redcedar and honey mesquite) have high potential for invasion and should not be considered for use in conservation plantings. However, if an intact keystone process will limit spread of a species, the risk of invasion is low and the species is acceptable for use in conservation plantings.

Summary

That eastern redcedar is native to North America has been used to justify extensive planting programs, a practice we now understand as ecologically misguided. No species, native or non-indigenous, should be used in planting programs without considering its invasive potential (i.e., by risk assessment). Increased dispersal from tree planting can be the catalyst in converting grassland to woodland when accompanied by change in ecosystem keystone processes. Consequently, tree planting in North American prairie represents a contradiction to conservation of imperiled prairie ecosystems. Indeed, woody plant invasions resulting from introduction of species for aesthetics, conservation, and agroforestry is a global problem (Richardson 1998, Reichard and White 2001, Rouget et al. 2002). If conservation of native species and native grasslands is considered an important goal in conservation, then programs and activities that facilitate the spread of invasive species, both native and non-indigenous, must be curtailed.

Literature cited

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? The American Naturalist 134:545-561.

Archer S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. Pages 13-68 *in* M. Vavra, W. Laycock, and R. Pieper, editors. Ecological Implications of Livestock Herbivory in the West. Society for Range Management, Denver, Colorado, USA.

Arend, J. L. 1950. Influence of fire and soil on distribution of eastern redcedar in the Ozarks. Journal of Forestry 48:129-130.

Baskin, Y. 2002. The greening of horticulture: new codes of conduct aim to curb plant invasions. Bioscience 52:464-471.

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. Journal of Vegetation Science 7:121-124.

Bragg, T. B., and L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19-24.

Brown, J. R., and S. Archer. 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. Vegetatio 73:73-80.

Chapman, R. N., D. M. Engle, R. E. Masters, and D. M Leslie Jr. 2004. Tree invasion constrains the influence of herbaceous structure in grassland bird habitats. Écoscience 11:55-63.

Coppedge, B. R., D. M. Engle, R. E. Masters, and M. S. Gregory. 2001a. Avian responses to landscape change in fragmented southern Great Plains grasslands. Ecological Applications 11:47-59.

Coppedge, B. R., D. M. Engle, S. D. Fuhlendorf, R. E. Masters, and M. S. Gregory. 2001b. Urban sprawl and juniper encroachment effects on abundance of wintering passerines in Oklahoma. Pages 225-242 *in* R. Bowman and J. Marzluff editors. Avian Ecology in an Urbanizing World. Kluwer, Boston, Massachusetts, USA.

Daehler, C. C., J. S. Denslow, S. Ansari, and H. C. Kuo. 2004. A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. Conservation Biology 18:360-368.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528-534.

de la Cretaz, A. L., and M. J. Kelty. 1999. Establishment and control of hay-scented fern: a native invasive species. Biological Invasions 1:223-236.

de Wit, M. P., D. J. Crookes, and B. W. van Wilgen. 2001. Conflicts of interest in environmental management: estimating the costs and benefits of tree invasion. Biological Invasions 3:167-178.

Droze, W. H. 1977. Trees, prairies and people: a history of tree planting in the Plains States. Texas Woman's University, Texas, USA.

Elton, C. S. 1958. The ecology of invasions by animals and plants. The University of Chicago, London, UK.

Engle, D. M., J. F. Stritzke, and P. L. Claypool. 1987. Herbage standing crop around eastern redcedar trees Journal of Range Management 40:237-239.

Engle, D. M., S. D. Fuhlendorf, and B. R. Coppedge. 2003. Conservation priorities on fragmented, homogenized Great Plains landscapes. Pages 1-6, *in* S. Foré editor. Proceedings of the 18th North American Prairie Conference.

Fowells, H. A. 1965. Silvics of forest trees of the United States. Agricultural Handbook 271. United States Department of Agriculture, Washington D.C., USA

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie Jr., and J. S. Shackford. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landscape Ecology 17:617-628.

Gehring, J. L., and T. B. Bragg. 1992. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. American Midland Naturalist 128:209-217.

Glantz, M. H. 1994. Drought, desertification and food production. Pages 9-30 *in* M. H. Glantz editor. Drought follows the plow: cultivating marginal areas. Cambridge, New York City, New York, USA.

Guyette, R., and E. A. McGinnes Jr. 1982. Fire history of an Ozark glade in Missouri. Transactions of the Missouri Academy of Science 16: 85-93.

Henzlick, R. E. 1965. Biogeographic extensions into a coniferous forest plantation in the Nebraska Sandhills. American Midland Naturalist 74:87-94.

Herkert, J. R. 1995. An analysis of Midwestern breeding bird population trends: 1966-1993. American Midland Naturalist 134:41-50.

Hoch, G. A., J. M. Briggs, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578-586.

Holthuijzen, A. M. A., and T. L. Sharik. 1985. The red cedar (*Juniperus Virginiana* L) seed shadow along a fenceline. American Midland Naturalist 113:200-202.

Holthuijzen, A. M. A., T. L. Sharik, and J. D. Fraser. 1987. Dispersal of eastern red cedar (Juniperus virginiana) into pastures - an overview. Canadian Journal of Botany 65:1092-1095.

Horncastle, V. J., Hellgren, E. C., Mayer, P. M., Ganguli, A. C., Engle, D. M. & Leslie, D. M. Jr. 2005. Implications of invasion by eastern redcedar

(*Juniperus virginiana*) on community structure of small mammals in the southern Great Plains. Journal of Mammalogy: (*in press*).

Hughes, G., and L. V. Madden. 2003. Evaluating predictive models with application in regulatory policy for invasive weeds. Agricultural Systems 76:755-774.

Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Review 61:369-394.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247-257.

Lesica, P., and S. Miles. 1999. Russian olive invasion into cottonwood forests along a regulated river in north-central Montana. Canadian Journal of Botany 77:1077-1083.

Martyn, A., J. Tyler, C. Offord, and R. McConchie. 2003. *Swainsona sejuncta*: a species of ornamental promise or a potential weed? Australian Journal of Experimental Agriculture 43:1369-1381.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8:677-681.

Myster, R. W. 1993. Tree invasion and establishment in old fields at Hutcheson Memorial Forest. The Botanical Review 59:251-272.

National Research Council. 2002. Predicting invasions of non-indigenous plants and plant pests. National Academy, Washington D.C., USA.

Norris, M. D., J. M. Blair, and L. C. Johnson. 2001a. Land cover change in eastern Kansas: litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. Canadian Journal of Botany 79:214-222.

Norris, M. D., J. M. Blair, L. C. Johnson, and R. B. McKane. 2001b. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Canadian Journal of Forest Research 31:1940-1946.

O'Leary, C. H., and D. W. Nyberg. 2000. Treelines between fields reduce the density of grassland birds. Natural Areas Journal 20:243-249.

Olson, T.E., and F. L. Knopf. 1986. Agency subsidization of a rapidly spreading exotic. Wildlife Society Bulletin 14:492-493.

Pheloung, P. C., P. A. Williams, and S. R. Hallow. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57:239-251.

Pimentel, D. 2002. Biological invasions: economic and environmental costs of alien plant, animal and microbe species. CRC, Boca Raton, Florida.

Reichard, S. H., and P. White. 2001. Horticulture as a pathway of invasive plant introductions in the United States. Bioscience 51:103-113.

Rejmánek, M., D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77:1655-1661.

Richardson, D. M. 1998. Forestry trees as invasive aliens. Conservation Biology 12:18-26.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93-107.

Rouget, M., D. M. Richardson, J. L. Nel, and B. W. Van Wilgen. 2002. Commercially important trees as invasive aliens – towards spatially explicit risk assessment at a national scale. Biological Invasions 4:397-412.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. Bioscience 44:418-421.

Samson, F., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past present and future. Wildlife Society Bulletin 32:6-15.

Schmidt, T. L., and E. C. Leatherberry. 1995. Expansion of eastern redcedar in the lower Midwest. Northern Journal of Applied Forestry 12:180-183.

Smith, S. D., and J. Stubbendieck. 1990. Production of tallgrass prairie herbs below eastern redcedar. Prairie Naturalist 22:13-18.

Tews, J., F. Schurr, and F. Jeltsch. 2004. Seed dispersal by cattle may cause shrub encroachment of *Grewia flava* on southern Kalahari rangelands. Applied Vegetation Science 7:89-102.

Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: more of the same? Ecography 18:390-402.

United States Department of Agriculture, United States Forestry Service. 1994. Directory of forest and conservation tree nurseries in the United States. United States Department of Agriculture, United States Forest Service, Pacific Northwest Region, State and Private Forestry, Cooperative Programs R6-CP-O2-94.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197-215.

Van Dersal, W. R. 1938. Utilization of woody plants as food by wildlife. Transactions of the 3rd North American Wildlife Conference 3:475-482.

Vermeire, L. T., R. K. Heitschmidt, P. S. Johnson, and B. K. Sowell. 2004. The prairie dog story: do we have it right? Bioscience 54:689-695.

Weltzin, J. F., S. Archer, R. K. Heitschmidt. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. Ecology 78:751-763.

Woodward, A. J. W., S. D. Fuhlendorf, D. M. Leslie Jr, and J. Shackford. 2001. Influence of landscape composition and change on lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations. American Midland Naturalist 145:261-274.

Table 1. State nurseries[a] that distribute eastern redcedar seedlings as a conservation species in the United States.

State	Easter Redcedar *Se*edlings Distributed 2001	Annual Average	# Of Years Distributing	Cost ($) / Seedling	Purpose
Colorado	200,000	200,000	44	0.40-1.00	windbreaks
Connecticut	4,000	4,000	6	0.50	wildlife habitat, windbreaks
Georgia	50,000	75,000	>41	0.50-1.00	privacy fencing, Christmas trees
Indiana	0	10,000	15	0.17	erosion control, windbreaks, mine reclamation
Iowa	93,200	100,000	20	0.20	wildlife habitat, erosion, and shelterbelts
Kansas	155,000	115,000	44	0.56-1.37	windbreaks, wildlife habitat
Maryland	20,000	50,000	6	0.04-0.12	windbreaks, privacy fencing, duck blinds
Minnesota	19,800	98,000	41	0.18	shelterbelts, windbreaks, wildlife habitat
Missouri	70,000	100,000	53	0.16	windbreaks, wildlife habitat
Nebraska	511,373	850,000	76	0.36-0.62	windbreaks, living snow fences, wildlife habitat
Nevada	368	400	- [b]	1.40	windbreaks

New Mexico	7,000	7,500	15-20	0.85-2.10	farmsteads, livestock protection, windbreaks
New York	25,000	25,000	15	0.30	windbreaks, beach stabilization, wildlife habitat
North Carolina	274,500	275,000	>40	0.20	privacy fencing, windbreaks
North Dakota	198,000	200,000	-[b]	0.19-0.50	windbreaks
Ohio	0	17,500	<5	0.24-0.35	mine reclamation, private landowner uses
Oklahoma	70,000	85,000	54	0.27-0.35	windbreaks, living snow fences
South Carolina	80,000	78,500	>20	0.20-0.50	reforestation, Christmas trees
South Dakota	500,000	500,000	43	0.45	windbreaks, wildlife habitat, CRP plantings
Texas	17,500	23,500	20	1.20-1.73	windbreaks
Utah	5,275	5,000	23	0.76	windbreaks, shelterbelts
Virginia	10,300	10,300	7	0.44-1.20	windbreaks, fencing, erosion control, wildlife habitat
Total	**2,311,316**	**2,829,700**			

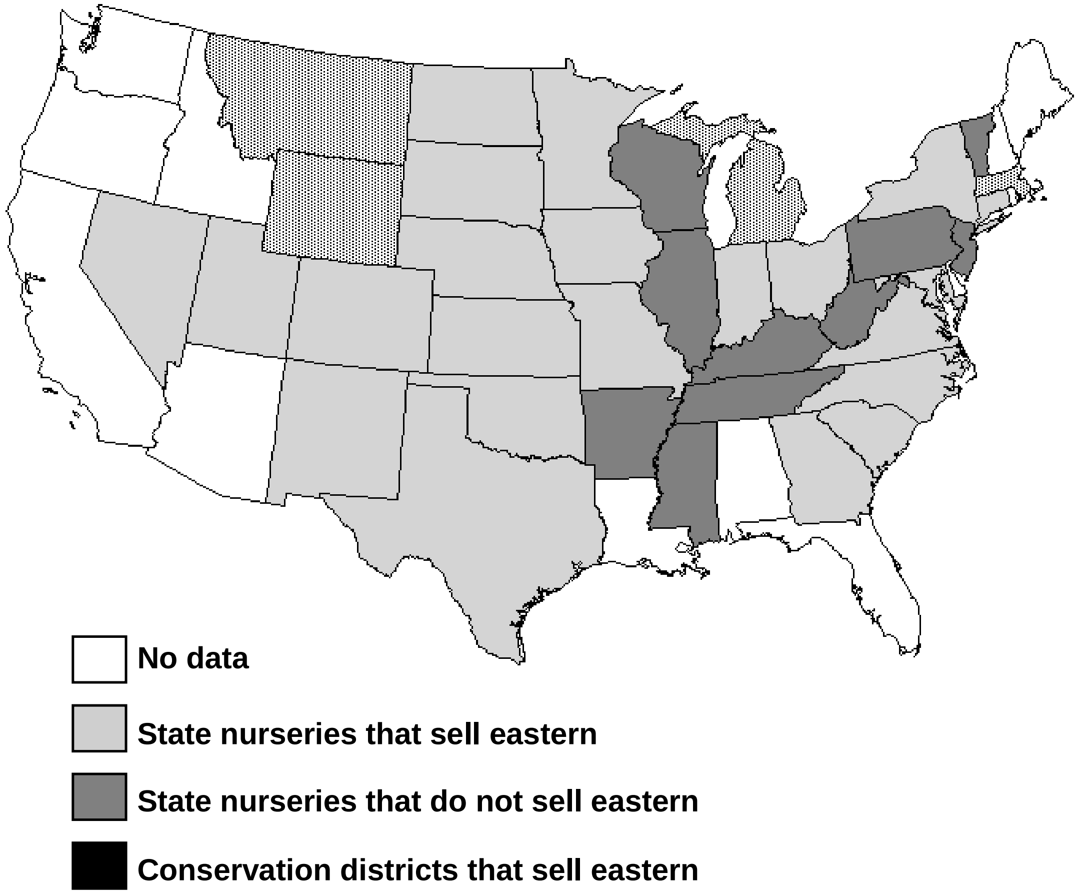
[a] Conservation districts typically obtain their seedlings from state nurseries therefore this table does not include their statistics.

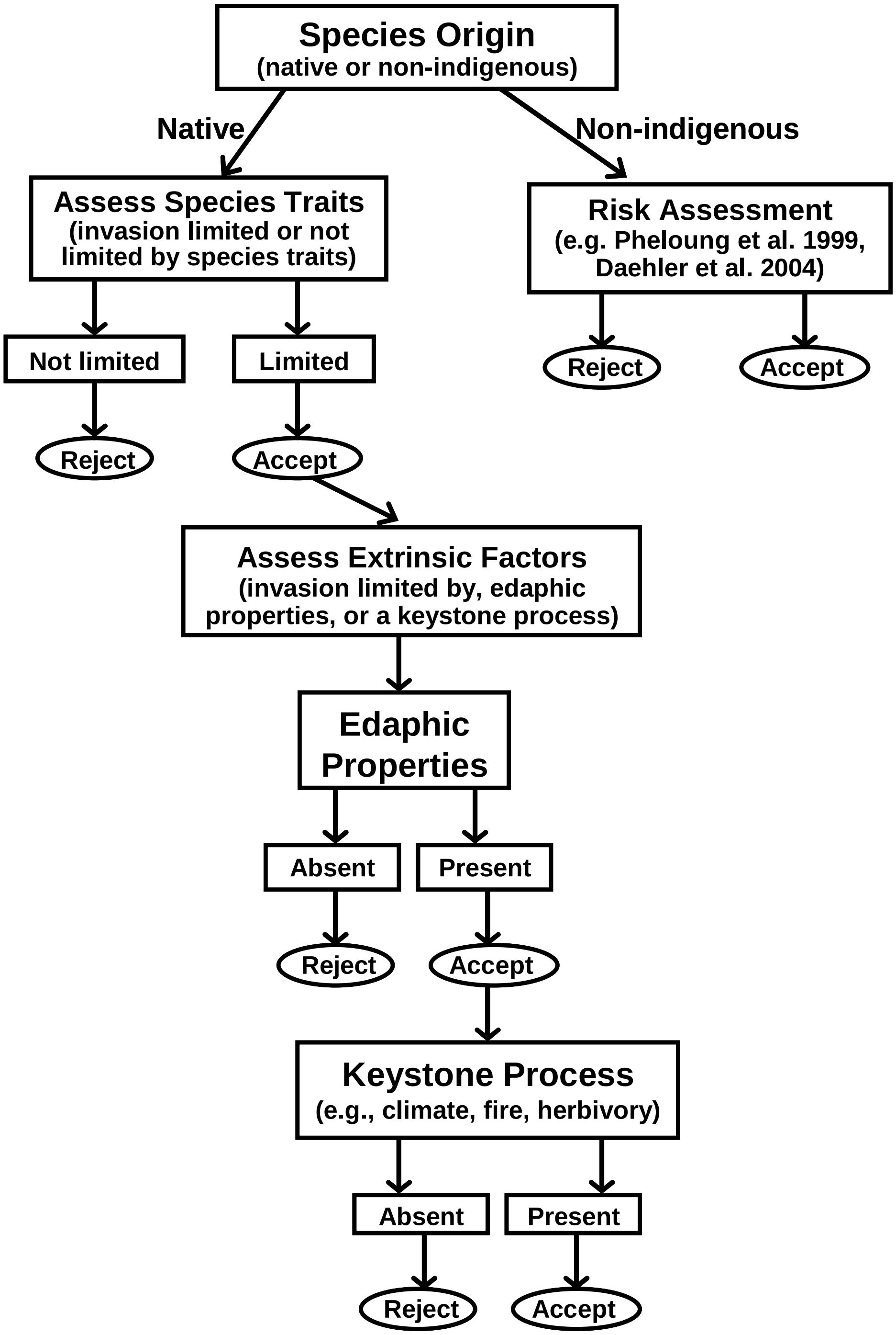
[b] information not available

Figure Captions

Figure 1. Survey results of eastern redcedar seedling distribution by state nurseries and local conservation districts within states. States without data do not have a state-operated nursery, the data were inaccessible, or the data were not compiled.

Figure 2. Proposed conceptual framework for evaluating native and non-indigenous species used in conservation plantings. In this framework non-indigenous species are evaluated through established risk assessment protocols and native species are evaluated through assessing the presence or absence of limiting factors such as species traits and extrinsic factors (edaphic properties and keystone processes). Species traits (limiting or non-limiting) and extrinsic factors (absent or present) are used to evaluate acceptability of the species for conservation planting.


No data
State nurseries that sell eastern
State nurseries that do not sell eastern
Conservation districts that sell eastern


Species Origin
(native or non-indigenous)
Native
Non-indigenous
Assess Species Traits
(invasion limited or not limited by species traits)
Risk Assessment
(e.g. Pheloung et al. 1999, Daehler et al. 2004)
Not limited
Limited
Reject
Accept
Reject
Accept
Assess Extrinsic Factors
(invasion limited by, edaphic properties, or a keystone process)
Edaphic Properties
Absent
Present
Reject
Accept
Keystone Process
(e.g., climate, fire, herbivory)
Absent
Present
Reject
Accept

VITA

Amy Christine Ganguli

Candidate for Degree of

Doctor of Philosophy

Thesis: PROXIMATE MECHANISMS OF CONTEMPORARY JUNIPERUS VIRGINIANA EXPANSION.

Major Field: Crop Science

Biographical:

Personal Data: Born in Middletown, Connecticut on April 5, 1975, the daughter of Dr. Prabhash and Fran Ganguli.

Education: Graduated Mercy High School, Middletown, Connecticut in May of 1993; received a Bachelor of Science in Wildlife Biology and Management from the University of Rhode Island in May of 1997; received a Masters of Science degree in Range Science from Texas Tech University in December of 1999. Completed the requirements for a Doctor of Philosophy degree in Plant Science with an emphasis in Rangeland Ecology and Management at Oklahoma State University in July, 2005.

Experience: Worked as a graduate research assistant at Texas Tech University, Department of Range, Wildlife and Fisheries Management; worked as a research associate at the University of Idaho, Rangeland Ecology and Management Department; employed as a graduate research assistant at Oklahoma State University, Department of Plant and Soil Sciences 2000 to present.

Professional Memberships: Society for Range Management, Ecological Society of America.

Name: Amy Christine Ganguli Date of Degree: July, 2005

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: PROXIMATE MECHANISMS OF CONTEMPORARY *JUNIPERUS VIRGINIANA* EXPANSION

Pages in Study: 104 Candidate for the Degree of Doctor of Philosophy

Major Field: Crop Science

Scope and Method of Study: The purpose of this study was to determine the influence of plant community traits and resource availability on *Juniperus virginiana* expansion and to examine conservation programs that promote the use of *J. virginiana* for conservation purposes. Survival and growth of transplanted *J. virginiana* seedlings were evaluated in three plant communities within an oak forest-tallgrass prairie ecotone. Understory canopy cover by species was measured on 1-m^2 quadrats surrounding each seedling. Soil chemical and physical properties (NO_3-N, NH_4-N, and soil texture) were measured around each seedling, and photosynthetic active radiation was measured above each seedling. We surveyed state nurseries to evaluate the extent of *J. virginiana* seedling distribution programs throughout the United States, identified major uses for the seedlings, and determined the duration of the distribution programs. Detrended correspondence analysis, chi-square analysis, logistic regression, regression, and path analysis were used to analyze data.

Findings and Conclusions: Greater levels of plant species diversity provide little safeguard to plant communities threatened by *J. virginiana* expansion. However, *J. virginiana* expansion may be limited in areas where plant species composition reflects the presence of abiotic stressors such as limited resource environments. *J. virginiana* seedling survival and seedling growth were inconsistently related to a single resource factor as a direct influence across plant communities and spatial scales. However, indirect and direct influence of a single belowground resource factor, soil clay content, emerged as an integrating resource factor that drives *J. virginiana* seedling survival and seedling growth. All of the plant communities we investigated are susceptible to *J. virginiana* expansion, differing only in the probable rates of conversion to *J. virginiana* woodland. *J. virginiana* is extensively used as a conservation species for windbreaks and wildlife habitat in the United States especially in the prairies of the Great Plains. Planting and subsequent expansion of eastern redcedar threatens remaining prairie fragments and other vegetation types in many areas of North America.

ADVISOR'S APPROVAL: ____