STUDIES OF EASTERN REDCEDAR ECOLOGY IN CENTRAL OKLAHOMA

By

JERAD SCOTT LINNEMAN

Bachelor of Science

University of Wisconsin-Green Bay

Green Bay, Wisconsin

1999

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of the requirements for
the Degree of
MASTER OF SCIENCE
May, 2004

STUDIES OF EASTERN REDCEDAR
ECOLOGY IN CENTRAL OKLAHOMA

Thesis Approved:

Thesis Advisor

Donald J. Turton

Alfred Carlozzi
Dean of the Graduate College

PREFACE

Invasive plant species have been widely studied throughout the world. General conclusions of these studies are remarkably similar. First, invading species tend to displace many of the native species that originally occupied the site. This displacement causes decreases in species richness and biological diversity that may affect higher biological levels. Second, invading plant species tend to modify micro-environmental conditions such as light, soil moisture, nutrient cycling and litter dynamics. Invading species may release allelopathic compounds. Several scientists have termed this epoch as the homogocene due to the "combining" of flora and fauna into what is increasingly a global species pool to the detriment of local or regional species pools. Successful invasions can be categorized into at least three main causes:

1. Although globalization is potentially good with respect to economic systems, its effects in biological systems are quite different. Biological entities are thrust into a situation where they must compete with species to which they have not adapted. Increased interspecific competition, caused by the degradation of isolating factors (such as oceans, mountains, or even climate), tends to be strongly influenced by human activity. Anthropogenically introduced species and their effects are well documented in the conservation literature and include examples such as sericea lespedeza (*Lespedeza cuneata*), garlic mustard (*Alliaria petiolata*) and kudzu (*Pueraria montana)*.

2. Another reason for invasion success is related to niche partitioning and/or utilization. Some invasive species are able to persist, or even expand their range, due to

the way in which they utilize resources. Invasive species may be more able to utilize an environmental resource but less able to utilize a different resource. As long as the native species is able to utilize a resource better than the invasive species it is possible that competitive displacement will not occur. On the other hand, if the invasive species is able to utilize a resource that is currently unused by any other species it is highly likely that the invasive species will persist and expand. An example of this is Japanese brome (*Bromus japonicus*). It is a winter annual grass species that is utilizing a set of environmental conditions/parameters that no native species has adapted to in Oklahoma. Although this is not problematic by itself, the question remains as to whether this species is immobilizing resources that would otherwise be used by native species later in the growing season.

3. A third factor strongly influencing species invasions is the amplification or removal of natural disturbance. Although tornados, mudslides and hurricanes disturb the natural vegetation of an area, these events are generally rare and localized. However, activities like agriculture and construction tend to create soil disturbances on temporal and spatial scales that may seem almost ubiquitous at times. These locations tend to support many ruderal species of which several are non-native.

Just as disturbance greater than that observed in nature can create appropriate habitat for invasive species, disturbance less than that observed in nature can also create conditions that favor invasive species. In the Great Plains of the United States, the suppression of wildfire has allowed several woody species to encroach on many of the remaining grasslands in the region. One invasive species is of particular interest, eastern redcedar (*Juniperus virginiana*). This evergreen tree was once confined to mesic forests, riparian zones and cliff sides due to the inability of wildfire to extend into these areas. However, since the elimination of fire redcedar has made substantial inroads into prairies and pastures throughout the Great Plains. Although this particular invasive species is native to the area, the effects it has on surrounding species are similar to those of exotic invasives. For instance, studies have shown reduced herb production as a result of redcedar invasion. Although reduced herb production is important to ranchers, conservationists are also concerned about the loss of native prairies and their constituent species.

The studies contained herein were designed to elucidate the effect of eastern redcedar encroachment on native prairie species. Alterations in species composition and individual species responses to redcedar encroachment were not the only issue of concern. Questions about why or how redcedar appears to outcompete these grassland species in an environment where the natural disturbance regime has been removed were also of interest. In particular, does redcedar alter environmental conditions that are characteristic of prairies? Does redcedar facilitate further encroachment of woody species or is it the result of previous encroachment of other species? On the other hand, is the overstory tree altering the environmental conditions or is the resultant litter modifying the environment? Assuming that there are effects of redcedar encroachment on native grassland species, are theses effects permanent? Will an original suite of species return if the trees are removed? If the overstory tree and/or its litter are not important, could it be that changes in nutrient availability or utilization favor redcedar?

THESIS ABSTRACT

This thesis is composed of four chapters: 1) the effects of *Juniperus virginiana* on micro-environment under the tree, 2) changes in community composition under the tree, 3) the role that the overstory tree and litter play in determining species composition, 4) the acquisition of nitrogen in different forms or concentrations.

Chapters 1 & 2 summarizes an observational study of environmental and species responses along transects extending to 1.5 times the canopy radius. Results show substantial changes in micro-environmental condition under the canopy. I found significant differences in soil acidity between male and female trees. Litter accumulations under redcedar canopies were larger than total prairie production and litter decomposition rates were 7.5-10% yr^{-1}. Species richness, stems per quadrat and vegetation cover all increased as distance increased. Graminoid and forb species dominated "prairie" quadrats and south transects, whereas woody species dominated "under" quadrats and north transects. Compositional trends were relatively weak due to the few stems per quadrat and/or insufficient time since invasion.

Chapter 3 summarizes a manipulative study where trees and/or litter were removed. Tree removal had a significant affect on stems per quadrat, vegetation cover and species composition. Litter removal effects were not as strong but included increased stems per quadrat and vegetation cover. Species richness increased one year after treatment application; however, it decreased in all treatments there after. Absolute cover of prairie species increased in the cut-no litter treatment whereas cover of woody species increased in the no cut treatment. These results are consistent with those of Chapter 2, which suggested that the woody tree species are favored underneath redcedar canopies.

Chapter 4 describes a greenhouse experiment where redcedar trees were grown in sterilized sand and supplied with different forms (NH_4^+:NO_3^-), ratios (3:1, 1:1, 1:3) and concentrations of nitrogen (1 mM, 2 mM, 3 mM). Nitrogen ratios, although being significantly different within a harvest, showed no consistent pattern related to growth over the course of the experiment. There was a consistent ordering of N proportion between NH_4^+ to NO_3^- treatments. This ordering suggests that N absorption was greater when NH_4^+ to NO_3^- ratios favored NH_4^+-N over NO_3^--N.

TABLE OF CONTENTS

Chapter 1—Environmental Conditions and Litter Production Underneath *Juniperus virginiana* L. Trees in Central Oklahoma....................1
Abstract....................2
Introduction....................2
Methods....................4
Results....................9
Discussion....................14
Acknowledgements....................21
Literature Cited....................22
Chapter 2—The Effect of *Juniperus virginiana* L. Trees on Plant Species Composition in a Central Oklahoma Grassland. 39
Abstract....................40
Introduction....................40
Methods....................42
Results....................45
Discussion....................50
Acknowledgements....................54
Literature Cited....................55
Appendix 1....................67
Chapter 3—The Effects of Removal of *Juniperus Virginiana* L. Trees and Litter from a Central Oklahoma Grassland....................69
Abstract....................70
Introduction....................70
Methods....................72
Results....................75
Discussion....................79
Acknowledgements....................82
Literature Cited....................83
Appendix 1....................95
Chapter 4—Differences in Growth and Nitrogen Uptake by *Juniperus virginiana* L. Trees Grown in a Greenhouse....................96
Abstract....................97
Introduction....................97
Methods....................99
Results....................102
Discussion....................106
Acknowledgements....................110
Literature Cited....................111
Appendix 1....................124

LIST OF FIGURES

Chapter 1—Environmental Conditions and Litter Production Underneath *Juniperus virginiana* L. Trees in Central Oklahoma.

Figure 1: Canopy cover of eastern redcedar as a function of distance from the trunk, expressed as a percentage of maximum canopy radius 28
Figure 2: A— Percent incoming solar radiation as a function of cedar canopy cover. Includes both north and south transects....29
Figure 2: B— Percent incoming solar radiation as a function of distance from the trunk, expressed as a percentage of unobstructed incoming light observed in the prairie....29
Figure 3: A—Soil temperature as a function of canopy cover....32
Figure 3: B—Soil temperature as a function of distance from the trunk. Positive distances represent the north transect direction whereas negative distances represent the south transect....32
Figure 4: Percent soil moisture as a function of distance....33
Figure 5: A—Box and whisker plots indicating median, quartiles and ranges for soil moisture based on quadrat categories....34
Figure 5: B—Comparison of total litter accumulation of three different canopy cover categories for one year....34
Figure 6: Change in the mass of oven dry litter from litter decomposition bags as a function of date for two years....35
Figure 7: Box and whisker plots indicating median, quartiles and ranges of solar radiation between quadrat categories....36
Figure 8: Box and whisker plots indicating median, quartiles and ranges of soil temperatures between quadrat categories....37
Figure 9: Average quadrat litter accumulation with 82% distance for the two years of the study....38

Chapter 2—The Effect of *Juniperus virginiana* L. Trees on Plant Species Composition in a Central Oklahoma Grassland.

Figure 1: Stem density (stems per 0.125 m^2) as a function of distance from the trunk (expressed as a percent of canopy radius) based on all samples....59
Figure 2: Species richness as a function of the log of stem density plus one....60
Figure 3: Species Richness (species per 0.125 m^2) as a function of percent distance from the trunk (expressed as a percent of canopy radius)....61
Figure 4: Vegetation cover for three growth forms as a function of distance. Also included is total vegetation cover....62
Figure 5: pCCA scatter plot of environmental variables along axis 1 and 2 displayed 63
Figure 6: pCCA biplot of manually selected environmental variables and species codes. 64
Figure 7: pCCA of canopy cover categories based on relative proportion of cover of each species within a quadrat....65

Chapter 3—The Effects of Removal of Juniperus Virginiana L. Trees and Litter from a Central Oklahoma Grassland.

Figure 1: Mean stems per quadrat of tree removal and litter removal treatments............87
Figure 2: Mean species richness (species per 0.25 m^2) and cumulative species richness. 88
Figure 3: Mean percent total cover of tree removal and litter removal treatments for 2.5 years...89
Figure 4: Mean percent forb cover of tree removal and litter removal treatments for 2.5 years...90
Figure 5: Mean percent graminoid cover of tree removal and litter removal treatments for 2.5 years..91
Figure 6: Mean percent woody cover of tree removal and litter removal treatments for 2.5 years...92
pRDA trajectory of tree and litter removal treatment centroids for each sampling period. 93
Figure 8: pRDA triplot of speceies codes, treatment centroids and supplemental environmental variables..94

Chapter 4—Differences in Growth and Nitrogen Uptake by *Juniperus virginiana* L. Trees Grown in a Greenhouse.

Figure 1: A— Average root dry weight of seven N concentrations and NH_4^+:NO_3^- ratios across seven tree harvests...115
Figure 1: B—Average shoot dry weight of seven N concentrations and NH_4^+:NO_3^- ratios across seven tree harvests...115
Figure 2: A— Average dry weight at Harvest 6 for different structures of plants grown at seven N concentrations and NH_4^+:NO_3^- ratios...116
Figure 2: B— Average dry weight at Harvest 7 for different structures of plants grown at seven N concentrations and NH_4^+:NO_3^- ratios...116
Figure 3: Root to shoot ratio of seven combinations of N concentrations and NH_4^+:NO_3^- ratios for seven harvests. 118
Figure 4: Leaf area ratio of seven combinations of N concentrations and NH_4^+:NO_3^- ratios for seven harvests. 119
Root length of plants grown at of seven combinations of N concentrations and NH_4^+:NO_3^- ratios. 123

LIST OF TABLES

Chapter 1—Environmental Conditions and Litter Production Underneath *Juniperus virginiana* L. Trees in Central Oklahoma.

Table 1: Variables significantly influencing light, soil temperature and soil moisture conditions for quadrat categories based on a multiple regression of each canopy cover category. 30

Chapter 2—The Effect of *Juniperus virginiana* L. Trees on Plant Species Composition in a Central Oklahoma Grassland.

Table 1: Mean stems per quadrat and species richness for each canopy cover category. 58
Table 2: Species occurrence frequencies by canopy cover category....66

Chapter 4—Differences in Growth and Nitrogen Uptake by *Juniperus virginiana* L. Trees Grown in a Greenhouse.

Table 1: A—Results for several plant variables recorded at Harvest 6....117
Table 1: B—Results for several plant variables recorded at Harvest 7....117
Table 2: Proportion of carbon pooled across treatments for each plant structure. 120
Table 3: Comparison of proportion nitrogen within each nitrogen treatment for all four plant structures based on trees with data for all Structures. 121

Chapter 1

Environmental Conditions and Litter Production Underneath *Juniperus virginiana* L. Trees in Central Oklahoma

By: JERAD S. LINNEMAN[1]

Oklahoma State University, Department of Botany, Stillwater, OK 74078

---

[1] Present address: Department of Botany, Oklahoma State University, Life Science East-#104, Stillwater, OK 74078. Telephone (405)744-5559; e-mail: ljerad@okstate.edu

Abstract

I conducted a study to describe the environmental conditions underneath eastern redcedar (*Juniperus virginiana*) trees, in comparison to those of the surrounding prairie. I found summer soil temperatures to be 20-30 C lower within the canopy radius as compared to open prairie. Incoming solar radiation under the canopy was only 5-10% of that of the open prairie. Total precipitation was 50-75% lower underneath the tree; however, this precipitation was spatially and temporally variable. Increased spatial variability of microclimatic conditions on the north side of trees indicates the possibility of a tree shadow effect. I found no significant trends in soil acidity underneath redcedar trees as compared to the open prairie. However, male trees were typically associated with more alkaline conditions compared to female trees. I found deep litter layers on the soil surface and large accumulations of litter in litter traps underneath the trees. Cedar litter decay was only 15-20% of the litter bag total mass over the two years of the study. Differences in environmental conditions and litter may influence species composition under redcedar trees.

Introduction

Invasion of woody species into grasslands is currently under extensive study; research includes studies from Argentina (Ghersa et al. 2002), Australia (Costello et al. 2000, Whiteman and Brown 1998), Canada (Peltzer and Köchy 2001) and the United States (Petranka and McPherson 1979, Callaway and Aschehoug 2000, Fitch et al. 2001, Briggs et al. 2002b). Several members of the genus *Juniperus* are widely recognized as having increased in abundance and are considered invasive within their native ranges.

Examples include: *Juniperus ashei* (Fuhlendorf 1992, Fuhlendorf et al. 1997), *J. communis* (Diotte and Bergeron 1989, Bakker et al. 1996), *J. monosperma* (Jameson 1966), *J. occidentalis* (Miller and Rose 1995, Miller et al. 2000) and *J. pinchotii* (McPherson and Wright 1990). It is interesting to note that no studies I am aware of show *Juniperus* species as an invader when introduced to a new continent.

Juniperus virginiana (eastern redcedar) is a drought tolerant tree whose original range in the United States includes every state east of the 100th meridian (Lawson 1990). Redcedar invasion in the Great Plains has had detrimental effects on native tallgrass prairies by reducing geographic range and by decreasing species richness (Holthuijzen and Sharik 1985, Engle et al. 1987, Smith and Stubbendieck 1990, Gehring and Bragg 1992, Hoch 2000, Briggs et al. 2002a).

Studies of microclimate in relation to cedar invasion are generally of two types. Several researchers demonstrated differences in water relations under redcedar versus open grasslands (Engle et al. 1987, Smith and Stubbendieck 1990, Axmann and Knapp 1993, Joy and Young 2002). In addition, Smith and Stubbendieck (1990) found large reductions in solar radiation underneath redcedar canopies. Other research has focused on how prescribed fire affects microclimatic conditions such as soil temperature (Hulbert 1969). However, there has been no attempt to account for a wider array of microclimatic factors that could be affecting species composition. Examples of these factors include soil temperature in unburnt prairies, soil acidity, precipitation and litter accumulation.

Litter dynamics have a strong influence on microclimate (Facelli and Pickett 1991). For example, thick litter layers tend to reduce evaporation thus helping to maintain soil moisture. In contrast, litter may reduce water inputs via litter absorption thus preventing water from reaching the soil surface. Litter cover could reduce soil temperatures by decreasing solar radiation hitting the soil surface or by increasing soil moisture and thereby increasing the amount of energy required to raise soil temperatures. Decreases in light can strongly affect germination and establishment under *Juniperus* (Yager and Smeins 1999). In addition, Myster (1994) found that the mechanical barrier litter imposes upon seedlings reduced germination and emergence of both *Cornus florida* and *J. virginiana* seedlings. Therefore, removal of accumulated litter and woody species are common rationales for prescribed fires in grasslands (Hulbert 1969, Knapp and Seastedt 1986, Höffmann 1996). On the other hand, litter decay may increase soil acidity as organic acids leach from the A-horizon or litter may decrease soil acidity by acting as a cation exchange buffer (Agbim 1987, Schlesinger 1997, Davy et al. 1998).

The purpose of this study was to describe environmental conditions and characteristics of leaf litter underneath eastern redcedar trees invading a grassland in north-central Oklahoma.

Methods

Study Site—I conducted this experiment at the James K. McPherson Botanical Preserve located 16 km west of Stillwater, Oklahoma (36°06'00"N, 97°12'30"W). After a brief period of row crop agriculture, the site was converted into pastureland and grazed until the 1960's. Oklahoma State University (OSU) purchased the land and managerial control was turned over to the Department of Botany. In 1995, the Department of Botany introduced a burning regime, consisting of a 3-5 year return interval, to the northwestern half of the preserve with the goals of stimulating the return of a native tallgrass prairie community and controlling redcedar invasion into the Preserve's grasslands.

Tree selection and classification—I selected four study sites based on location within the unburned portion of the Preserve and distance between clusters of potential study trees. Three of the four study sites occurred along the eastern edge of the preserve, whereas one site was along the northern edge

I selected potential study trees based on four criteria: (1) distance between study trees and any adjacent redcedars of at least 1.5 times the radius of the study tree, (2) a distance of no less than 2 times the canopy radius of the study tree to the canopy edge of any adjacent trees greater than one meter in height in the north and south compass direction, (3) a minimum canopy radius of 60 cm in the north and south direction of any study tree and (4) no overstory species for each study tree. Based on these criteria, I selected forty-eight potential study trees. I recorded canopy diameter in the north-south and east-west directions, tree height, stem diameter at both 10 cm and breast height (DBH) and gender of each potential study tree. I classified tree gender as male, female, or juvenile (those trees without observable cones). For trees with multiple stems at breast height, I recorded separate DBH measurements for each primary stem. No potential study tree had several distinct stems rising from ground level.

I averaged canopy diameter measurements for both the north-south and east-west axes for each potential study tree and ranked them from smallest to largest. I assigned all potential trees to one of four arbitrary size classes (1-4) based on average canopy diameter; after which I randomly selected five trees within each size class for further study.

Sampling design—Sampling was based on a belt transect of contiguously placed quadrats in both the north and south compass direction for each study tree. I selected these directions because in a similar study Fuhlendorf (1992) found that the north/south distinction had stronger relationships with other factors than the east/west direction. Each quadrat measured 50 cm by 25 cm on a side with the 50 cm sides abutting adjacent quadrats. The number of quadrats directly underneath the canopy of the cedar tree determined the radius in each direction for environmental sampling. Environmental sampling, including estimated canopy cover, extended to 1.5 times the canopy radius. Based on the results from personal observations and the literature, I assigned the following categories to all quadrats: 'under' the canopy (0-60% of the canopy radius), 'edge' quadrats (60-90% of the canopy radius) and 'prairie' quadrats (greater that 90% of the canopy radius).

Light—I obtained light data from every quadrat in the study using a LICOR LOGGER (LI-1000) with a cosine corrected quantum sensor (LI-192SA). Sampling occurred between 1100 and 1600 hrs to reduce variability related to diurnal changes in solar intensity. I recorded all light measurements at 10-15 cm above the ground. For each transect, I also collected three unobstructed measurements for comparison between measurements collected in each quadrat. These unobstructed measurements were recorded prior to, during and after sampling each transect. All measurements are in photon flux density (μmol m^{-2} s^{-1}) which is the same as units for photosynthetically active radiation (PAR).

Soil Temperature—I collected soil temperatures using the OMEGASCOPE (OS531) hand-held infrared thermometer (±0.1 C) from the soil core holes left after removal of soil samples for pH analysis (described below). I report soil temperatures from a depth of 10-15 cm measured between 1030 and 1530 hrs collected on 18 May 2001.

Soil Moisture—I obtained soil moisture data from a gravimetric analysis of soil samples gathered on May 18, 2002 from each quadrat of every study tree. Prior to sampling, I removed all surface plant litter from the coring area. The soil-coring device consisted of a 3.7 cm (ID) copper tube with an end cap. All samples were dried for 72 hrs at 75 C, after which percent soil moisture was calculated from the difference in sample weights and was expressed as a percent of field condition mass.

Rain—I positioned rain gauges under one randomly selected tree from each size class. Each rain gauge consisted of a plastic 50 ml graduated centrifuge tube (Fisher 06-443-20 & 21) which was placed in holes drilled in a wooden board. Each rain gauge was centered in the middle of each quadrat and the volume of water recorded every 24 hrs during rain events from September 2001 through mid May 2002. I converted all volumes to centimeters of precipitation. I obtained supplemental data (including wind direction and speed) for each rain event from the Marena Mesonet Station (Oklahoma Mesonet, Oklahoma Climatological Survey) located approximately 4 km from the study site.

Soil Acidity—I gathered soil for pH analysis from the center of each quadrat, using the soil-coring device describe above, to a depth of 10-15 cm. I processed the soil samples using a modified 1:1 suspension protocol (Thomas 1996); I increased both soil and water sample size to 15 ml as opposed to 10 ml. Measurements were recorded with an ORION PERFECT LOG R METER (MODEL 370) and a Ag-AgCl glass probe. Prior to processing, I calibrated the pH meter with stock buffer solutions of pH 4 and 7.

Litter Accumulation—I positioned litter trap trays contiguously in a belt transect under one randomly selected tree from each size class. Each tray measured 24x26 cm. Each tray also had several small cuts along the lower edge of the sides to allow drainage. Litter from the trays was collected every four months. In the lab, I separated the litter into five categories: cedar litter, deciduous plant litter, grass litter, female cones and an 'other' category that included items such as galls, dry sap and bark. This material was dried for 72 hrs at 75 C and then re-weighed.

Litter Decomposition—In the spring of 2001, I collected litter underneath cedar trees in the surrounding area and filled litter decomposition bags (Singh and Gupta 1977, Kemp et al. 1994). Litter mats (a layer composed of cedar "needles" possessing structural integrity) were removed and taken to the lab where they were stored in a refrigerator at 5 C. This litter was considered to be in field-condition. A sample of the field-condition litter was weighed and dried at 75 C. The litter was re-weighed and the proportion of water present was calculated. I filled each litter decomposition bag with approximately 17 g of field-condition litter in order to equal 7 g of oven-dry litter.

Litter decomposition bags, measuring 9.5x11cm, were made of "No-See-Um" netting from Ocean Electronics. I placed six decomposition bags within the litter layer under each tree on September 3, 2001. I randomly removed one bag from underneath each tree at the beginning of January, May and September for the next two years. In the lab, I removed all the litter from the bag, dried it for 72 hrs at 75 C, and weighed it. I encountered two problems with the litter bags. Litterbags collected at each sampling time had oven dry weights that were higher than the 7 g of oven-dry litter that I originally placed in the bags. Secondly, several litterbags disappeared over the course of the study.

Although these losses only accounted for slightly more that 4% of all litterbags, losses increased to 15% in the last sampling period. Therefore, litter decay rates described below are based on a fitted linear regression to the average mass for collected litterbags within a single sampling period instead of determining interval specific decay rates.

Statistical Analysis—I conducted multiple linear regressions and paired *t*-tests using SPSS (Version 11.0). Additionally, I have included standardized "beta" (*b*) coefficients along with statistical significances. For all analyses that included transect direction, I used a dummy variable that included both north (1) and south (0). Therefore, transect direction effects in linear regressions may refer to either compass direction. Because this was an exploratory study rather than inferential study, I have not included corrections for multiple comparisons nor for spatial autocorrelation (Legendre and Legendre 1998, Hallgren et al. 1999).

Results

Canopy Cover—Not surprisingly, canopy cover was highly related to distance from the trunk. In general, maximum canopy cover was present at 60-80% of the distance whereas south sides had increased canopy cover and increased cover at increased distances (Fig. 1). For both north and south transect directions, rapid reductions in canopy cover occurred at 70-80% distance with the canopy cover absent by 100% distance.

Light—Photon flux density ranged from a minimum of 11 μmol m^{-2} s^{-1} underneath the tree to a maximum of 1956 μmol m^{-2} s^{-1} in the open prairie. There was a very slight effect of date in the complete data set; however, this relationship was undetectable when quadrat categories ('under', 'edge', 'prairie') were analyzed separately. Sampling time did not significantly influence incoming radiation overall or by quadrat category. However, in the complete data set, three variables were highly significant in influencing incoming radiation. Canopy cover and transect direction had a significant negative effect (b=-0.595, p<0.001 and b=-0.229, p<0.001 respectively) on photon flux density. On the other hand, distance from the trunk had a significant positive effect (b=0.213, p=0.001) on photon flux density.

Canopy cover had the most direct influence on incoming solar radiation. At positions with maximum canopy cover, incoming radiation reaching the ground level was only 5-10% of that reaching the ground level in the open prairie (Fig. 2A). Additionally, maximum reductions in incoming radiation were skewed towards the north side of trees with substantial increases not occurring until ~80% of the radius for north transect in contrast to only ~60% for south transects (Fig. 2B).

Canopy cover, transect direction and distance from trunk were also significant factors influencing photon flux density when both the 'edge' and 'prairie' quadrat categories were considered separately (Table 1). However, aside from juvenile effects, no recorded variables had a significant effect on incoming light for the 'under' category.

Soil Temperature—Soil temperatures ranged from a minimum of 3 C to a maximum of 83 C. As with the results from photon flux density, transect direction (b=0.060, p< 0.001), distance from the trunk (b=-0.354, p< 0.001) and canopy cover (b=-0.153, p< 0.001) were significant factors influencing soil temperature (Fig. 3A). Soils under canopy cover were 20-30 C cooler than soil temperatures in the open prairie. North transects were ~10-20% cooler than south transects at most distances (Fig. 3B). Additionally, the lowest soil temperatures recorded were on the north side of trees at ~80% of the canopy radius. Litter depth had no significant influence on soil temperature.

There was also no significant effect of sampling day in relation to soil temperature for the entire data set.

Time of day did have a significant effect on soil temperature when 'under' quadrats were analyzed separately. Temperatures recorded earlier in the day were higher (p<0.001) than those gathered later in the day. In addition, the ground under smaller trees tended to be warmer than under larger trees (p=0.014). As with the complete data set, 'under' quadrats were negatively influenced by north transect direction (p<0.001) and canopy cover (p=0.004) but not distance from the trunk (Table 1), whereas 'edge' quadrats were negatively influenced only by north transect direction (p<0.001). 'Prairie' quadrats were negatively influenced by north transect direction (p<0.001) and positively influenced by distance from the trunk (p<0.001).

Soil Moisture—Soil moisture values ranged from as low as 5% to as high as 40% of field condition sample weight, however most values were 10-15%. Results from the complete data set showed that canopy diameter positively influenced soil moisture (b=0.243, p<0.001) whereas distance from the trunk negatively influenced soil moisture (b=-0.354, p=0.001, Fig. 4A). In general, soil moisture was 3-5% lower in the open prairie as compared to underneath the tree (Fig. 5A).

Canopy cover negatively influenced 'under' quadrats whereas 'edge' quadrats were not significantly influenced by any variable (Table 1). 'Prairie' quadrats were positively influenced by north transect direction (p=0.023), canopy diameter (p<0.001) and litter depth (p=0.001). North transects, larger trees and increased litter depth all resulted in increased soil moisture. Conversely, distance from the trunk had a negative affect (p=0.005) on soil moisture for 'prairie' quadrats indicating that soils in quadrats closer to the canopy edge contained more water than those further away.

Precipitation—Results of rainfall data showed that only distance from the trunk was significantly related to precipitation accumulation (b=0.887, p=0.001). However, distance from the trunk was only important for the entire data set and not any quadrat category. Total rainfall underneath the tree for the duration of this experiment ranged from as little as 50% to as high as 100% of accumulations outside of the canopy. However, rainfall accumulations under trees were generally 50-75% of accumulations in the open prairie. No variable significantly influenced rainfall accumulations for any quadrat category.

Analysis of each rain event day showed that there were significant differences in rainfall between north and south transects. However, neither north nor south transects continuously received more rain than the other on a regular basis. Data from the Marena Mesonet Station regarding wind speed and direction showed no clear pattern with respect to the relationship between observed accumulations and transect direction.

Soil Acidity—There were no significant trends in soil acidity underneath trees as compared to the open prairie. However, based on the complete data set, canopy diameter (b=0.191, p<0.001) and male trees (b=0.256, p<0.001) were positively related to soil pH. This result also held for 'under' quadrats (b=0.287, p=0.002 & b=0.254, p=0.006 respectively) but not for 'edge' quadrats. Soil pH in 'prairie' quadrats were positively associated with male trees (b=0.293, p<0.001) but not canopy diameter. Average soil pH around males trees was 6.83 (standard deviation of 0.97, N=125) whereas around female trees pH was 6.13 (standard deviation of 0.63, N=289). No other variables (including litter depth) were significantly related to soil acidity.

Litter Accumulation—Animal and/or wind disturbance of litter traps was common, particularly for traps outside of the canopy. Thus, analyses presented here are restricted to those traps within 82% of the distance from the trunk. Litter accumulation was positively affected by canopy cover for both cedar litter (b=0.442, p<0.001) and female cones (b=0.618, p=0.035), but canopy cover was negatively related to grass (b=-0.469, p=0.002) and deciduous (b=-0.356, p=0.012) litter accumulations. Both female cones and the 'other' category (which tended to be primarily composed of bark chips and dried sap) were negatively related to percent distance. Transect direction had no affect on litter accumulation for any litter category except for female cones, which was significantly greater towards the south.

Total yearly litter accumulation under the canopy in 2002, for all traps within 82% of the canopy radius, ranged from 26.6 g m^{-2} yr^{-1} to 1129.6 g m^{-2} yr^{-1} of which cedar litter accounted for 80-99% of the total. Across ten 'prairie' quadrats that had one complete year of data, total accumulations ranged from 12.1 g m^{-2} yr^{-1} to 130.1 g m^{-2} yr^{-1} of which cedar litter accounted for 2-10% (and rarely up to 90%) of the total. A comparison of canopy cover categories illustrates the dramatic reductions in litter accumulation in 'prairie' quadrats as compared to 'under' quadrats (Fig. 5B). 'Under' quadrats had litter accumulations of approximately 1-1.5 orders of magnitude more than 'prairie' quadrats.

Litter Decomposition—At every sampling interval, the oven-dry weight of litter in every litter decomposition bag was greater than the original 7 g placed within them

(Fig. 6). Preweighed reserved litterbags were reweighed and the original starting amount of approximately 7 g of oven-dry litter was confirmed. Increased mass was possibly due to an accumulation of fine dust, soil particulate matter and/or the invasion of fungal hyphae. However, based on linear regression, litter mass decreased at a rate of approximately 15-20% of oven-dry litter over two years.

Discussion

Microclimate—The observed reductions in incoming radiation under redcedar trees are dramatic but not unexpected. Joy and Young (2002) reported photosynthetically active radiation (PAR) for open sites in the range of 1313-1673 μmol m^{-2} s^{-1} and PAR under redcedar canopies less than 400 μmol m^{-2} s^{-1}. Yager and Smeins (1999) also reported PAR under *Juniperus* canopies to be 40-580 μmol m^{-2} s^{-1}. Although the results from this study generally agree with those of others, the variability of PAR values was quite high. In general, 'under' quadrats do not show as much variability in light received as compared to 'prairie' quadrats (Fig. 7). However, several 'under' and 'edge' quadrats received such high amounts of PAR that they were classified not only as outliers but also as extreme outliers during statistical analysis. This indicates that (1) solar angle in association with compass direction may significantly influence PAR, (2) *Juniperus* canopies are not uniform and therefore (3) any particular spot may receive a substantial amount of PAR at any one time during the day. Overall reductions in PAR of 90-95% in this study, 71-98% in Yager and Smeins (1999) and 70-80% in Joy and Young (2002) all suggest that reduced PAR by itself could significantly decrease total plant density and cover.

Reduced soil temperatures are one consequence of reduced PAR reaching the soil surface (Knapp and Seastedt 1986). Soil temperatures in this study had a wider range than those reported by either Hulbert (1969) who found soil temperatures ranging from 8-28 C or Joy and Young (2002) who found soil temperatures ranging from 31-45 C. I found the lowest soil temperatures in this study underneath cedar trees towards the north side; however, soil temperatures began decreasing at 120-130% distance in both transect directions. Therefore, although reductions in soil temperature seem to generally follow reductions in PAR (Fig. 7 & 8) it is still difficult to say definitively that cedar canopy directly caused these reduced soil temperatures because the reductions started occurring outside of the canopy diameter. Because litter depth had no significant influence on soil temperature, it is highly likely that lower soil temperatures are either caused by reduced PAR reaching the soil surface or increased soil moisture content acting as a heat sink and thereby reducing soil temperature.

Observed soil moisture values under redcedar in this study were similar to those reported by Smith and Stubbendieck (1990). However soil moisture in 'prairie' quadrats was 5-10% lower than values reported for an undisturbed prairie by Hulbert (1969) and Smith and Stubbendieck (1990). Unlike the results from Smith and Stubbendieck (1990), I found that 'prairie' quadrats contained less moisture than 'under' quadrats. Although they claimed that soil moisture values under redcedar trees consistently came closer to -1.5 MPa, it is likely that for my study such low soil water potentials would only be observed outside of the canopy and cedar litter influence.

Reduced PAR and soil temperatures likely reduce evaporation under cedar trees, as evidenced by a 3-5% higher soil moisture content under cedar trees. Reduced evaporation may potentially equalize the 25-50% reduction in total rainfall compared to the open prairie. In fact, results from Hulbert (1969) suggested that litter cover increases soil moisture content. Axmann and Knapp (1993) claimed that one potential reason for displacement of *Andropogon gerardii* by redcedar could be due to the ability of redcedar to maintain higher xylem pressure potential than *A. gerardii* during hot summer months. However, these higher pressure potentials may not strictly be due to morphological or physiological characteristics as Axmann and Knapp (1993) claimed but may simply be due to increased soil moisture caused by reduced PAR, reduced soil temperatures and thick litter layers. Additionally, microclimatic conditions such as reduced PAR, reduced soil temperature and increased soil moisture do not seem to fit the characteristic habitat requirements of a C_4 species adapted to hot and dry grasslands. On the other hand, my results and those of Hulbert (1969) both suggest that the shady, cooler and wetter conditions typical of 'under' quadrats would appear to favor woody species in an unburned grassland.

Although precipitation is the ultimate source of soil moisture, it does not appear that the observed temporal or spatial variability in total accumulations is the likely reason for decreased vegetation under redcedar trees. Spatial variability was more pronounced during larger rain events under cedar trees. However, due to the overall amount of precipitation in larger events, differences in accumulations between different distances and transect directions are likely to have little effect as evidenced by higher soil moisture content underneath cedar trees regardless of transect direction. Smaller rain events did produce a more pronounced effect and are thus the likely cause of increased spatial variability. In the end, precipitation effects may be extremely difficult to elucidate without direct on-site measurements of both wind speed and direction.

Soil Acidity—Soil acidity did not change in a predictable manner as a function of litter depth. Older research (Spurr 1940, Arend and Collins 1949) has suggested that alkaline soil conditions result from the presence of redcedar. Arend (1950) further suggested that the reason for redcedar creating conditions that are more basic is due to the relatively high leaf calcium content. If high leaf calcium content is responsible for increased alkalinity, larger trees and 'under' quadrats should be most affected and litter depth should then be positively correlated with increasing pH. My results do not support this prediction. On the other hand, if cedar litter contains immobilized calcium and the litter does not release the calcium until it decomposes, then litter depth may be unrelated to soil acidity because of the slow rate of cedar litter decay.

The observation of a significant gender effect on soil pH suggests that reproductive structures may have a differential effect on soil acidity. Because male trees tended to have more basic soil conditions than female or juvenile trees, it is possible that male cones contain more immobilized calcium than the cedar's foliage. Additionally, female cones may contain more acidic constituents the foliage and thus reduce the pH of soils below them. However, slight changes in soil pH may be difficult to demonstrate statistically in circumneutral to slightly basic soils typical of this part of Oklahoma. On the other hand, it is possible that male and female trees germinate and/or establish themselves preferentially in areas based on soil pH. To date, I have found no literature that suggests either gender having a higher germination or establishment probability in specific soil acidity conditions.

Litter—Not surprisingly, cedar litter accumulations underneath the canopy, although highly variable, were larger than accumulations in open tallgrass prairie. 'Prairie' litter accumulations averaged only 39.24 g m^{-2} yr^{-1} (Fig. 5B) which is significantly less than reported litter accumulations in the literature. An Osage (Oklahoma) prairie varied from 100 to 450 g m^{-2} yr^{-1} (Sims et al. 1978, Sims and Singh 1978). Engle et al. (1987) found that herbaceous biomass ranged from 150 to 350 g m^{-2} yr^{-1}. This dramatic difference between reported accumulations and my results is likely due to two factors. First, missing data precluded detailed, balanced results. Second, I used a litter trap method as opposed to a clipped biomass approach by the previous researchers. This means that litter accumulations would only be composed of material falling into the trap from around the edges.

On the other hand, a comparison of litter inputs underneath cedar canopies and the surrounding prairie show that cedar litter accumulations of approximately 500-600 g m^{-2} are 2 to 3 times higher than reported values for production in adjacent open prairie sites (Sims et al. 1978, Sims and Singh 1978, Engle et al. 1987). Such large inputs of litter are likely to have dramatic effects on species composition and diversity especially if little to no litter removal occurs. Sydes and Grime (1981) found that deciduous litter inputs of 400 to 600 g m^{-2} dramatically reduced herbaceous vegetation. Several other researchers have also found that litter negatively affects recruitment, herb density and biomass (Facelli 1994, Foster and Gross 1997, Yager and Smeins 1999).

The large pulse in redcedar litter accumulations during the May through September sampling period observed in this study (Fig. 9) are similar to those reported for redcedar by Norris et al. (2001). The timing of these pulses is also consistent with those reported by Enright (1999) and Saito (1997) for other conifers and angiosperms. The timing of litter accumulation pulses may further exacerbate reduced recruitment, germination and establishment rates in the next growing season. Carson and Peterson (1990) suggest that litter removal in the fall leads to increased plant density and species richness because seeds requiring particular cues to break dormancy do not or are not able to receive these cues when they are buried within the litter matrix. In addition, litter tends to act as a mechanical barrier that seedlings must penetrate to become established; therefore, even if seeds do germinate within the litter matrix they are not likely to survive unless they have relatively larger food reserves that would allow the seedlings to reach both the soil surface and incoming solar radiation (Facelli and Pickett 1991).

Although litter decomposition bags showed decreases of 15-20% in mass over the entire study, the unaccounted for initial increase in mass is problematic. At this time, I can only speculate what caused this. First, two unpaved roads border the study site (approximately 80 m to the closest tree) and could potentially be a source of fine dust. This dust could enter the litter layer during a rain event and could then be washed into the litter contained within the litterbag. An alternative explanation is that soil particles under the litter could have entered the litterbags during rain events. In addition, the increased weight of wet litter in the decomposition bags may have caused the decomposition bags to settle into the viscous soil. Several times I observed litterbags at or in the soil-litter boundary; this indicates that the bags moved downward from their original position within the litter matrix.

If my litter decomposition rates are representative of actual decomposition rates, then this study suggests a litter decay rate that is approximately 20% lower than that reported by Norris et al. (2001). Assuming a decay rate of 7.5-10% yr^{-1}, total net litter accumulation underneath redcedar trees is approaching the upper limit of gross annual native prairie production. In addition, there is a reduced probability of litter removal underneath cedar trees by prescribed fire due to standard practice of spring burning when cedar litter mats are moist. The lack of fine fuels under cedar trees would not be likely to support a fire. Assuming a successful prescribed fire under typical fire conditions, cedar litter combustion under burnt cedar trees is ~60% whereas litter combustion under unburned trees is typically less than 40%. (John Weir, personal communication).

Large litter depositions and slow decomposition rates should lead to a rapid accumulation of litter on the soil surface. Observed accumulation rates were lower when tree size was relatively small and/or canopy cover was relatively sparse. Accumulated litter from the smallest trees in this study was less than larger trees over the majority of samplings. However, the smaller trees were more prone to large litter accumulation pulses during the summer interval. This suggests that small trees may not be producing as much litter throughout the year that relatively larger amounts of litter are accumulating during key times.

In general, environmental conditions under redcedar trees are more similar to those in forested areas than open tallgrass prairie. Incoming solar radiation under the canopy was only 5-10% of unobstructed areas. Reduced PAR reaching the soil surface leads to lower soil temperatures and increased soil moisture underneath redcedar trees. However, high temporal and spatial variability in rainfall does not appear to influence soil moisture. Soil acidity appears to be unrelated to any other environmental variable measured in this study including canopy cover and litter depth. Average annual litter accumulation under redcedar trees was approximately 50-350 g m^{-2} yr^{-1} higher than that reported for several tallgrass prairies within Oklahoma. Litter decomposition rates of 7.5-10% yr^{-1} indicate the potential for litter to accumulate quickly to levels detrimental to prairie species.

Species richness and community composition are likely to be affected by these microclimatic conditions and litter dynamics. In Chapter 2, I found species richness tended to be much lower underneath redcedar trees and there appeared to be a trend favoring woody species with relatively large carbohydrate reserves. In addition, plant cover tended to decrease dramatically as cedar canopy increased thus resulting in little to no vegetation cover under redcedar trees. As a whole, my results imply that *J. virginiana* has the ability to alter microclimatic and litter dynamics to such a degree that theses changes adversely affect species richness and community composition within the influence of the tree.

Acknowledgements—I thank my advisor, Dr. Michael Palmer, for his continuous advice regarding experimental design, statistical analysis and editorial comments. I also thank Dr. Sam Fuhlendorf and Dr. Ron Tyrl for editorial comments. In addition, Jared Laufenberg, Cathy Sonlietner and Andy Potter aided in collection of various field samples. I thank John Weir for his personal communication regarding litter combustion due to prescribed fire. The Payne County Audubon Society and the OSU Botany Department's James K. McPherson Fund provided funding for this study.

Literature Cited

Agbim, N.N. 1987. Dry season decomposition of leaf litter from five common plant species of West Africa. *Bio. Agric. Hortic.*, **4**:213-224.

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

Arend, J.L. and R.F. Collins. 1949. A site classification for eastern redcedar in the Ozarks. *Proc. Soil Sci. Soc. Am.*, **13**:510-511.

Axmann, B.D. and A.K. Knapp. 1993. Water relations of *Juniperus virginiana* and *Andropogon gerardii* in an unburned tallgrass prairie watershed. *Southwestern Nat.*, **38**:325-330.

Bakker, J.P., E.S. Bakker, E. Rosen, G.L. Verweij and R.M. Bekker. 1996. Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. *J. Veg. Sci.*, **7**:165-176.

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

Briggs, J.M., A.K. Knapp and B.L. Brock. 2002b. Expansion of woody plants in tallgrass prairie: A fifteen-year study of fire and fire-grazing interactions. *Am. Midl. Nat.*, **147**:287-294.

Callaway, R.M. and E.T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. *Science,* **290**:521-523.

Carson, W.P. and C.J. Peterson. 1990. The role of litter in an old-field community: Impact of litter quality in different seasons on plant species richness and abundance. *Oecologia*. **85**:8-13.

Costello, D.A., I.D. Lunt and J.E. Williams. 2000. Effects of the invasion by the indigenous shrub *Acacia sophorae* on plant composition of costal grasslands in south-eastern Australia. *Biol. Cons.*, **96**:113-121.

Davy, A.J., S.J. Dunsford and A.J. Free. 1998. Acidifying peat as an aid to the reconstruction of lowland health on arable soil: Lysimeter experiments. *J. Appl. Ecol.*, **35**:649-659.

Diotte, M. and Y. Bergeron. 1989. Fire and the distribution of *Juniperus communis* L. in the boreal forest of Quebec, Canada. *J. Biogeogr.*, **16**:91-96.

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

Enright, N. J. 1999. Litterfall dynamics in a mixed conifer-angiosperm forest in northern New Zealand. *J. Biogeogr.*, **26**:149-157.

Facelli, J.M. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology*, **75**:1727-1735.

Facelli, J.M. and S.T.A. Pickett. 1991. Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.*, **57**:1-32.

Fitch, H.S., P. von Achen and A.F. Echelle. 2001. A half century of forest invasion on a natural area in northeastern Kansas. *Trans. KS. Acad. Sci.*, **104**:1-17.

Foster, B.L. and K.L. Gross. 1997. Partitioning the effects of plant litter biomass and litter on *Andropogon gerardii* in old-field vegetation. *Ecology*, **78**:2091-2104.

Fuhlendorf, S.D. 1992. Influence of age/size and grazing history on understory relationships of Ashe Juniper. [Thesis]. College Station (TX): Texas A&M University.

Fuhlendorf, S.D., F.E. Smeins and C.A. Taylor. 1997. Browsing and tree size influences on Ashe juniper understory. *J. Range Manage.*, **50**:507-512.

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

Ghersa, C.M., D.O. Ferranro, M. Omacini, M.A. Martinez-Ghersa, S. Pereaman, E.H. Satorre and A. Soriano. 2002. Farm and landscape level variables as indicators of sustainable land-use in the Argentine Inland-Pampa. *Agric. Ecosyst. Environ.*, **93**:279-293.

Hallgren, E., M.W. Palmer and P. Milberg. 1999. Data diving with cross-validation: an investigation of broad-scale gradients in Swedish weed communities. *J. Ecol.*, **87**:1-16.

Hoch, G.A. 2000. Patterns and mechanisms of eastern redcedar (*Juniperus virginiana*) expansion into tallgrass prairie in the Flint Hills Kansas [Dissertation]. Manhattan (KS): Kansas State University.

Hoffmann, W.A. 1996. The effects of fire and cover on seedling establishment in a neotropical savanna. *J. Ecol.*, **84**:383-393.

Holthuijzen, A.M.A. and T.L. Sharik. 1985. Colonization of abandoned pastures by eastern redcedar (*Juniperus virginiana* L.). *Can. J. For. Res.*, **15**:1065-1068.

Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology*, **50**:874-877.

Jameson, D.A. 1966. Pinyon-Juniper litter reduces growth of blue grama. *J. Range Manage.*, **19**:214-217.

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

Kemp, P.R., D.G. Waldecker, C.E. Owensby, J.F. Reynolds and R.A. Virginia. 1994. Effects of elevated CO_2 and nitrogen fertilization pretreatments on decomposition on tallgrass prairie leaf litter. *Pl. Soil*, **165**:115-127.

Knapp, A.K. and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioSci.*, **36**:662-667.

Lawson, E.R. 1990. *Juniperus virginiana* L. Eastern Redcedar, p. 131-139 *in* R.M. Burns and B.H. Honkala, coordinators. Silvics of North America: Volume 1, Conifers. U.S. Forest Service Agriculture Handbook 654. Washington DC.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. Elsevier, Amsterdam.

McPherson, G.R. and H.A. Wright. 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in western Texas. *Am. Midl. Nat.*, **123**:144-151.

Miller, R.F. and J.A. Rose. 1995. Historic expansion of *Juniperus occidentalis* (Western Juniper) in southeastern Oregon. *Gt. Basin Nat.*, **55**:37-45.

Miller, R.F., T.J. Svejcar and J.A. Rose. 2000. Impacts of western juniper on plant community composition and structure. *J. Range Manage.*, **53**:574-585.

Myster, R.W. 1994. Contrasting litter effects on old field tree germination and emergence. *Vegetatio*, **114**:169-174.

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

Peltzer, D.A. and M. Köchy. 2001. Competitive effects of grasses and woody plants in mixed-grass prairie. *J. Ecol.*, **89**:519-527.

Petranka, J.W. and J.K. McPherson. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. *Ecology*, **60**:956-965.

Schlesinger, W.H. 1997. Biogeochemistry: An analysis of global change. Academic Press, San Diego.

Sims, P.L., J.S. Singh and W.K. Lauenroth. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. *J. Ecol.*, **66**:251-285.

Sims, P.L. and J.S. Singh. 1978. The structure and function of ten western North American grasslands. II. Intra-seasonal dynamics in primary producer compartments. *J. Ecol.*, **66**:547-572.

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

Singh, J.S. and S.R. Gupta. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. *Bot. Rev.* **43**:449-528.

Spurr, S.H. 1940. The influence of two *Juniperus* species on soils reaction. *Soil Sci.* **50**:289-294

Sydes, C. and J.P. Grime. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. *J. Ecol.*, **69**:237-248.

Thomas, G.W. 1996. Soil pH and Soil Acidity, p. 485-489 *in* D.L. Sparks and J.M. Bartels, editors. Methods of Soil Analysis: Part 3 Chemical Methods. Soil Science Society of America, Inc. & American Society of Agronomy, Inc. Madison WI.

Whiteman, G. and J.R. Brown. 1998. Assessment of a methods for mapping woody plant density in a grassland. *J. Arid Environ.*, **38**:269-282.

Yager, L.Y. and F.E. Smeins. 1999. Ashe juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak savanna. *Southwestern Nat.*, **44**:6-16.

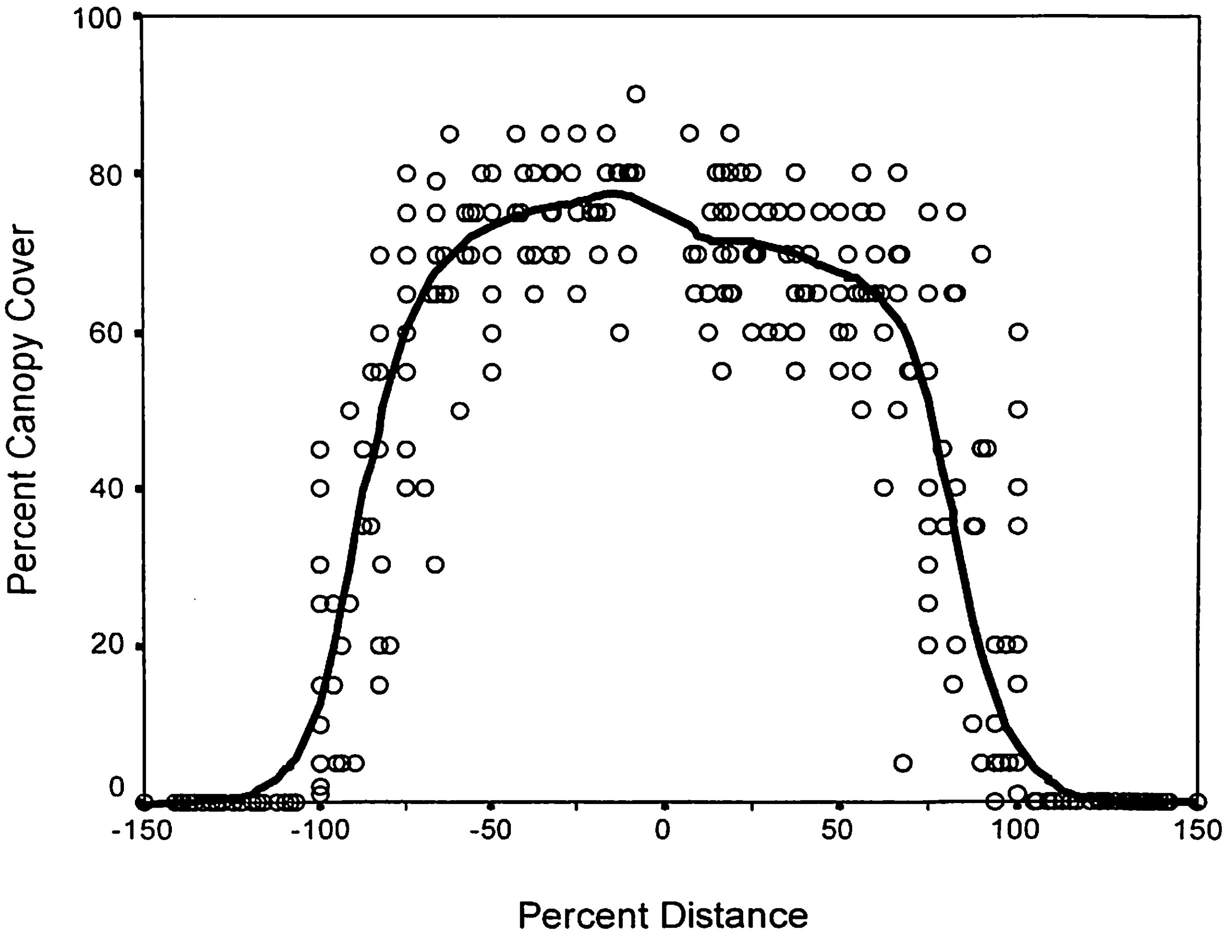

Figure 1: Canopy cover of eastern redcedar as a function of distance from the trunk (expressed as a percent of canopy radius). Positive distances represent the north transect direction whereas negative distances represent the south transect. The trendline for this figure is a Lowess curve

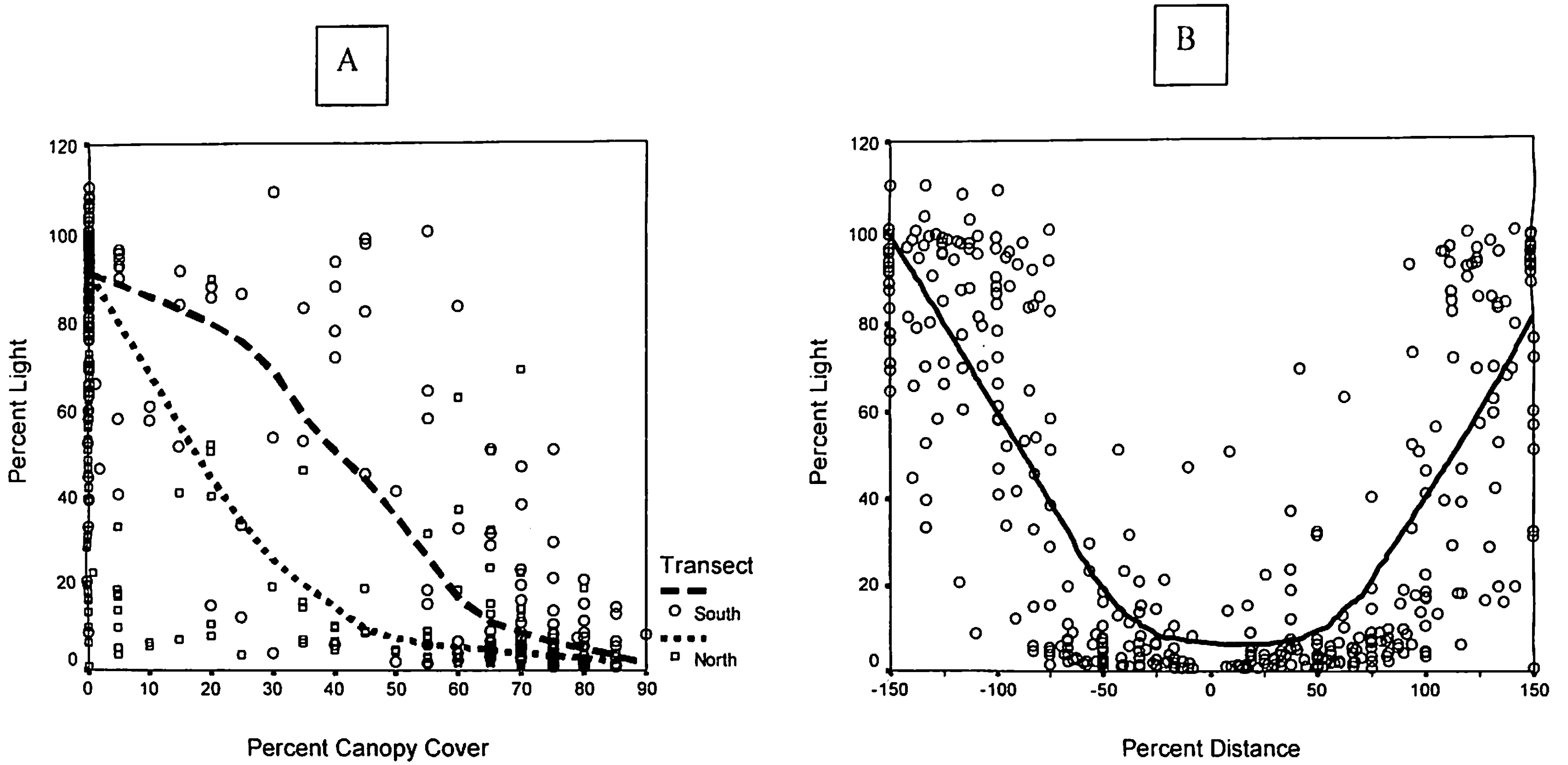

Figure 2: A—Percent incoming solar radiation as a function of cedar canopy cover. Includes both north and south transects. Trendlines for both figures are based on a Lowess curve. B—Percent incoming solar radiation (expressed as a percentage of unobstructed incoming light observed in the prairie) as a function of distance from the trunk (expressed as a percent of canopy radius). Positive distances represent the north transect direction whereas negative distances represent the south transect. Trendline is based on a Lowess curve.

Table 1: Variables significantly influencing light, soil temperature and soil moisture conditions for quadrat categories based on a multiple regression of each canopy cover category. Several nominal variables were used in these analyses including: transect direction (north), tree gender (male & juvenile) and date (8th, 14th, 17th and 20th). Asterisks indicates only two quadrats were present in this analysis for the marked variable

Quadrat Categories	Analysis	R	Variable	Standardized Coefficients	Significance
Under	Light	0.315	North Transect	-0.056	0.555
			Average Canopy Diameter	0.227	0.253
			Male Trees	0.024	0.871
			Juvenile Trees *	0.236	0.031
			Time of Day	0.155	0.505
			Date-8th	0.245	0.510
			Date-14th	0.121	0.288
			Date-17th	0.217	0.294
			Date-20th	0.101	0.453
			Absolute Distance	0.045	0.615
			Canopy Cover	-0.056	0.648
Edge	Light	0.645	North Transect	-0.469	0.000
			Average Canopy Diameter	0.054	0.785
			Male Trees	0.122	0.445
			Time of Day	0.287	0.239
			Date-8th	0.060	0.625
			Date-14th	0.184	0.087
			Date-17th	0.043	0.717
			Date-20th	0.050	0.763
			Absolute Distance	0.229	0.042
			Canopy Cover	-0.255	0.040
Prairie	Light	0.561	North Transect	-0.381	0.000
			Average Canopy Diameter	-0.108	0.429
			Male Trees	-0.072	0.473
			Juvenile Trees	-0.049	0.516
			Time of Day	-0.002	0.990
			Date-8th	-0.100	0.208
			Date-14th	-0.121	0.135
			Date-17th	-0.069	0.598
			Date-20th	-0.140	0.086
			Absolute Distance	0.191	0.008
			Canopy Cover	-0.251	0.000
Under	Soil Temperature	0.596	North Transect	-0.408	0.000
			Time of Day	-0.469	0.000
			Male Trees	-0.312	0.001
			Juvenile Trees *	-0.073	0.360
			Average Canopy Diameter	-0.223	0.014
			Absolute Distance	-0.078	0.301
			Canopy Cover	-0.267	0.004
			Litter Depth	-0.146	0.063

Table 1: Continued

Quadrat Categories	Analysis	R	Variable	Standardized Coefficients	Significance
Edge	Soil Temperature	0.829	North Transect	-0.721	0.000
			Time of Day	-0.132	0.123
			Male Trees	-0.144	0.077
			Average Canopy Diameter	-0.023	0.809
			Absolute Distance	0.109	0.183
			Canopy Cover	-0.125	0.190
			Litter Depth	-0.195	0.051
Prairie	Soil Temperature	0.723	North Transect	-0.576	0.000
			Time of Day	0.076	0.188
			Male Trees	-0.119	0.051
			Juvenile Trees	-0.078	0.163
			Average Canopy Diameter	0.412	0.000
			Absolute Distance	-0.045	0.470
			Canopy Cover	-0.016	0.785
			Litter Depth	0.067	0.182
Under	Soil Moisture	0.321	North Transect	-0.142	0.121
			Male Trees	-0.082	0.421
			Juvenile Trees *	-0.162	0.074
			Average Canopy Diameter	0.193	0.062
			Absolute Distance	-0.138	0.121
			Canopy Cover	-0.273	0.009
			Litter Depth	-0.061	0.512
Edge	Soil Moisture	0.250	North Transect	0.101	0.410
			Male Trees	-0.034	0.804
			Average Canopy Diameter	0.243	0.114
			Absolute Distance	-0.064	0.648
			Canopy Cover	-0.052	0.729
			Litter Depth	-0.024	0.881
Prairie	Soil Moisture	0.451	North Transect	0.147	0.023
			Male Trees	-0.129	0.096
			Juvenile Trees	-0.006	0.929
			Average Canopy Diameter	0.367	0.000
			Absolute Distance	-0.209	0.005
			Canopy Cover	-0.071	0.338
			Litter Depth	0.214	0.001

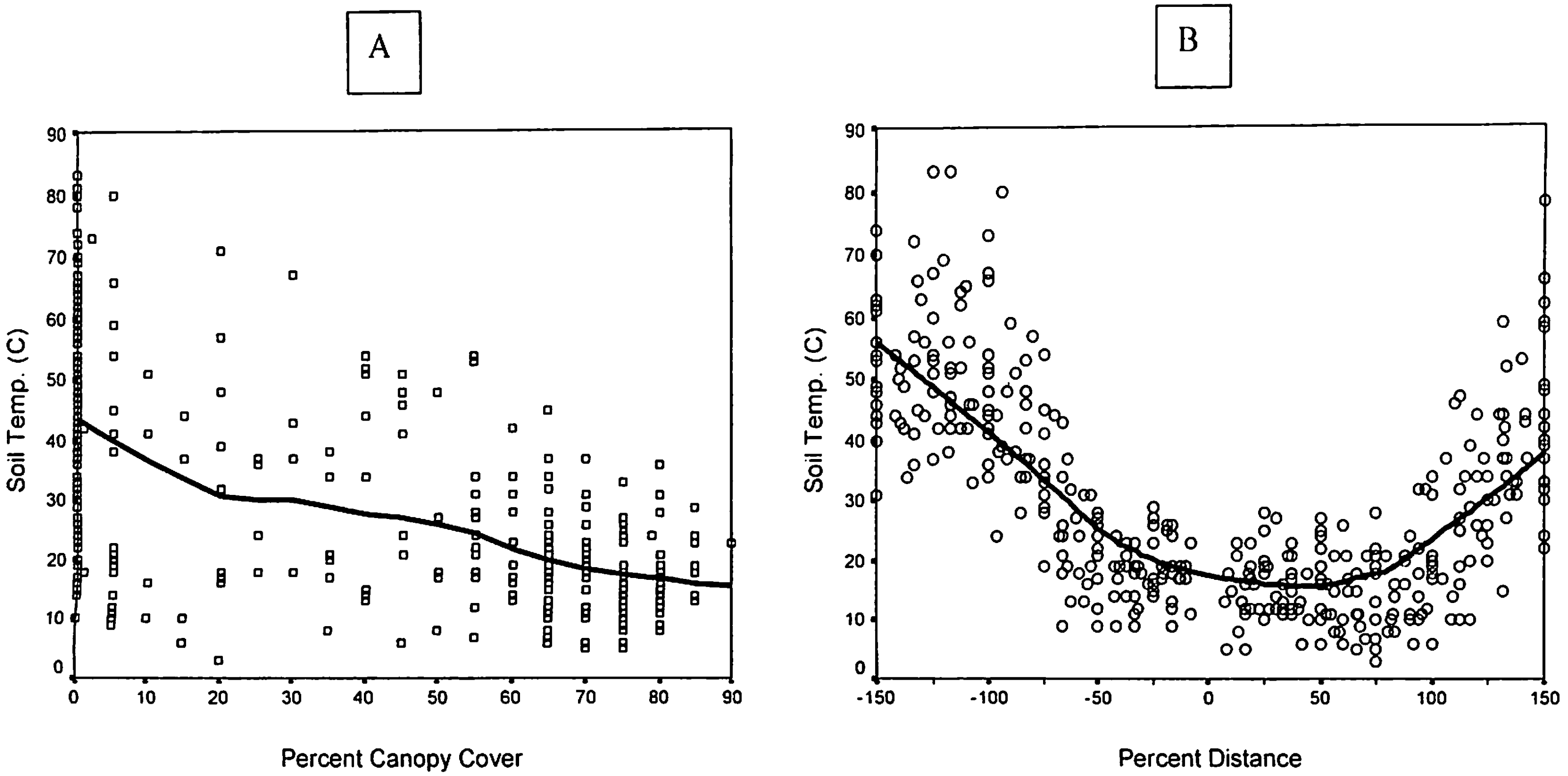

Figure 3: A—Soil temperature as a function of canopy cover. B—Soil temperature as a function of distance from the trunk (expressed as a percent of canopy radius). Positive distances represent the north transect direction whereas negative distances represent the south transect. Trendlines for both figures are based on a Lowess curve.

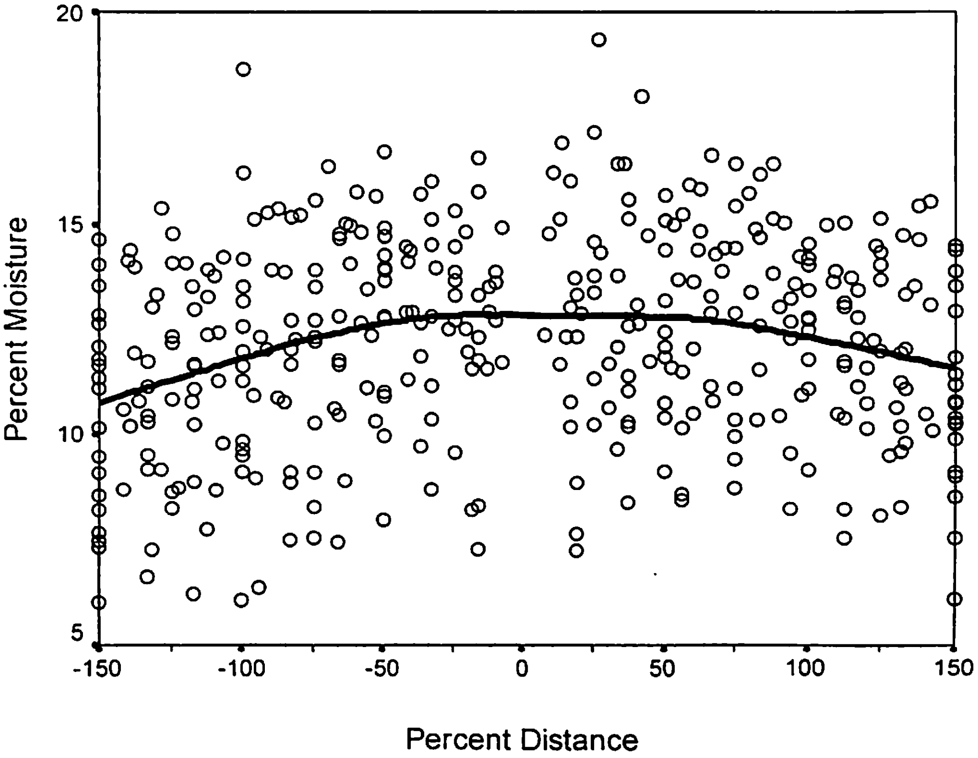

Figure 4: Percent soil moisture as a function of distance from the trunk (expressed as a percent of canopy radius). Positive distances represent the north transect direction whereas negative distances represent the south transect. Trendline for this figure is based on a Lowess curve.

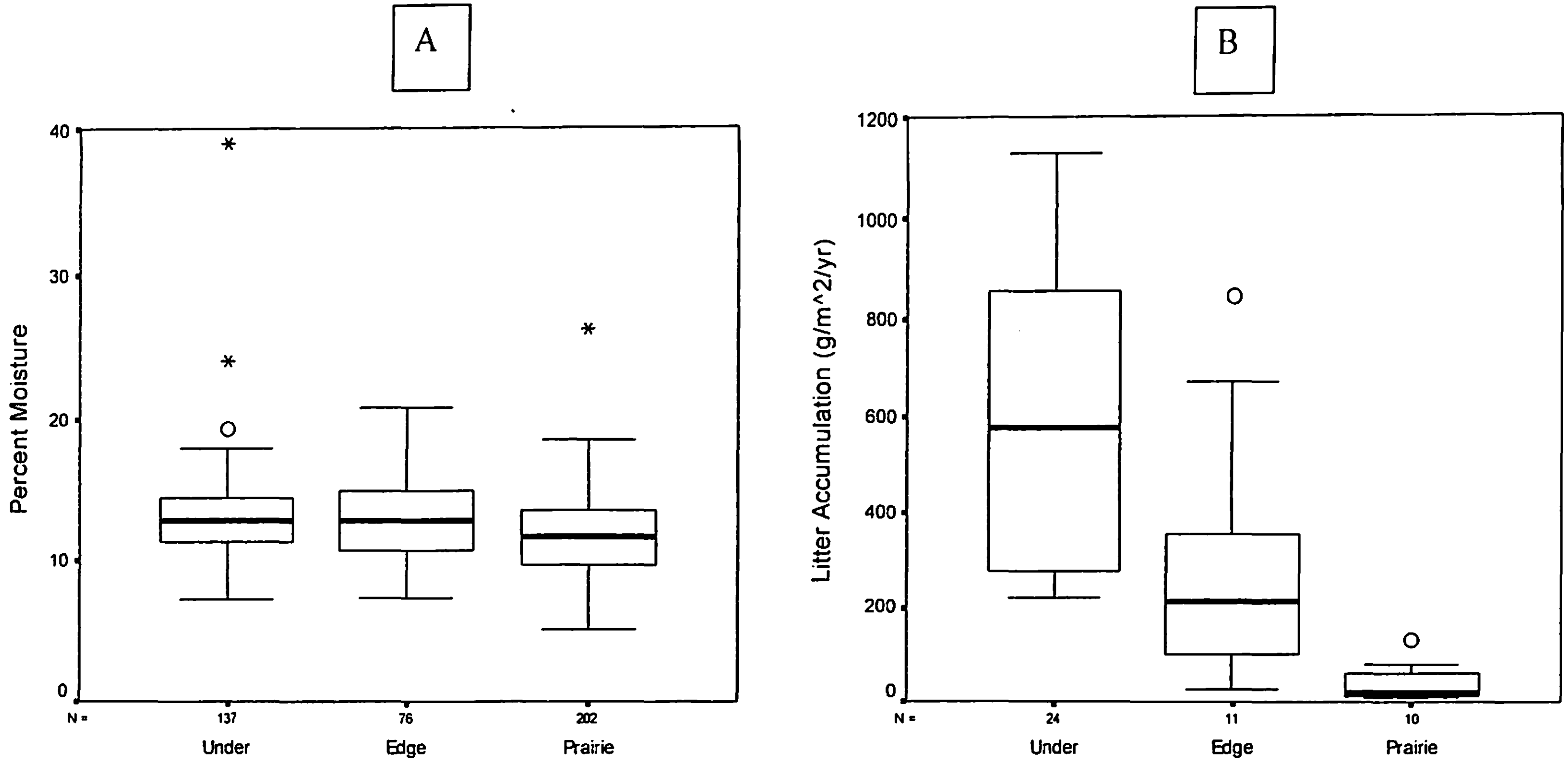

Figure 5: A—Box and whisker plots indicating median, quartiles and ranges for soil moisture based on quadrat categories. Circles represent outliers whereas stars represent extreme outliers. Also included is the number of quadrats of each category. B—Comparison of total litter accumulation of three different canopy cover categories for one year. 'Under' and 'edge' data is based 2002 whereas prairie data is based on any continuous year of data. Circles indicate outliers (1.5-3.0 times interquartile range) whereas stars indicate extreme outliers (>3.0 times interquartile range). Also included is the number of quadrats of each category.

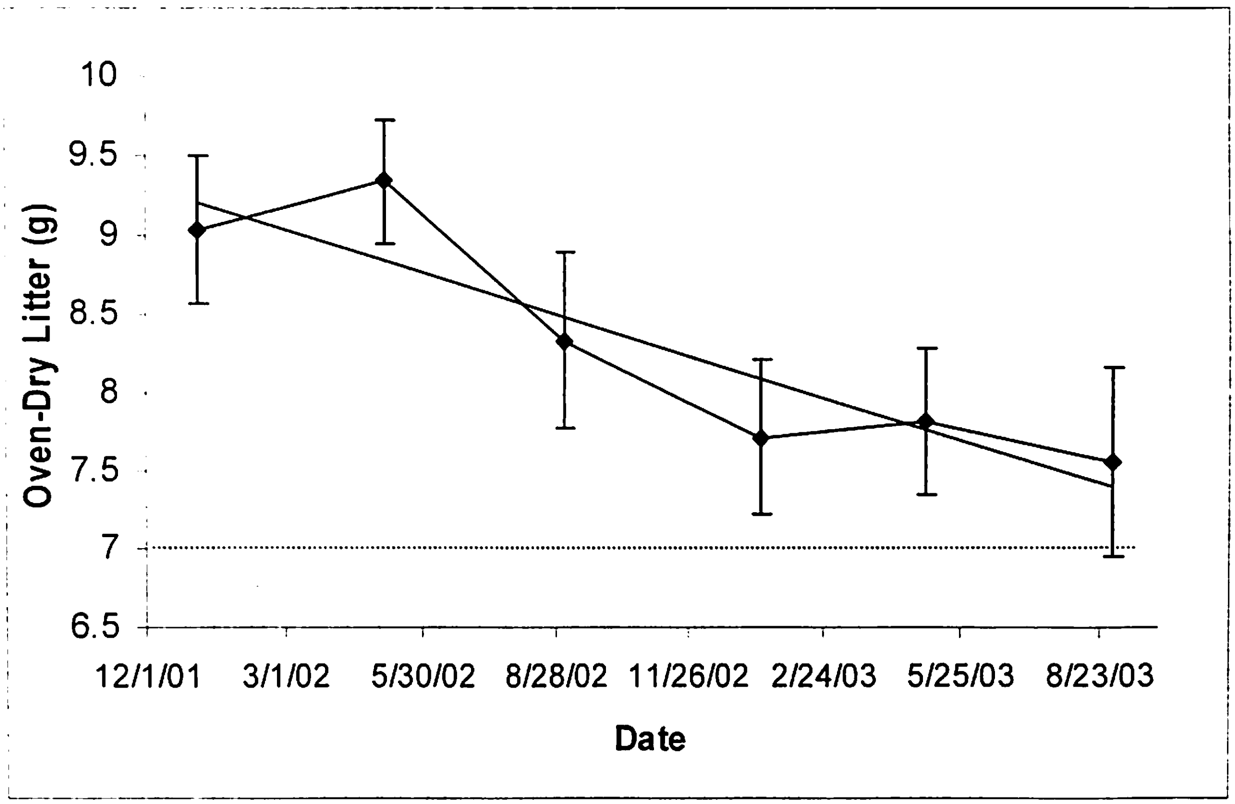

Figure 6: Change in the mass of oven dry litter from litter decomposition bags as a function of time for two years. Also included within this figure is a linear trend line and standard error bars for each sampling. The corresponding coefficient of determination for the linear trend line was 0.8313. The dashed line indicates the calculated original mass of litter in each litterbag.

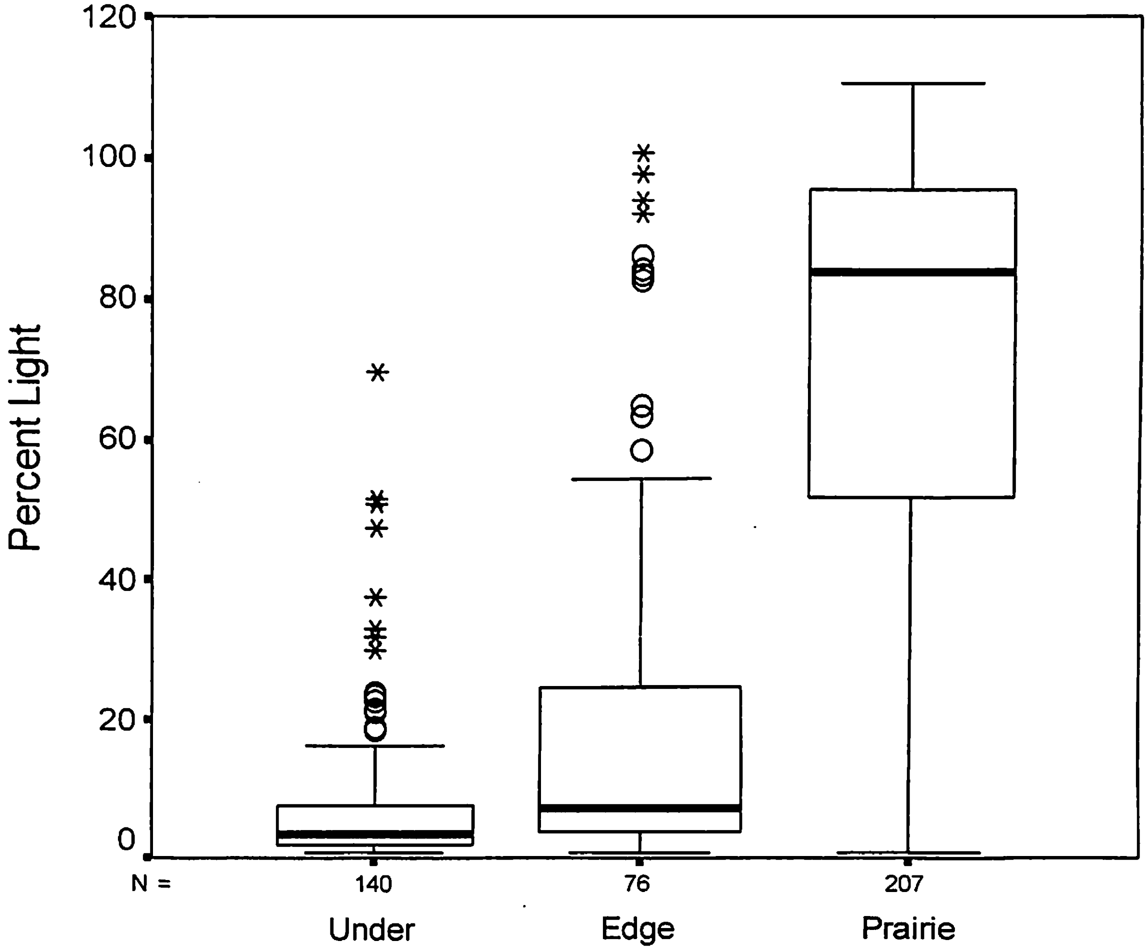

Figure 7: Box and whisker plots indicating median, quartiles and ranges of solar radiation between quadrat categories. Circles indicate outliers (1.5-3.0 times interquartile range) whereas stars indicate extreme outliers (>3.0 times interquartile range). Also included is the number of quadrats of each category.

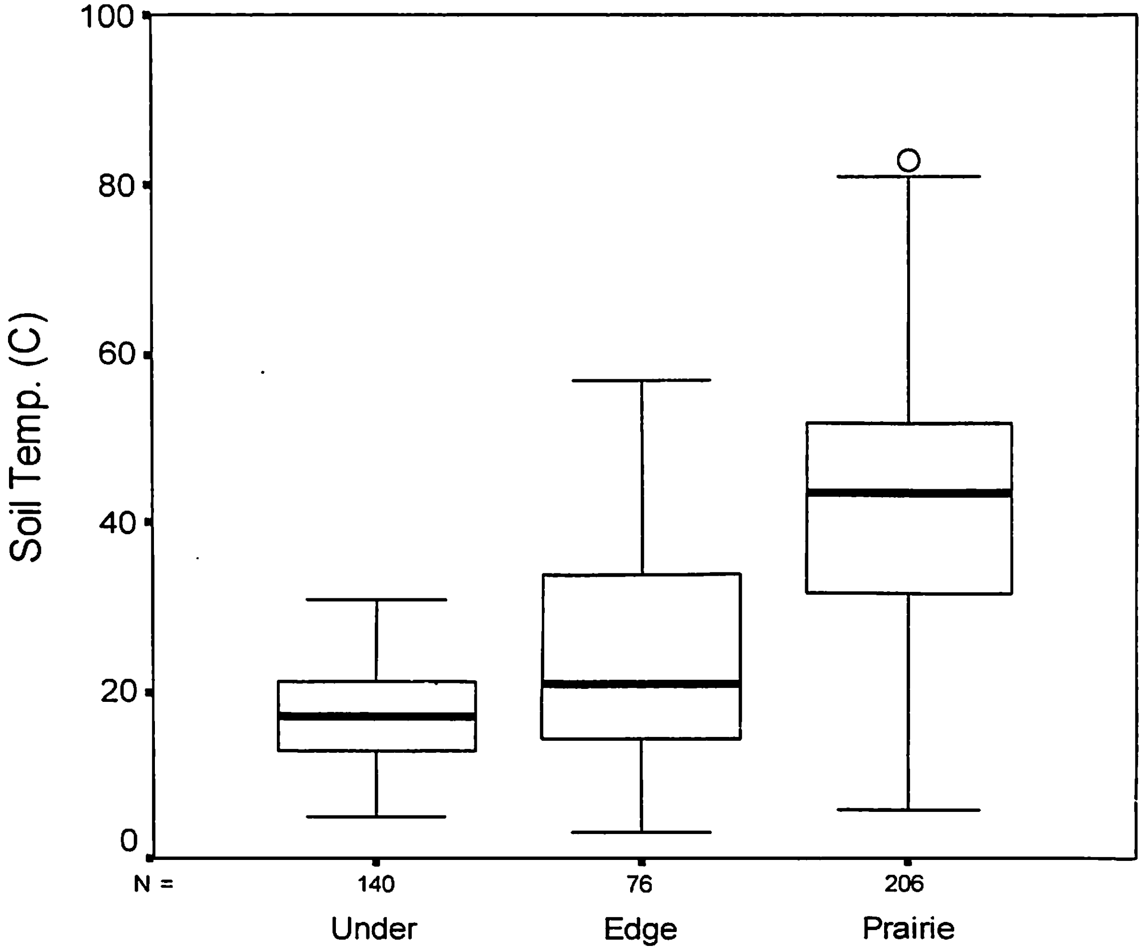

Figure 8: Box and whisker plots indicating median, quartiles and ranges of soil temperatures between quadrat categories. Circles indicate outliers. Also included is the number of quadrats of each category.

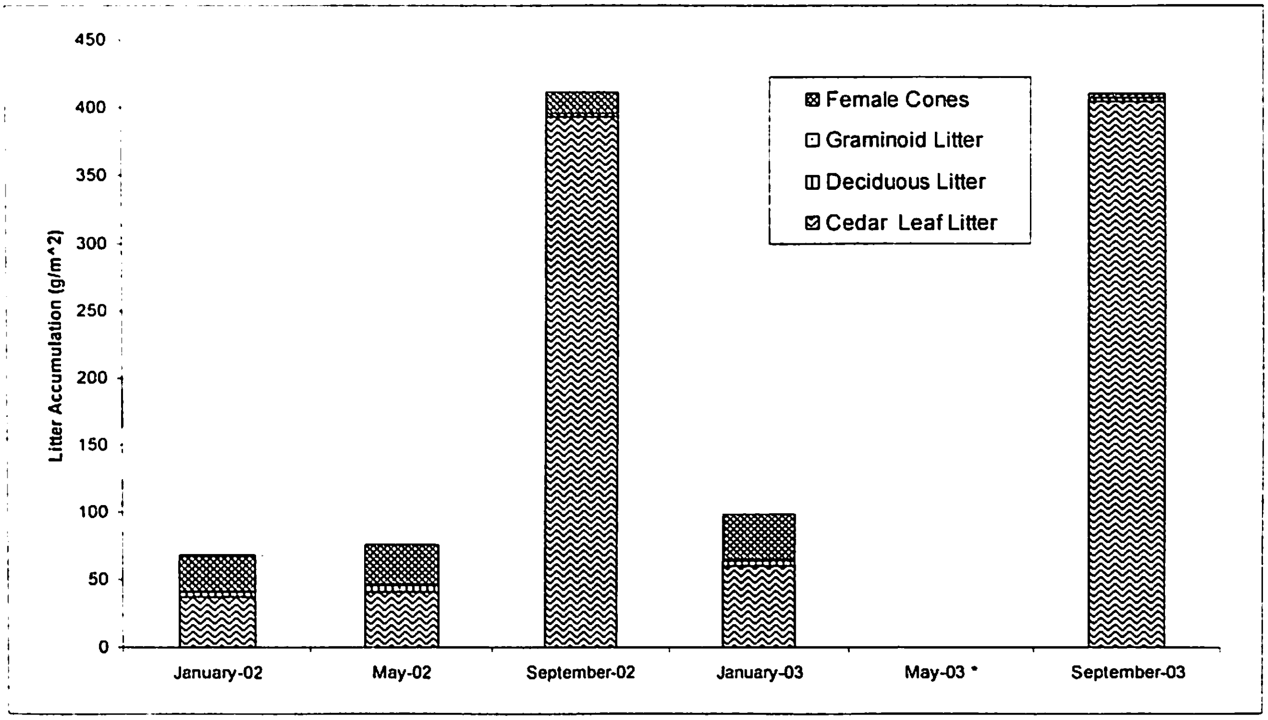

Figure 9: Average accumulation of quadrat litter within 82% distance from the trunk for the two years of the study. May 2003 was removed from analysis due to missing data.

Chapter 2

The Effect of *Juniperus virginiana* L. Trees on Plant Species Composition in a Central Oklahoma Grassland

By: JERAD S. LINNEMAN[1]

Oklahoma State University, Department of Botany, Stillwater, OK 74078

---

[1] Present address: Department of Botany, Oklahoma State University, Life Science East-#104, Stillwater, OK 74078. Telephone (405)744-5559; e-mail: ljerad@okstate.edu

Abstract

I studied species composition under *Juniperus virginiana* trees that invaded an unburned central Oklahoma grassland within the last 20-30 years. Species richness and stem density increased as distance from the trunk increased. Stem density was also higher towards the south side of trees. Graminoid, forb and total cover were significantly affected by distance from the trunk and transect direction. Ordination revealed at least two main environmental gradients, "openness" and compass direction, influencing species composition. Woody species tended to be most abundant underneath cedar canopies whereas grass and forb species were most abundant in the prairie. Woody and shade tolerant species dominated north transects and quadrats underneath the tree. Conversely, forbs dominated edge quadrats whereas graminoids dominated south transects and prairie quadrats. However, overall compositional trends were relatively weak because of few stems per quadrat and/or insufficient time since redcedar invasion.

Introduction

Within the last few decades, there has been a reduction in the number and size of native grasslands in North America. Urbanization has had a major effect on the conversion of native grasslands into housing developments as many people move out into what was once countryside (Samson and Knopf 1994, Licht 1997, Smith 1998). Changes in land use have also converted previously ungrazed native prairies into pasturelands as an increasing population demands more food (Licht 1997, Coppedge et al. 2001). However, the most widely accepted reason for the reduction in prairie area and vegetation quality is the anthropogenic removal of periodic fire from this system (Bragg and Hulbert 1976, Smith and Stubbendieck 1990, Licht 1997). The elimination of fire has not only caused a decrease in species richness in these unburned prairies but also the conversion of grasslands into forests (Axmann and Knapp 1993, Briggs et al. 2002a, Briggs et al. 2002b).

To the detriment of native grasslands in the Great Plains, one tree species has dramatically expanded its range in the absence of periodic fire. The rapid invasion of eastern redcedar (*Juniperus virginiana*) into the grasslands of North America has stimulated a large amount of research. Researchers have suggested that reductions in prairie species abundance and altered prairie community composition are related to a multitude of environmental factors that occur under *J. virginiana*. Such altered environmental factors include soil moisture (Engle et al. 1987, Facelli and Pickett 1991b), incoming solar radiation (Smith and Stubbendieck 1990, Facelli and Pickett 1991a & b) and soil temperature (Weaver and Rowland 1952, Hulbert 1969).

Besides changes in the microclimate resulting from redcedar trees, cedar litter may alter prairie litter dynamics by increasing litter accumulations and retarding litter decomposition. These alterations in microclimate and litter dynamics may be detrimental to prairie species richness and diversity (Knapp and Seastedt 1986, Facelli and Pickett 1991b, Myster 1994). Facelli and Pickett (1991b) suggested that not only does litter affect environmental conditions but it also affects the plant community. Litter can prevent germination or establishment by acting as a mechanical barrier that seedlings must penetrate to reach the soil surface or incoming light. For instance, Myster (1994) found significant decreases in *J. virginiana* and *Cornus florida* emergence caused by increased litter on the soil surface.

A number of studies have demonstrated the effects of eastern redcedar on grasslands. Studies by Engle et al. (1987) and Smith and Stubbendieck (1990) have shown dramatic reductions in standing biomass underneath redcedar trees. Other studies suggested that *J. virginiana* adversely affects species at specific locations (Jameson 1966, Smith and Stubbendieck 1990, Gehring and Bragg 1992). There is a shift in the dominant photosynthetic pathway as redcedar canopies close (Briggs et al. 2002). The result is a larger proportion of C_4 species outside of the canopy as compared to more C_3 species under redcedar trees.

In Chapter 1, I demonstrated how *J. virginiana* influenced the environment. In this study, I examine species richness and community composition under *Juniperus virginiana* trees in contrast to the open prairie in a central Oklahoma grassland. I also relate environmental variables to these observed trends.

Methods

Study Site—I conducted this experiment at the James K. McPherson Botanical Preserve located 16 km west of Stillwater, Oklahoma (36°06'00"N, 97°12'30"W). After a brief period of row crop agriculture, the site was converted into pastureland and grazed until the 1960's. Oklahoma State University (OSU) purchased the land and managerial control was turned over to the Department of Botany. In 1995, the Department of Botany introduced a burning regime, consisting of a 3-5 year return interval, to the northwestern half of the preserve with the goals of stimulating the return of a native tallgrass prairie community and controlling redcedar invasion into the Preserve's grasslands.

Tree selection and classification—I selected four study sites based on location within the unburned portion of the Preserve and distance between clusters of potential study trees. Three of the four study sites occurred along the eastern edge of the preserve, whereas one site was along the northern edge.

I selected potential study trees based on four criteria: (1) distance between study trees and any adjacent redcedars of at least 1.5 times the radius of the study tree, (2) a distance of no less than 2 times the canopy radius of the study tree to the canopy edge of any adjacent trees greater than one meter in height in the north and south compass direction, (3) a minimum canopy radius of 60 cm in the north and south direction of any study tree and (4) no overstory species for each study tree. Based on these criteria, I selected forty-eight potential study trees. I recorded canopy diameter in the north-south and east-west directions, tree height, stem diameter at both 10 cm and breast height (DBH) and gender of each potential study tree. I classified tree gender as male, female, or juvenile (those trees without observable sexual organs). For trees with multiple stems at breast height, I recorded separate DBH measurements for each primary stem. No potential study tree had several distinct stems rising from ground level.

I averaged canopy diameter measurements for both the north-south and east-west axes for each potential study tree and ranked them from smallest to largest. I assigned all potential trees to one of four arbitrary size classes (1-4) based on average canopy diameter; thereafter I randomly selected five trees within each size class for further study.

Sampling design—Sampling was based on a belt transect of contiguously placed quadrats in both the north and south compass direction for each study tree. I selected these directions because in a similar study Fuhlendorf (1992) found that the north/south distinction had stronger relationships with other factors than the east/west direction. Each quadrat measured 50 cm by 25 cm on a side with the 50 cm sides abutting adjacent quadrats. The number of quadrats directly underneath the canopy of the cedar tree determined the radius in each direction for environmental sampling. Environmental sampling, including estimated canopy cover, extended to 1.5 times the canopy radius. Based on the results from personal observations and the literature, I assigned the following categories to all quadrats: 'under' the canopy (0-60% of the canopy radius), 'edge' quadrats (60-90% of the canopy radius) and 'prairie' quadrats (greater that 90% of the canopy radius).

I identified each plant species rooted inside the quadrat and estimated its cover to the nearest percent for any cover less than 5% and to the nearest 5% for any cover over 5%. I collected unknown species for later identification. Species nomenclature and codes follow that of the USDA PLANTS database (USDA 2004). Species present in the study along with their corresponding codes are listed in Appendix 1. In addition, at several locations within this paper I refer to the response of *J. virginiana* redcedar seedlings and not the study tree or any of its structures.

At the time of vegetation sampling, I collected other measurements from each quadrat including percent canopy cover, litter depth, height to nearest foliage, percent of litter that is cedar, percent litter cover and percent plant cover. See Chapter 1 for more details.

Statistical Analysis—Statistical analysis consisted of multiple regressions and paired *t*-tests. I used SPSS (Version 11.0) to conduct both analyses. Additionally, I have included standardized "beta" (*b*) coefficients along with statistical significances. Due to the exploratory nature of many analyses within this study, I have not included any correction for multiple comparisons nor spatial autocorrelation.

I analyzed compositional data using direct gradient analysis. Direct gradient analysis uses species data and directly relates it to measured environmental variables. I selected partial Canonical Correspondence Analysis (pCCA) because of its ability to factor out covariables. Manual forward selection within pCCA was used to identify the most important environmental variables by selecting only those variables explaining residual variation. All ordinations were conducted using CANOCO FOR WINDOWS 4.5 (ter Braak and Šmilauer 2002) on both the absolute cover of each species as well as the relative proportion of cover of that species within a sample. Since the results of both absolute and relative analyses were similar, I present only the relative analysis here unless otherwise stated.

I developed *a priori* hypotheses about differences in both canopy cover and north versus south transect direction. I hypothesized that decreased canopy cover and south transects would have a positive relationship to stem density, vegetation cover and species richness. All ordination analyses are merely exploratory and, I have not included corrections for multiple comparisons nor for spatial autocorrelation (Legendre and Legendre 1998, Hallgren et al. 1999).In addition, environmental variables included in these analyses may only be acting as a proxy for the true environmental gradient(s).

Results

Density and Richness— Stems per quadrat was positively related to percent distance (b=0.652, p<0.001) and to south transects (b=-0.170, p<0.001) for the entire data set. A paired t-test of transect direction by each canopy cover category ('under', 'edge', 'prairie') showed that stems per quadrat was significantly higher on the south side of trees for 'edge' (p=0.001) and 'prairie' (p=0.029) quadrats. South quadrats had approximately 25% more stems than north quadrats (Fig. 1).

A common drawback of fine-scale studies of species richness is an inherent correlation between richness and density (Oksanen 1996); a phenomenon known as the 'rarefaction effect' (Palmer et al. 2000). As my data reveal a strong rarefaction effect (Fig. 2), I factored out the effects of stems per quadrat by including it in a multiple regression of species richness.

Multiple regressions showed percent distance from the trunk (b=0.141, p=0.004, Fig. 3) and both male (b=0.077, p=0.049) and juvenile trees (b=0.079, p=0.022) were all positively related to species richness for the entire data set. However, when each canopy cover category was analyzed separately, percent distance (b=0.190, p=0.005) and juveniles trees (b=0.161, p=0.023) were significant only for 'prairie' quadrats.

Total species richness ranged from 0-16 per 0.125m^2 quadrat with mean quadrat richness ranging from 2.9-7.5 (Table 1). Results from a paired t-test of mean quadrat richness for both transect directions by each canopy cover category showed that there were no significant differences in richness between the north and south transects for any category.

Vegetation Cover—A paired t-test of total vegetation cover showed that percent of vegetation cover was significantly higher on the south side for both 'edge' and 'prairie' quadrats (p=0.002 and 0.02 respectively, Fig. 4). In addition, total cover was positively affected by increasing distance based on the entire data set (b=0.583, p<0.001), however only for 'under' quadrats was total cover positively affected by distance (b=0.277, p=0.001). Larger trees also had significantly less total cover for all quadrats

(b=-0.110, p=0.017) and specifically for 'under' and 'edge' quadrats (b=-0.250, p=0.006 and b=-0.329, p=0.008, respectively).

Results from a paired t-test showed that forb cover was significantly higher on the south side for both 'edge' and 'prairie' quadrats (p=0.01 and 0.006 respectively). In addition, distance also had a significant positive effect on forb cover (b=0.412, p<0.001) for the entire data set; however distance was only significant for 'prairie' quadrats (b=0.011, p<0.001).

A paired t-test showed that graminoid cover was significantly higher on the south side for only 'edge' quadrats (p=0.014). Increasing percent distance was positively related to graminoid cover for the complete data set (b=0.481, p<0.001). In addition, both 'under' and 'edge' quadrats were positively affected by distance (b= 0.371, p<0.001 and b=0.227, p=0.013, respectively).

Although woody cover could be locally high, in general it was sporadic and contributed little to total plant cover over all quadrats. A paired t-test showed no significant differences between woody cover in north and south transects for any canopy cover category. In addition, percent distance had no significant effect on woody cover.

Direct Gradient Analysis—Partial Canonical Correspondence Analysis (pCCA) revealed two main compositional gradients in the data. The first axis was related to cedar canopy cover, whereas the second axis was related to transect direction (Fig. 5). The eigenvalues of the third and fourth axes were approximately equal to that of Axis 2 and were related to openness and bare ground respectively. Four of the twenty-one environmental variables included in the analysis showed significant partial effects and were therefore included in a pCCA; the south dummy variable was also included because both north and south comprise a single environmental variable. The five included variables accounted for more than 46% of the total explained variance and represent the two most dominant gradients present in the CCA, those being openness and compass direction (Fig. 6).

Using manual forward selection, I tested each environmental variable within each canopy category. In 'under' quadrats only litter depth significantly influenced (p=0.006) species composition. 'Edge' quadrats were not significantly influenced by any variable whereas 'prairie' quadrats were significantly influenced by soil pH (p=0.002), percent bare ground (p=0.023) and litter depth (p=0.044).

In general, species such as *Amphiachyris dracunculoides*, *Sabatia campestris* and *Diodia teres* dominated warmer sites towards the south whereas species such as *Gamochaeta purpurea*, *J. virginiana* and *Quercus stellata* dominated cooler sites under cedar canopy towards the north. In addition, species such as *Ambrosia psilostachya*, *Digitaria cognata* and *Sporobolus compositus* dominated sites with higher soil pH whereas *Symphoricarpos orbiculatus*, *Paspalum setaceum* and *Acacia angustissima* dominated sites with more acidic soils (Fig. 6).

Two *a priori* hypotheses were considered at the onset of this study. First, there are differences in species composition based on transect compass direction. Second, species are affected by distance from the trunk of the tree. I tested these hypotheses separately for 'under', 'edge' and 'prairie' quadrats. Results from the pCCA of transect direction showed that certain species marginally "preferred" (p=0.046) particular sides of the tree. For example, species with general habitat preferences for woodlands such as *S. orbiculatus*, *J. virginiana* and *A. gracilens* dominated the north side whereas species with general habitat preferences for more open upland sites like *P. setaceum, H. drummondii* and *Artemisia ludoviciana* dominated the south side. By itself, transect direction only accounted for 6.4% of the total explained variance in the data set.

The results of the pCCA on the relative proportion of species cover based on canopy cover categories showed a significant effect (*p*=0.001) of distance on species composition. However, canopy cover categories ('under', 'edge', 'prairie') only explained 19.7% of the non-residual variation. *Quercus stellata*, *C. festucacea* and *Gamochaeta purpurea*, all showed an affinity towards 'under' quadrats (Fig. 7), whereas less frequent woody species such as *Rhus copallinum*, *J. virginiana* and *Prunus mexicana* were more common in 'under' quadrats. Species typical of open prairies or pasturelands such as *Sorghastrum nutans*, *Ambrosia psilostachya* and *S. campestris* were more common in 'prairie' quadrats. Although none of the most frequent species occurred preferentially in 'edge' quadrats, a few rarer species (*Bothriochloa ischaemum*, *Chenopodium album*, *Oxalis violacea* and *Vernonia baldwinii*) did favor 'edge' quadrats.

'Under', 'edge' and 'prairie' quadrats were analyzed separately with pCCA to determine what environmental variables could be responsible for any changes in species composition as distance from the trunk increased. Litter depth was the only significant factor (*p*=0.006) influencing species composition in 'under' quadrats. On the other hand, soil pH (*p*=0.002), bare ground (*p*=0.023) and litter depth (*p*=0.044) all significantly influenced species composition in 'prairie' quadrats. No environmental variable significantly influenced species composition in 'edge' quadrats.

Woody species such as *R. copallinum, J. virginiana* and *Ulmus rubra* were predominantly found in 'under' quadrats whereas species like *Paspalum setaceum* and

Symphyotrichum ericoides dominated quadrats that were more open. However, although species composition changed as distance increased the compositional trend was weak as evidenced by the frequency of each species by quadrat category. Table 2 presents the most frequent species quadrat occurrences greater than 10% for at least one canopy cover category. Only three species were found in a single canopy cover position. *Parietaria pensylvanica* was only found in 'under' quadrats, *Solanum carolinense* was only found in 'edge' quadrats and *Symphyotrichum oblongifolium* was only found in 'prairie' quadrats.

Five species had their highest frequencies in 'under' quadrats including: *J. virginiana*, *Lamium amplexicaule*, *Lespedeza procumbens*, *Q. stellata* and *U. rubra*. However, none of these five species were in the top five most frequent species for 'under' quadrats. As distance from the tree increased, woody species became less frequent whereas forb and graminoid species became more frequent. Three of the five woody species present in 'edge' quadrats had their highest frequencies at this location (*Cercis canadensis*, *Cornus drummondii* and *S. orbiculatus*). However, unlike 'under' quadrats where tree species were the dominant woody vegetation, woody vegetation in 'edge' quadrats primarily consisted of shrubs. In addition, seven forbs and two graminoids had their highest frequencies in 'edge' quadrats. In 'prairie' quadrats, no woody species were one of the most frequent species aside from *S. orbiculatus*. Six of the seven most abundant species present in 'prairie' quadrats were graminoids including three of the tallgrass prairie's "big four" (*Schizachyrium scoparium*, *Andropogon gerardii* and *Sorghastrum nutans*). Additionally, seventeen forb species and nine grass species had their highest frequencies in prairie quadrats.

Discussion

Although I expected differences in both stem density and species richness between quadrats underneath the tree and the open prairie, both (as well as forb and grass cover) slowly increased even at 1.5 times the canopy radius. These results are similar to those of Engle et al. (1987) who suggested that herbage standing crop significantly increased as distance from the drip line increased from 3 m to 5 m. In this study, incoming solar radiation and soil temperature also were still increasing beyond 1.5 times the radius, particularly along the south transect, whereas soil moisture continued to decrease. These results suggest that a single tree's influence extends greatly beyond its canopy diameter and the sampling distance in this study. Two possible explanations could include the slow return to typical microenvironment conditions and/or increasing inter-specific root competition.

The results of this study also imply that the tree shadow (predominantly on the north side) influences both stem density and vegetation cover. These results are consistent with those of Gehring and Bragg (1992) who suggested that vegetation cover was lower on the north and east sides compared to south and west sides. Additionally, edge quadrats on the south side received more incoming solar radiation then their counterparts on the north side (Chapter 1). Several researchers have suggested that reductions in incoming radiation could substantially reduce total plant density and cover (Yager and Smeins 1999, Joy and Young 2002). Differences in solar radiation could explain the increased amount of forb and grass cover in south quadrats and the compositional trend towards open and/or upland species in south quadrats whereas woodland species were most frequent in north quadrats.

Overall, species composition showed only a weak trends as a function of distance. Tree species were much more likely to occur underneath redcedar trees as compared to any other location; however, no single woody species occurred in more than 8% of the quadrats as compared to dominant species such as *S. scoparium* and *D. oligosanthes* both of which occurred in approximately 33% of the 'under' quadrats. With the exception of tree species, my results mirror those of Briggs et al. (2002) who found that species present in the prairie were not consistently different from those found in a closed canopy redcedar forest. 'Edge' quadrats, although still being influenced by canopy cover in this study, were comparatively similar to 'prairie' quadrats. 'Edge' and 'prairie' quadrats were dominated by grass species such as *S. scoparium*, *S. compositus* and *D. oligosanthes* that occurred in 42%-69% of the quadrats. In each canopy cover category, grass species typically associated with the prairie were the most frequent.

In this study, C_4 species frequency increased as distance increased; photosynthetic pathway classification followed that of Sage et al. (1999). However, the number of C_4 species and the specific C_4 species remained the same across all distances. What was striking was that C_4 grass species, most commonly associated with the tallgrass prairie, rapidly became the most frequent as distance increased. My results agree with those of Briggs et al. (2002) who suggested a compositional trend towards C_4 species occurs as distance from closed canopies increased. On the other hand, the C_3 species *D. oligosanthes*, *Erigeron strigosus* and *Scleria pauciflora* were always frequent in each quadrat category. As stated by Gehring and Bragg (1992), factors other than photosynthetic pathway probably drive species responses as distance from the trunk increases.

With the exception of woody plants, species growing underneath redcedar trees appear to largely be a random subset of the species from the surrounding matrix. Therefore, those species with the highest frequencies prior to redcedar establishment and growth are still likely to be the most frequent underneath cedar canopies as each tree grows. My results agree with those of Gehring and Bragg (1992) who suggested that frequency of tree species increases underneath redcedar trees. Both Myster (1994) and Facelli (1994) found that woody species were less inhibited by deep litter layers than herbaceous species because of their relatively larger seed mass and subsequently increased carbohydrate reserves. Therefore, if seeds from woody species became lodged within the litter layer underneath a cedar tree they would likely have a higher probability of establishment than a grass or forb species.

Conversely, the results from this study show little to no trend in non-woody species composition under cedar trees that have encroached within the last 20-30 years. This result differs from Gehring and Bragg (1992) who observed significant changes within only 10-20 years since encroachment. Although tree frequency did increase under cedar trees in this study, the vast majority of species present in 'under' quadrats were also present in the open prairie. Increased time since initial invasion should lead to a more highly pronounced trend in composition due to the exclusion of prairie species from underneath redcedar canopies. Results from Briggs et al. (2002) suggested that within 40 years of encroachment nearly all grassland species are likely to be eliminated.

In conclusion, cedar canopies reduced both stem density and species richness. Since the majority of species were present in few quadrats and that the most frequent species were consistently grasses associated with the prairie, the composition under cedar trees appears to be an idiosyncratic subset of the species present before encroachment. Although no strong compositional trend or species transition zones were observed in this study there does appear to be a slight preference of woody and/or shade tolerant species for conditions under cedar trees. In addition, forbs and graminoids tend to be more frequent as distance increased. Distance and transect direction had a strong influence on vegetation cover and were both related to species composition. North and south transects have strong differences in several microclimatic variables (Chapter 1) which may help to account for the observed differences in species composition. These differences in microclimate also extend far beyond areas in close proximity to the canopy. Additionally, a tree shadow effect was observed towards the north side for several environmental variables as well as vegetation cover. With the additional results of Chapter 3, one item related to species composition and overstory redcedar cover seems consistent; without redcedar removal, grasslands and pasturelands will continue to lose grassland species in favor of forest species.

Acknowledgements—I thank my advisor, Dr. Michael Palmer, for his continuous advice regarding experimental design, statistical analysis and editorial comments. I also thank Dr. Sam Fuhlendorf and Dr. Ron Tyrl for editorial comments. In addition, Jared Laufenberg aided with the collection of various field samples. The Payne County Audubon Society and the James K. McPherson Fund, administered by the Department of Botany at Oklahoma State University, provided funding for this study.

Literature Cited

Axmann, B. D. and A. K. Knapp. 1993. Water relations of *Juniperus virginiana* and *Andropogon gerardii* in an unburned tallgrass prairie. *Southwest Nat.*, **38**:325-330.

Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.*, **29**:19-23.

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

Briggs, J.M., A.K. Knapp and B.L. Brock. 2002b. Expansion of woody plants in tallgrass prairie: A fifteen-year study of fire and fire-grazing interactions. *Am. Midl. Nat.*, **147**:287-294.

Coppedge, B.R., D.M. Engle, S.D. Fuhlendorf, R.E. Masters and M.S. Gregory. 2002. Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA. *Landscape Ecol.*, **16**:677-690.

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

Facelli, J.M. and S.T.A. Pickett. 1991a. Plant litter: Light interception and effects on an old-field plant community. *Ecology*, **72**:1024-1031.

Facelli, J.M. and S.T.A. Pickett. 1991b. Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.*, **57**:1-32.

Facelli, J.M. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology,* **75**:1727-1735.

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

Hallgren, E., M.W. Palmer and P. Milberg. 1999. Data diving with cross-validation: an investigation of broad-scale gradients in Swedish weed communities. *J. Ecol.,* **87**:1-16.

Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology,* **50**:874-877.

Jameson, D.A. 1966. Pinyon-Juniper litter reduces growth of blue grama. *J. Range Manage.,* **19**:214-217.

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

Knapp, A.K. and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioSci.,* **36**:662-667.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. Elsevier, Amsterdam.

Licht, D.S. 1997. Ecology & Economics of the Great Plains. University of Nebraska Press, Lincoln, NB

Myster, R.W. 1994. Contrasting litter effects on old field tree germination and emergence. *Vegetatio,* **114**:169-174.

Oksanen, J. 1996. Is the humped relationship between species richness and biomass an artifact due to plot size? *J. Ecol.*, **84**:293-295.

Palmer, M.W., D.B. Clark and D.A. Clark. 2000. Is the number of tree species in small tropical forest plots nonrandom? *Comm. Ecol.*, **1**:95-101.

Sage, R.F., M. Li and R.K. Monson. 1999. The taxonomic distribution of C_4 photosynthesis, p. 551-584. In: Sage, R.F. and R.K. Monson. C_4 plant biology. Academic press, San Diego

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

Smith, D.D. 1998. Iowa prairie: Original extent and loss, preservation and recovery attempts. *J. Iowa Acad. Sci.*, **105**:94-108.

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

ter Braak, C.J.F. and P. Šmilauer. 2002. Canoco for Windows 4.5. Biometris-Plant Research International. Wageningen, Netherlands.

USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Weaver, J.E. and N.W. Rowland. 1952. Effect of excessive natural mulch on the development, yield, and structure of a native grassland. *Bot. Gaz.*, **114**:1-19.

Yager, L.Y. and F.E. Smeins. 1999. Ashe juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak savanna. *Southwestern Nat.*, **44**:6-16.

Table 1: Mean stems per quadrat (stems per 0.125 m^2) and species richness (species per 0.125 m^2) for each canopy cover category including standard deviation

	Minimum Stems	Maximum Stems	Mean Stems and Standard Deviation	Minimum Richness	Maximum Richness	Mean Richness and Standard Deviation
Under	0	40	8.2±9.1	0	10	2.9±2.5
Edge	2	74	30.8±19.7	1	15	6.1±3.0
Prairie	4	160	51.0±26.7	2	16	7.5±2.9

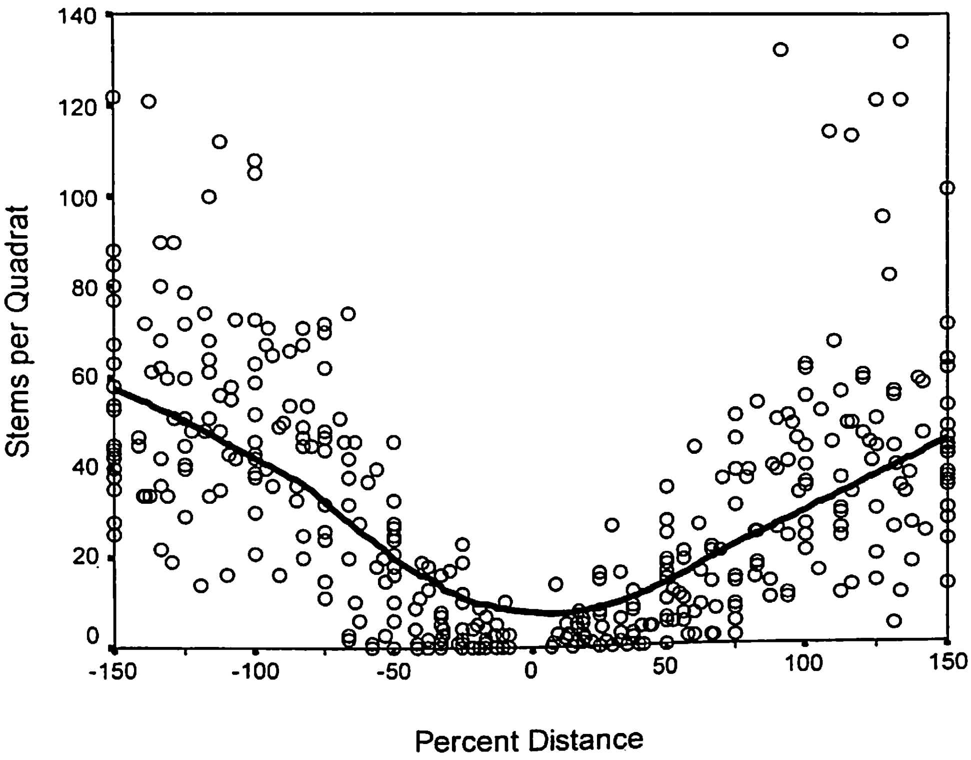

Figure 1: Stems per quadrat (stems per 0.125 m^2) as a function of distance from the trunk (expressed as a percent of canopy radius) based on all samples. Negative percent distance indicates south transects direction and positive values indicate north transects direction. A Lowess trendline has been included

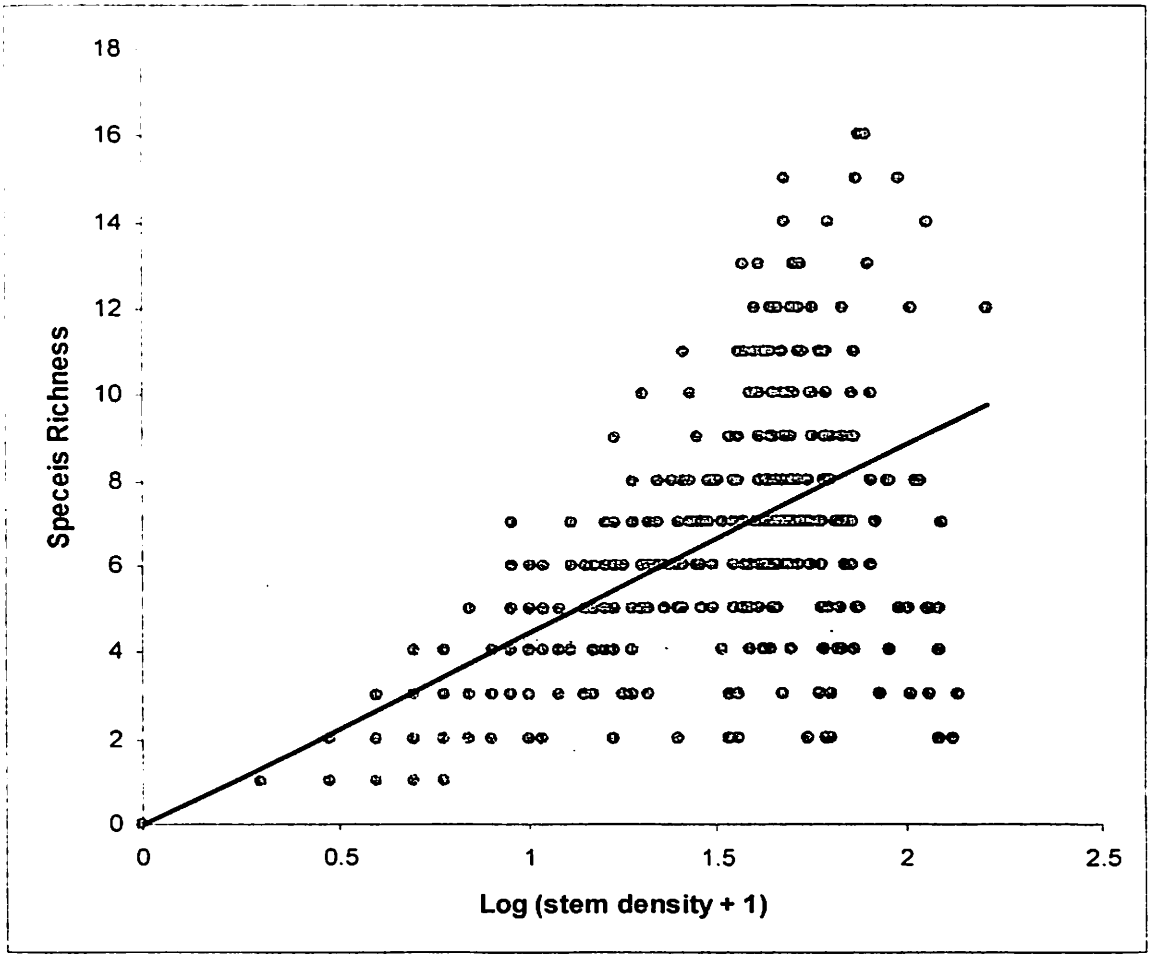

Figure 2: Species richness as a function of the log of stems per quadrat plus one. The linear regression line was forced to start at the origin thus yielded a coefficient of determination of 0.5226.

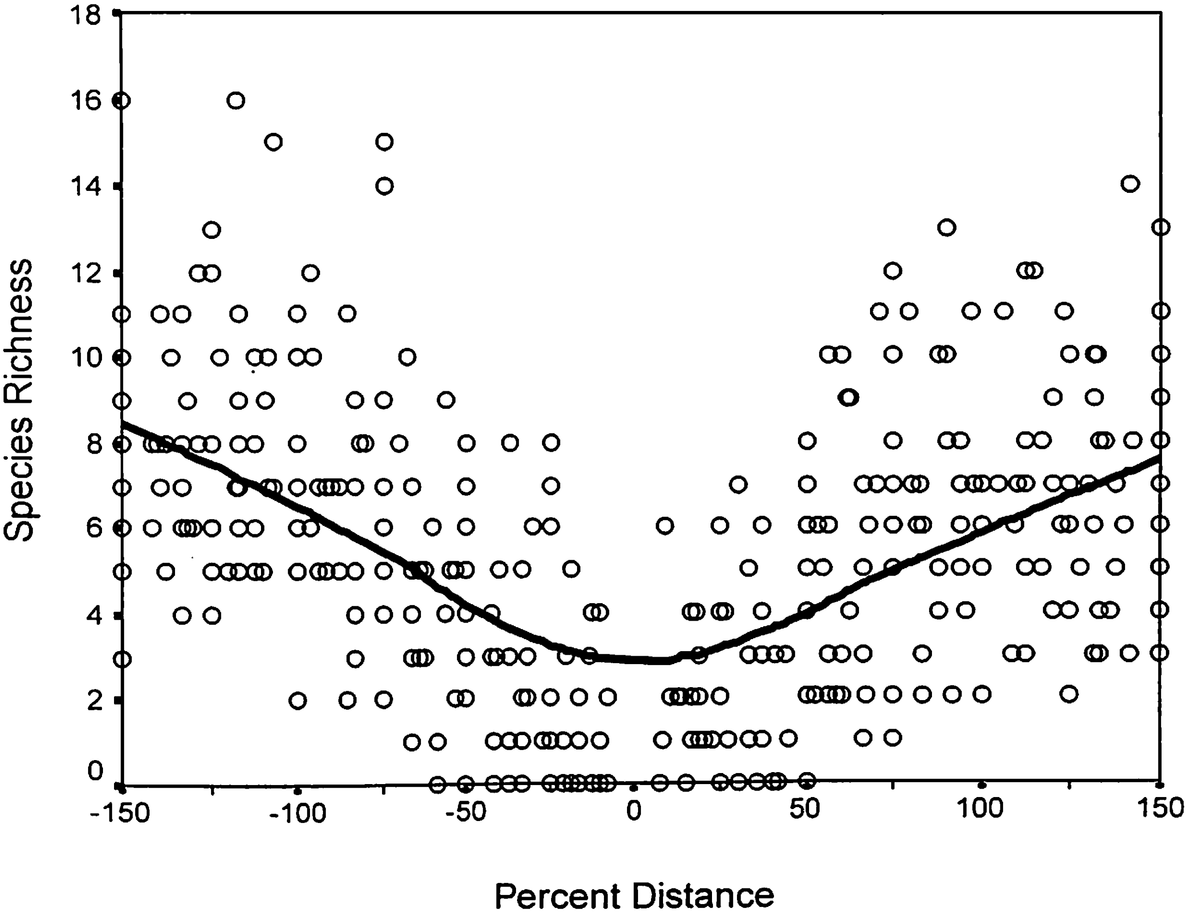

Figure 3: Species Richness (species per 0.125 m^2) as a function of percent distance from the trunk (expressed as a percent of canopy radius). Negative percent distance indicates south transects direction and positive values indicate north transects direction. A Lowess trendline has been included.

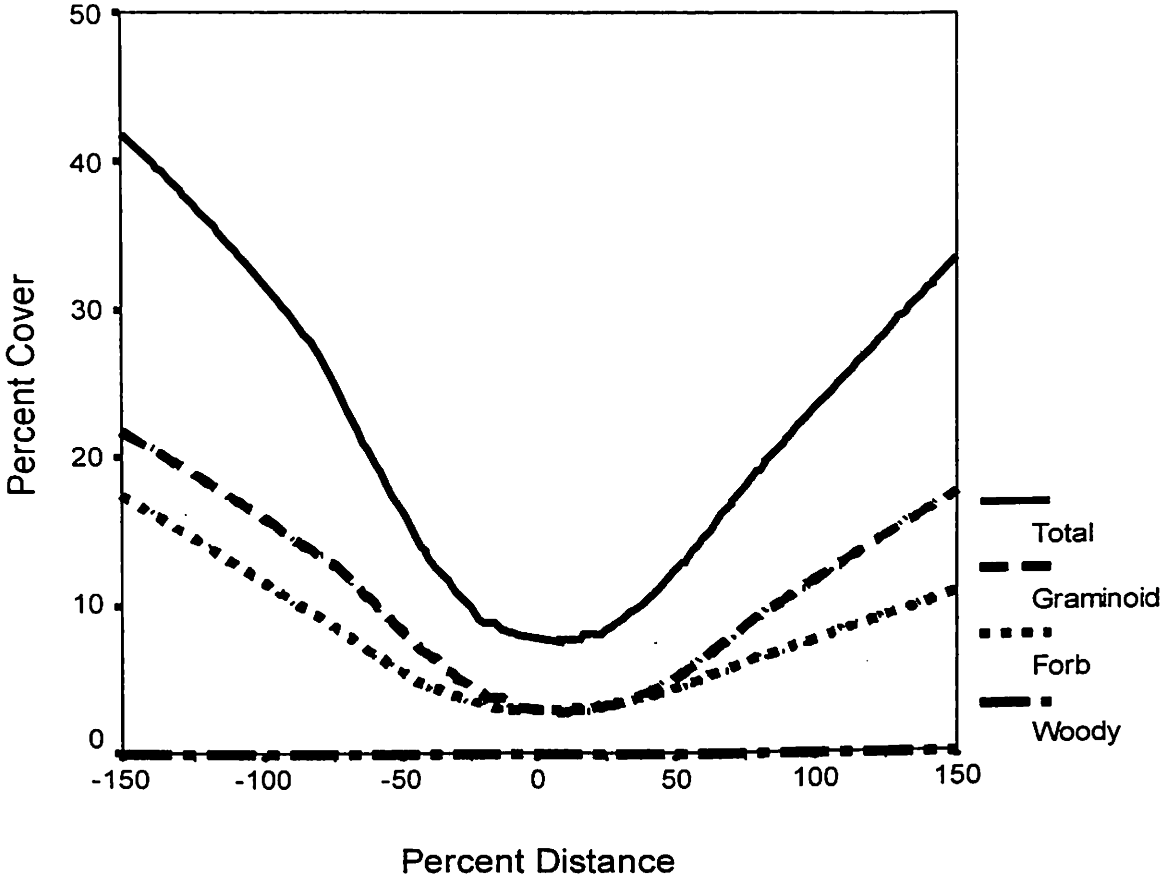

Figure 4: Vegetation cover for three growth forms as a function of distance. Also included is total vegetation cover. The trendlines for this figure are Lowess curves. In addition, data points were excluded from this figure to aid visibility.

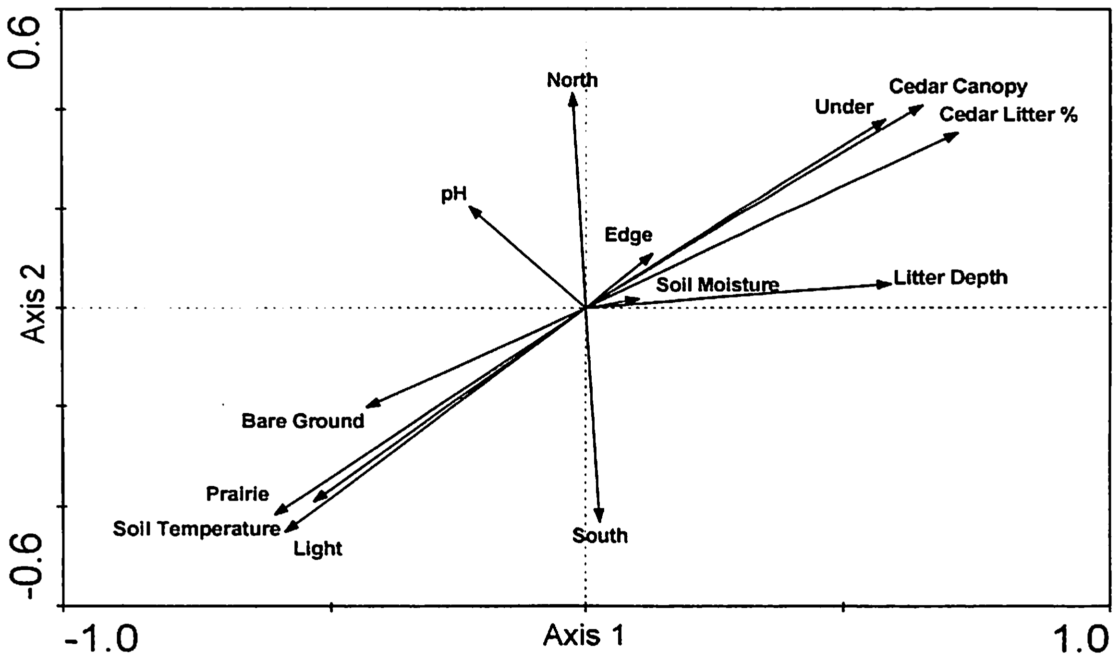

Figure 5: pCCA scatter plot of environmental variables along Axis 1 and 2. Arrow length indicates the relative strength of each particular variable.

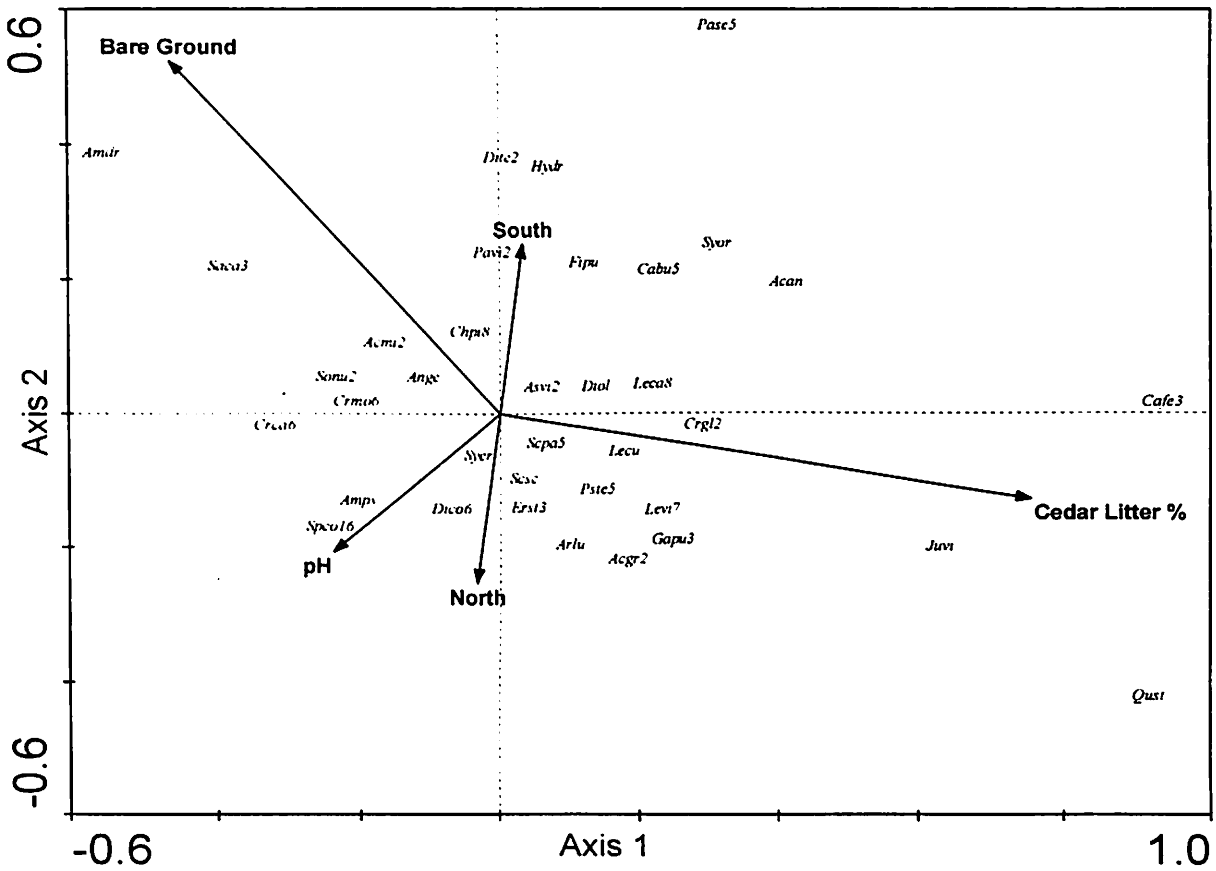

Figure 6: pCCA biplot of manually selected environmental variables and species codes. Axis 1 and 2 are displayed. Arrow length indicates relative strength of environmental variables whereas the species codes represent the relative multi-dimensional position of each species in ordination space. Species codes are indexed in Appendix 1.

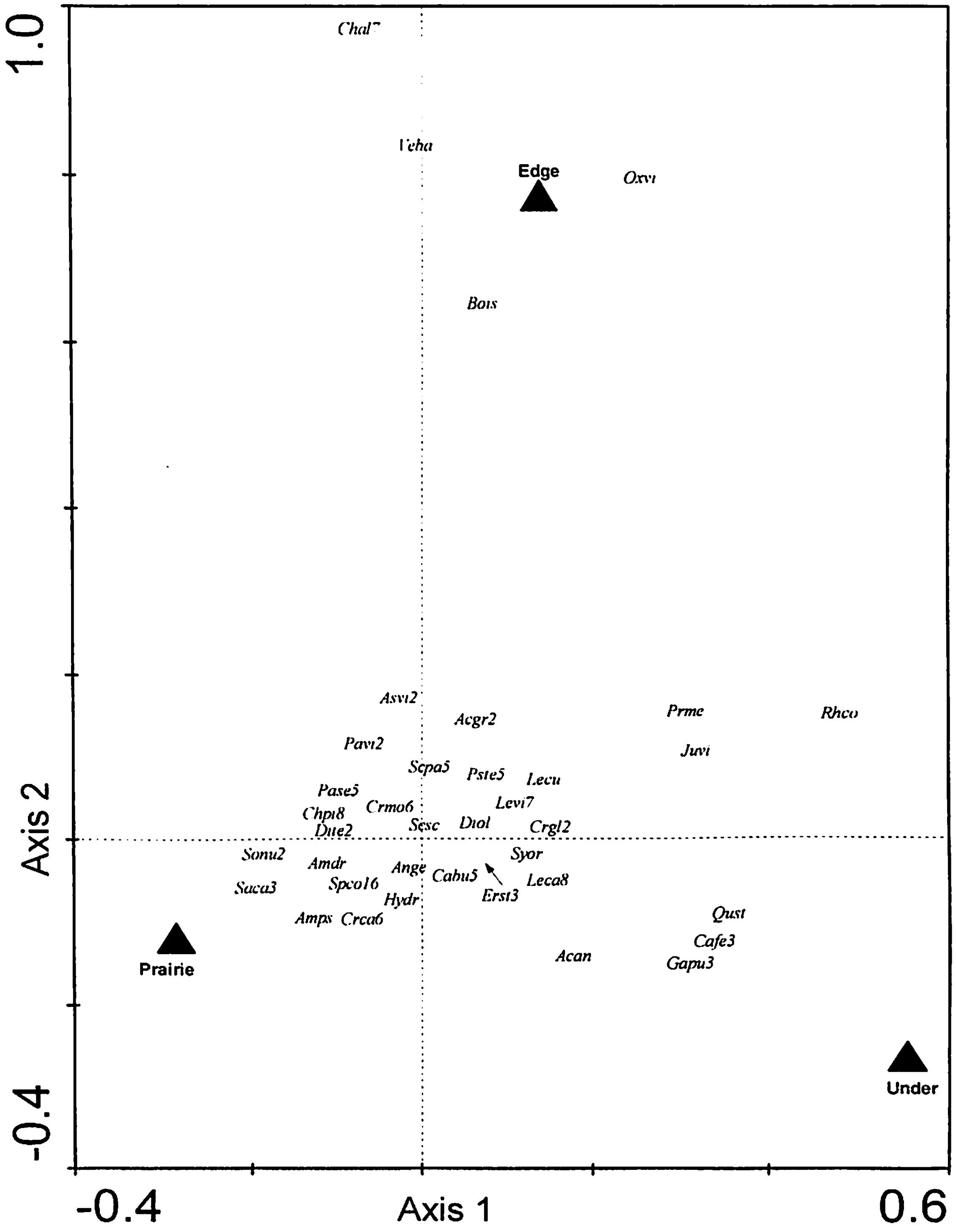

Figure 7: pCCA of canopy cover categories based on relative proportion of cover of each species within a quadrat. Axis 1 & 2 are displayed. See Appendix 1 for species codes.

Table 2: Species occurrence frequencies by canopy cover category. This table includes all species with occurrence frequency of at least 10% of at least one canopy cover category.

Species Name	USDA Code	Photosynthetic Pathway	Under %	Edge %	Prairie %
Acacia angustissima	Acan	3	7.14	17.11	11.17
Acalypha gracilens	Acgr2	3	8.57	19.74	18.45
Achillea millefolium	Acmi2	3	4.29	17.11	12.14
Ambrosia psilostachya	Amps	3	6.43	10.53	28.16
Amphiachyris dracunculoides	Amdr	3	2.86	10.53	18.45
Andropogon gerardii	Ange	4	7.86	28.95	33.50
Asclepias viridis	Asvi2	3	2.86	10.53	3.88
Carex bushii	Cabu5	3	6.43	10.53	19.90
Chrysopsis pilosa	Chpi8	3	8.57	21.05	23.79
Croton capitatus	Crca6	3	3.57	10.53	15.53
Croton glandulosus	Crgl2	3	16.43	23.68	27.67
Croton monanthogynus	Crmo6	3	5.00	18.42	29.61
Dichanthelium oligosanthes	Diol	4	32.14	43.42	42.72
Diodia teres	Dite2	3	2.86	17.11	18.45
Erigeron strigosus	Erst3	3	11.43	27.63	39.81
Hypericum drummondii	Hydr	3	4.29	5.26	19.90
Lespedeza cuneata	Lecu	3	5.71	13.16	8.74
Lespedeza virginica	Levi7	3	5.71	10.53	12.14
Sabatia campestris	Saca3	3	0.00	9.21	18.45
Schizachyrium scoparium	Scsc	4	33.57	64.47	69.42
Scleria pauciflora	Scpa5	3	10.00	25.00	30.10
Sorghastrum nutans	Sonu2	4	4.29	19.74	30.10
Sporobolus compositus	Spco16	4	10.00	50.00	58.74
Symphyotrichum ericoides	Syer	3	5.00	21.05	29.13

Appendix 1:USDA PLANT species codes, habit, and photosynthetic pathway.

Species	USDA Code	Habit	Photosynthetic Pathway
Acacia angustissima	Acan	Forb	3
Acalypha gracilens	Acgr2	Forb	3
Achillea millefolium	Acmi2	Forb	3
Ambrosia psilostachya	Amps	Forb	3
Amphiachyris dracunculoides	Amdr	Forb	3
Andropogon gerardii	Ange	Graminoid	4
Apocynum cannabinum	Apca	Forb	3
Artemisia ludoviciana	Arlu	Forb	3
Asclepias viridis	Asvi2	Forb	3
Bothriochloa ischaemum	Bois	Graminoid	4
Carex bushii	Cabu5	Graminoid	3
Carex festucacea	Cafe3	Graminoid	3
Cercis canadensis	Ceca4	Woody	3
Chamaecrista fasciculata	Chfa2	Forb	3
Chenopodium album	Chal7	Forb	3
Chrysopsis pilosa	Chpi8	Forb	3
Cornus drummondii	Codr	Woody	3
Croton capitatus	Crca6	Forb	3
Croton glandulosus	Crgl2	Forb	3
Croton monanthogynus	Crmo6	Forb	3
Dichanthelium oligosanthes	Diol	Graminoid	4
Digitaria cognata	Dico6	Graminoid	4
Diodia teres	Dite2	Forb	3
Elymus canadensis	Elca4	Graminoid	3
Erigeron stigosus	Erst3	Forb	3
Fimbristylis puberula	Fipu	Graminoid	4
Gamochaeta purpurea	Gapu3	Forb	3
Geum canadensis	Geca7	Forb	3
Hypericum drummondii	Hydr	Forb	3
Juniperus virginiana	Juvi	Woody	3
Lamium amplexicaule	Laam	Forb	3
Lespedeza capitata	Leca8	Forb	3
Lespedeza cuneata	Lecu	Forb	3
Lespedeza procumbens	Lepr	Forb	3
Lespedeza virginica	Levi7	Forb	3
Liatris punctata	Lipu	Forb	3
Linum imbricatum	Liim	Forb	3
Oxalis violacea	Oxvi	Forb	3
Panicum virgatum	Pavi2	Graminoid	4
Parietaria pensylvanica	Pape5	Graminoid	3
Paspalum setaceum	Pase5	Graminoid	4
Psoralidium tenuiflorum	Pste5	Forb	3
Quercus stellata	Qust	Woody	3
Sabatia campestris	Saca3	Forb	3
Schizachyrium scoparium	Scsc	Graminoid	4
Scleria pauciflora	Scpa5	Graminoid	3

Appendix 1: Continued

Solanum carolinense	Soca3	Forb	3
Sorghastrum nutans	Sonu2	Graminoid	4
Sporobolus compositus	Spco16	Graminoid	4
Symphoricarpos orbiculatus	Syor	Woody	3
Symphyotrichum ericoides	Syer	Forb	3
Symphyotrichum oblongifolium	Syob	Forb	3
Ulmus rubra	Ulru	Woody	3
Vernonia baldwinii	Veba	Forb	3

Chapter 3

The Effects of Removal of *Juniperus Virginiana* L. Trees and Litter from a Central Oklahoma Grassland.

By: JERAD S. LINNEMAN[1]

Oklahoma State University, Department of Botany, Stillwater, OK 74078

---

[1] Present address: Department of Botany, Oklahoma State University, Life Science East-#104, Stillwater, OK 74078. Telephone (405)744-5559; e-mail: ljerad@okstate.edu

Abstract

I studied species composition after *Juniperus virginiana* tree and litter removal in a central Oklahoma grassland. Tree removal had the most significant effect on stems per quadrat and vegetation cover. Litter removal effects were not as strong. However, stems per quadrat and vegetation cover in litter removal treatments were higher than in litter intact treatments. Species richness increased for all treatments in the first year post-treatment; after which species richness declined at every sampling period and in every treatment for the duration of the study. Absolute cover of typical prairie species increased in the cut-no litter treatment whereas cover of woody forest species increased in the no cut-no litter treatment. I suggest that even without prescribed fire, redcedar tree removal may result in a return of prairie vegetation. However, additional efforts besides tree removal may be required to restore some invaded grasslands.

Introduction

For the last several decades, there has been a growing interest in management techniques required to maintain and/or restore vegetation. The two most common problems faced in grassland restoration, besides habitat destruction, are the loss of native species diversity due to the encroachment of woody species. Concerns about decreased diversity and the invasion of exotic woody species have spurred extensive study throughout the world including Argentina (Ghersa et al. 2002), Australia (Costello et al. 2000, Whiteman and Brown 1998), Canada (Peltzer and Köchy 2001), French Prealps (Barbaro et al. 2001), South Africa (Homles et al. 2000, Homles and Marais 2000) and the United States (Petranka and McPherson 1979, Callaway and Aschehoug 2000, Fitch et al. 2001, Briggs et al. 2002b).

In the United States, two examples of fire adapted vegetation types that have received much attention regarding restoration are the longleaf pine sandhill vegetation of northwestern Florida (Kush et al. 1999, Provencher et al. 2000 and Provencher et al. 2001) and the tallgrass prairie of the eastern Great Plains (Axmann and Knapp 1993, Briggs et al. 2002a, Briggs et al. 2002b). In both instances the elimination of fire has caused a decrease in species richness and facilitated their conversion into forests. Tallgrass prairie researchers have suggested that reductions in abundance and altered community composition are related to a multitude of environmental factors associated with woody invasion. Examples of such altered environmental factors including soil moisture (Engle et al. 1987, Facelli and Pickett 1991b), solar radiation (Smith and Stubbendieck 1990, Facelli and Pickett 1991a & b) and soil temperature (Weaver and Rowland 1952, Hulbert 1969). In addition, leaf litter from woody species may alter grassland litter dynamics (Facelli and Pickett 1991b).

Two management techniques are typically employed to combat woody species encroachment in tallgrass prairies, particularly of eastern redcedar (*Juniperus virginiana*). Removal of larger trees is usually accomplished via mechanical felling with either chainsaws, large cutting machinery or cabling. When fuel loads are sufficient, prescribed fire will usually remove smaller trees. Although felling and prescribed fire are effective in reducing redcedar abundance in prairies, the continuous application of this management technique has left a significant gap in our understanding about the role redcedar litter plays in tallgrass prairie restoration. In particular, we do not understand the role of the overstory tree versus the leaf litter in determining species composition.

I conducted this study to disentangle the effects of redcedar overstory canopy and accumulated litter on prairie species richness and composition. Elucidating these effects will allow for a more informed approach to redcedar removal and prairie restorations.

Methods

Study Site— I conducted this experiment at the James K. McPherson Botanical Preserve located 16 km west of Stillwater, Oklahoma (36°06'00"N, 97°12'30"W). After a brief period of row crop agriculture, the site was converted into pastureland and grazed until the 1960's. Oklahoma State University (OSU) purchased the land and managerial control was turned over to the Department of Botany. In 1995, the Department of Botany introduced a burning regime, consisting of a 3-5 year return interval, to the northwestern half of the preserve with the goal of stimulating the return of a native tallgrass prairie community.

Tree Selection and Classification— I selected 47 potential study trees based on several criteria including tree isolation, minimization of surrounding tree effects, the existence of an intact litter layer underneath the tree, and tree size. I recorded canopy diameter in the north-south and east-west direction, height, stem diameter at both 10 cm and breast height (DBH) and gender. For those trees with multiple stems, I recorded separate diameter measurements for each primary stem, which I later converted into basal area (BA) at 10 cm and breast height respectively. I randomly assigned all trees into two groups (cut and no cut); ten study trees were then randomly selected from each group.

Sampling Design—Sampling design was based on a two by two factorial design of tree removal and litter removal. Underneath each study tree, I positioned two 50 cm by 50 cm quadrats so that each quadrat was completely under the canopy of the overstory redcedar. In addition, I positioned the two quadrats in such a way to maintain homogenous litter cover between quadrats and to minimize inter-quadrat variation in vegetation. After permanently marking each quadrat, I randomly assigned a litter removal treatment to one of the two quadrats under each tree. I conducted an initial vegetation sampling in May 2001, prior to treatment application. All subsequent sampling occurred biennially in May and September of 2002-2003.

Sampling of species composition consisted of identifying each plant species rooted inside the quadrat and estimating its percent cover to the nearest percent for any cover less than 5% and to the nearest 5% for any cover over 5%. I marked unknown species for later identification. Species nomenclature and code symbols follow that of the USDA PLANTS database (USDA 2004). In addition, at several locations within this paper I refer to the response of *J. virginiana* redcedar seedlings and not the study tree or any of its structures.

Experimental Treatments—The tree removal treatment was applied using a chainsaw and pruning shears between 17 and 19 May, 2001. I removed crowns and branches from the top down, with the aid of rigging equipment, to minimize the amount of disturbance to the litter layer and vegetation in the quadrats. I removed litter from litter removal quadrats by hand, taking care to minimize disturbance to vegetation. However, plants that had germinated in the litter layer and had not reached the soil surface were removed along with the litter during the initial treatment. The litter removal treatment was applied between 21 and 24 May, 2001. Treatment acronyms for tree and litter removal are: (CN) cut-no litter, (CL) cut-litter, (NN) no cut-no litter, (NL) no cut-litter; i.e. the control.

At each post-treatment sampling, I removed newly accumulated litter from the litter removal quadrats after observing vegetation. On a few occasions I removed branches from surrounding trees that started to grow over the tree removal quadrats.

Statistical Analyses—Statistical analysis included the use of both ANOVA and ordination techniques. I performed a repeated measures ANOVA using PROC MIXED for each environmental variable recorded using SAS (Version 8). For each environmental variable, initial (pre-treatment) observations were used as a baseline for all subsequent samplings (post-treatment). Based on results of Chapter 1, Preliminary ANOVAs included tree gender as an explanatory variable. However, because gender showed no significant main or interaction effects, I removed gender and re-ran all ANOVAs.

I analyzed compositional data using direct gradient analysis. Direct gradient analysis uses species data and directly relates it to measured environmental variables, in this case dummy variables representing the treatments. I selected partial Redundancy Analysis (pRDA) because it is generally considered more appropriate in short-term experimental studies where species responses are believed to be linear and over relatively short gradients. All ordinations were conducted using CANOCO FOR WINDOWS 4.5 (ter Braak and Šmilauer 2002) on absolute cover of each species within a sample.

I developed *a priori* hypotheses about the potential affect of treatment application on species cover. I hypothesized that, tree removal and litter removal would have a positive effect on stems per quadrat, vegetation cover and species richness. In addition, the combination of tree removal with litter removal, conditions most similar to open prairie (i.e. CN), would have the largest effect whereas the combination of no tree removal and no litter removal, the control condition (i.e. NL), would have no effect or the least positive affect on species. I have not included any correction factors for statistical problems associated with multiple comparisons (Legendre and Legendre 1998, Hallgren et al. 1999).

Results

Density and Richness—There were significant differences in stem density (p<0.001) between all quadrats prior to treatment application. However, the difference between the means of the densest and sparsest treatments was only 2.5 stems per quadrat. Both the cut-litter (CL) and cut-no litter (CN) treatments had the lowest stems per quadrat prior to treatment application. Stems density increased for all treatments except no cut-litter (NL) treatment by the second sampling. This increase was roughly 2-2.5 fold thus resulting in an increase of 10-13 stems per treatment (Fig. 1). Significant differences (p=0.0052) in density between NL & NN (no cut-no litter) only occurred in May 2002. On the other hand, there were significant differences in stems density between litter treatments within the cut treatment, CL & CN, in September 2002 (p=0.0366) and 2003 (p=0.0483). The cut treatment had a much more pronounced effect on density regardless of litter treatment. In September and May 2002-2003, there were significant differences between both CN & NN (p=0.006, 0.004, 0.001 respectively) and CL & NL (p=0.0052, 0.003, 0.0159 respectively).

As with density, there were significant differences in initial species richness (p<0.001) between all quadrats prior to treatment application. Again, the magnitude of the mean difference was quite small, fewer than 1.0 species per treatment. Additionally, the CL & CN treatments again had the lowest richness. The increase in species richness by the second sampling was not as dramatic as that observed in stems per quadrat by the same sampling. Generally increases in mean species richness were in the order of 0.4-1.25 species per quadrat (Fig. 2). Significant differences in species richness between NL & NN only occurred in September 2002 (p=0.0244); however May 2002 was marginally insignificant (p=0.0533). Conversely, significant differences in species richness between CL & CN occurred in both May 2002 (p=0.0381) and September 2002 (p=0.0026). The cut treatment had a slightly weaker influence on species richness as compared to stems per quadrat. Significant differences in species richness were observed between CN & NN in September 2002 (p=0.0055) and 4 (p=0.0007). Significant differences in species richness were also observed between CL & NL in September 2002 (p=0.0457) and September 2003 (p=0.0358).

Vegetation Cover—There was no significant difference in total vegetation cover prior to treatment application. There was a substantial increase in total cover through Samplings 2 & 3 in both the CL & CN treatments (Fig.3). This increase in total cover was in the order of 8.75-11.25%. On the other hand, total cover in both the NN & NL treatments only increased by ~2%. No significant differences in total cover were observed between the NL & NN treatments at any sampling. On the other hand, there was a significant difference between the CL & CN treatments in September 2003 (p=0.0024). Although litter removal did not have a major affect on total cover, tree removal did. Significant differences between CN & NN were observed in September and May 2002-2003 (p=0.001, 0.0023, <0.001 respectively). In addition, significant differences between CL & NL were also observed in September and May 2002-2003 (p=0.0071, 0.0075, 0.0318 respectively).

Unlike total vegetation cover, there were significant differences ($p<0.001$) in initial mean forb cover between treatments; however these differences were only 0.125%. Forb cover in both of the cut treatments, CL & CN, increased over the duration of the study although both no cut treatments, NL & NN, were relatively static throughout the study (Fig. 4). There were no significant differences in forb cover for NL or NN treatments at any time, whereas a significance difference between CL & CN only occurred in September 2002 ($p=0.0056$). The tree removal treatment yielded a significant difference between CN & NN in May 2002 ($p<0.0001$) and September 2002 ($p=0.0486$), whereas a significant difference between CL & NL occurred only in May 2003 ($p=0.0131$).

Graminoid cover responded similarly to forb cover with significant differences in initial mean graminoid cover between treatments ($p=0.0164$). Once again, the differences between treatments were small (0.15%). Graminoid cover increased over the first post-treatment sampling for all treatments (Fig. 5). Graminoid cover was not significantly affected by litter in NL or NN treatments. However, litter had a significant effect in September 2003 ($p=0.0012$) in the CL & CN treatment. The tree removal treatment had a stronger affect with significant differences in graminoid cover between CN & NN in September and May 2002-2003 ($p=0.0253$, 0.0092, <0.0001 respectively) and between CL & NL in September 2002 ($p=0.0133$). Marginal insignificance was also observed between CL & NL in May, 2003 ($p=0.052$).

Significant differences in woody cover ($p=0.0197$) were also present at the onset of this study. However, differences in mean woody cover between treatments were once again small (0.15%). Woody cover increased in all treatments over the duration of this study although these increases were only in the 0.5-2.0% range (Fig. 6). In fact, no significant differences were found between any combination of litter removal and/or tree removal treatments at any sampling.

Direct Gradient Analysis—Partial Redundancy Analysis (pRDA) was conducted to test *a priori* hypotheses regarding the effects of tree removal, litter removal and their interaction at each sampling. Results of pRDA only showed significant differences in absolute species cover between litter removal treatments in May, 2002 and September, 2002 ($p<0.001$). Conversely, pRDA showed significant differences ($p<0.001$) in absolute species cover between tree removal treatments at every post-treatment sampling period. The litter removal x tree removal interaction effect was only significant in September 2002 ($p=0.029$). Therefore, it appears that tree removal does have a stronger effect on species composition over time than litter removal. When treatment centroids by sampling period are plotted in ordination space three items become apparent. First, tree removal results in an increased magnitude of movement of treatment centroids over time (Fig. 7 a&b). Second, litter removal also results in an increased magnitude of movement of treatment centroids over time (Fig. 7 a&b). Finally, the overall amount of movement of cut treatments was greater than litter removal treatments.

A pRDA scatter plot of absolute species cover, treatment centroids and passive environmental variables based on all post-treatment samplings is displayed in Figure 8. The four dummy treatment variables accounted for 5.4% of the total explained species variance. Although woody cover was not significantly affected by tree removal or litter removal treatments at any sampling, woody forest species such as *Cercis canadensis, Celtis occidentalis, Parthenocissus quinquefolia, Quercus stellata, Juniperus virginiana* seedlings and *Ulmus rubra* all dominated the no cut treatments with a slight higher cover in the litter treatment (NL). Alternatively, grasses typical of the open prairie such as *Tridens flavus, Eragrostis spectabilis, Dicanthelium oligosanthes, Sorghastrum nutans, Bothriochloa saccharoides* and *Sporobolus compositus* dominated the tree removal treatments. In addition, each one of these graminoids (with the exception of *T. flavus*) also had higher absolute cover in the litter removal treatment (CL). Sedges such as *Carex festucacea* and *Carex bushii* both dominated the NN treatment. On the other hand, forb species typically associated with pastures such as *Ambrosia* sp., *A. psilostachya, Amphiachyris dracunculoides, Acalypha gracilens* and *Croton monanthogynus* dominated the CN treatment.

Discussion

Increases in stem density and species richness were expected as a result of litter removal and tree removal treatments. My results are similar to those of Monk and Gabrielson (1985) who observed a stronger influence of overstory cover compared to litter cover on old field vegetation. For all manipulated quadrats (CL, CN and NN) increased stems per quadrat is more likely to be due to increased perennial graminoid stems than to woody or forb stems. Reductions in stems per quadrat in NL & NN treatments after September 2002 are likely the result of continued overstory tree presence and its associated reductions in solar radiation. Studies by Monk and Gabrielson (1985), Yager and Smeins (1999), Joy and Young (2002) have all suggested that reductions in light similar to those observed in this study, via canopy cover data from Chapter 1, resulted in significant decreases in plant density and cover. On the other hand, I believe that reductions in stems per quadrat in September 2003 for CL and only the slight increase for CN were caused by relatively little precipitation received in 2002-2003. Total precipitation recorded at the Marena Mesonet Station, located approximately 4 km from the study site, was 24.82 in. from October 2002 to September 2003. This precipitation total is only 64-69% of annual precipitation for the site of 36-39 in. (Oklahoma Mesonet, Oklahoma Climatological Survey).

By comparison, the decreases in species richness over the course of this study suggest relatively little recruitment of new species occurred regardless of treatment. Provencher et al. (2000) found that species richness also decreased after the application of felling and slash burning in Florida's sandhill vegetation. However, Provencher et al. (2000) observed an increase in species richness two years after treatment application. Results from pRDA (Fig. 8) suggest a transition from pre-treatment species composition dominated by mesic or forest species to post-treatment tallgrass prairie species. It is possible that during this transition, forest species were lost faster than prairie species were added; therefore, we observe a decrease in species richness. However, the majority of species present in each treatments cumulative species pool were, on average, not present in each quadrat. Generally only 10-20% of each treatments cumulative species pool was observed in each quadrat (Figure 2). It should be noted that species richness may be strongly linked to density (i.e. rarefaction effect) and thus the richness-per-quadrat should not be interpreted independently of stem counts (Palmer et al. 2000). This suggests that given more time species richness may increase as these rare species become more universally distributed into cut quadrats.

In Chapter 2, I suggested that species composition underneath redcedar trees may be a largely random subset of the species from the surrounding matrix. The results from this study to suggest that this subset of species appears to be nonrandom and comprised of two main types. The first group appears to be remnant prairie grasses whereas the second is disturbance-loving forbs. The absolute cover of almost all graminoid species increased as a result of tree removal. Of particular interest is that the most abundant graminoid species were native tallgrass prairie species such as *S. nutans* and *S. compositus*. Conversely, the positive response of disturbance favoring forb species like *A. dracunculoides, A. psilostachya* and *C. monanthogynus* may lead to further reductions in species richness if they become dominant. Several researchers including Clary (1971), Clary and Jameson (1981), Brockway et al. (1998) and Provencher (2000) have all observed increases in graminoid and forb cover following overstory tree removal. Annual species increased in dominance in cut treatments however, few annuals dominated cover in any treatment. Although the response of disturbance loving forbs may be problematic in the short term, the increases in absolute cover of native tallgrass prairie species suggest that even without follow-up prescribed fire treatments, community composition may return to its pre-invasion condition given time.

The long-term effects of eastern redcedar in grasslands are unclear. The results from this study along with those in Chapter 2 suggest the continued presence of eastern redcedar in grasslands may (1) facilitate the forestation of grasslands or at least (2) continue to reduce the tallgrass prairie species pool in invaded grasslands. Briggs et al. (2002a) suggested that species present in the prairie were not consistently different from those found in a closed canopy redcedar forest. However, both this study and Chapter 2 show an apparent shift in community composition away from tallgrass prairie species toward forest tree species such as *C. canadensis, C. occidentalis, J. virginiana, Q. stellata* and *U. rubra*. Although complete extirpation of native tallgrass prairie species is not likely in the short term, areas with extensive invasion and subsequent tree removal may require seeding of prairie species to spur the return of characteristic prairie vegetation. This will inevitably increase the cost of restoration beyond the high cost of tree removal (Bidwell et al. 2002).

Continued invasion by eastern redcedar into grasslands in the Great Plains has serious implications not only for the existence of these grassland but also for biodiversity and potential future restorations. Tree removal, even when not followed by prescribed fire, in redcedar invaded grasslands should cause both an increase in stems per quadrat and an increase in species richness several years after treatment application. Litter removal, either via mechanical means or by prescribed fire, should accelerate the return of tallgrass prairie vegetation. Without tree removal, these grasslands will continue to lose native prairie species in favor of mesic and/or forest species. In addition, as invading redcedar trees grow thereby eliminating native prairie species and reducing the geographical extent of native grasslands, it is possible that future prairie restoration efforts may require seed inputs beyond what is available from surrounding sources via natural dispersal.

Acknowledgements—I thank my advisor, Michael Palmer, for his continuous advice regarding experimental design, statistical analysis along with Dr. Sam Fuhlendorf for their editorial comments. In addition, Jared Laufenberg aided with tree removal. Mark Payton's help with SAS analyses and programming was greatly appreciated. The Payne

County Audubon Society and the James K. McPherson Fund, administered by the Department of Botany at Oklahoma State University, provided funding for this study.

Literature Cited

Axmann, B.D. and A.K. Knapp. 1993. Water relations of *Juniperus virginiana* and *Andropogon gerardii* in an unburned tallgrass prairie watershed. *Southwestern Nat.*, **38**:325-330.

Barbaro, L., T. Dutoit and P. Cozic. 2001. A six-year experimental restoration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps. *Biodiv. Conserv.*, **10**:119-135.

Bidwell, T.G., D.M. Engle, R.E. Masters and J.R. Weir. 2002. Fire effects in Oklahoma. Oklahoma Cooperative Extension Service. F-2877

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

Briggs, J.M., A.K. Knapp and B.L. Brock. 2002b. Expansion of woody plants in tallgrass prairie: A fifteen-year study of fire and fire-grazing interactions. *Am. Midl. Nat.*, **147**:287-294.

Brockway, D.G., K.W. Poutcalt and R.N. Wilkins. 1998. Restoring longleaf pine wiregrass ecosystems: plant cover, diversity and biomass following low-rate hexazinone application on Florida sandhills. *For. Eco. Manage.*, **103**:159-175.

Callaway, R.M. and E.T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. *Science*, **290**:521-523.

Clary, W.P. 1971. Effects of Utah juniper removal on herbage yields from Springerville soils. *J. Range Manage.*, **24**:373-378.

Clary, W.P. and D.A. Jameson. 1981. Herbage production following tree and shrub removal in the pinyon-juniper type of Arizona. *J. Range Manage.*, **34**:109-113.

Costello, D.A., I.D. Lunt and J.E. Williams. 2000. Effects of the invasion by the indigenous shrub *Acacia sophorae* on plant composition of costal grasslands in south-eastern Australia. *Biol. Cons.*, **96**:113-121.

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

Facelli, J.M. and S.T.A. Pickett. 1991a. Plant litter: Light interception and effects on an old-field plant community. *Ecology,* **72**:1024-1031.

Facelli, J.M. and S.T.A. Pickett. 1991b. Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.*, **57**:1-32.

Fitch, H.S., P. von Achen and A.F. Echelle. 2001. A half century of forest invasion on a natural area in northeastern Kansas. *Trans. KS. Acad. Sci.,* **104**:1-17.

Ghersa, C.M., D.O. Ferranro, M. Omacini, M.A. Martinez-Ghersa, S. Pereaman, E.H. Satorre and A. Soriano. 2002. Farm and landscape level variables as indicators of sustainable land-use in the Argentine Inland-Pampa. *Agric. Ecosyst. Enviro.*, **93**:279-293.

Hallgren, E., M.W. Palmer and P. Milberg. 1999. Data diving with cross-validation: an investigation of broad-scale gradients in Swedish weed communities. *J. Ecol.*, **87**:1-16.

Homles, P.M. and C. Marais. 2000. Impacts of alien plant clearance on vegetation in the mountain catchments of the Western Cape. *S. African For. J.,* **189**:113-117.

Homles, P.M., D.M. Richardson, B.W. Van Wilgen and C. Gelderblom. 2000. Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. *Aust. Ecol.,* **25**:631-639.

Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology,* **50**:874-877.

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

Kush, J.S., R.S. Meldahl and W.D. Boyer. 1999. Understory plant community response after 23 years of hardwood control treatments in natural longleaf pine (*Pinus palustris*) forests. *Can. J. For. Res.,* **29**:1047-1054.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. Elsevier, Amsterdam.

Monk, C.D. and F.C. Gabrielson. 1985. Effects of shade, litter and root competition on old-field vegetation in South Carolina. *Bull. Torrey Bot. Club,* **112**:383-392.

Palmer, M.W., D.B. Clark and D.A. Clark. 2000. Is the number of tree species in small tropical forest plots nonrandom? *Comm. Ecol.,* **1**:95-101.

Peltzer, D.A. and M. Köchy.{make sure to have the umlaut in the text} 2001. Competitive effects of grasses and woody plants in mixed-grass prairie. *J. Ecol.,* **89**:519-527.

Petranka, J.W. and J.K. McPherson. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. *Ecology,* **60**:956-965.

Provencher, L., B.J. Herring, D.R. Gordon, H.L. Rodgers, G.W. Tanner, L.A. Brennan and J.L. Hardesty. 2000. Restoration of northwest Florida sandhills through harvest of invasive *Pinus clausa*. *Res. Ecol.,* **8**:175-185.

Provencher, L., B.J. Herring, D.R. Gordon, H.L. Rodgers, G.W. Tanner, L.A. Brennan and J.L. Hardesty. 2001. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. *Res. Ecol.,* **9**:13-27.

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

ter Braak, C.J.F. and P. Šmilauer. 2002. Canoco for Windows 4.5. Biometris-Plant Research International. Wageningen, Netherlands.

USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Weaver, J.E. and N.W. Rowland. 1952. Effect of excessive natural mulch on the development, yield, and structure of a native grassland. *Bot. Gaz.,* **114**:1-19.

Whiteman, G. and J.R. Brown. 1998. Assessment of a method for mapping woody plant density in a grassland. *J. Arid Environ.,* **38**:269-282.

Yager, L.Y., F.E. Smeins. 1999. Ashe juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak savanna. *Southwestern Nat.,* **44**:6-16.

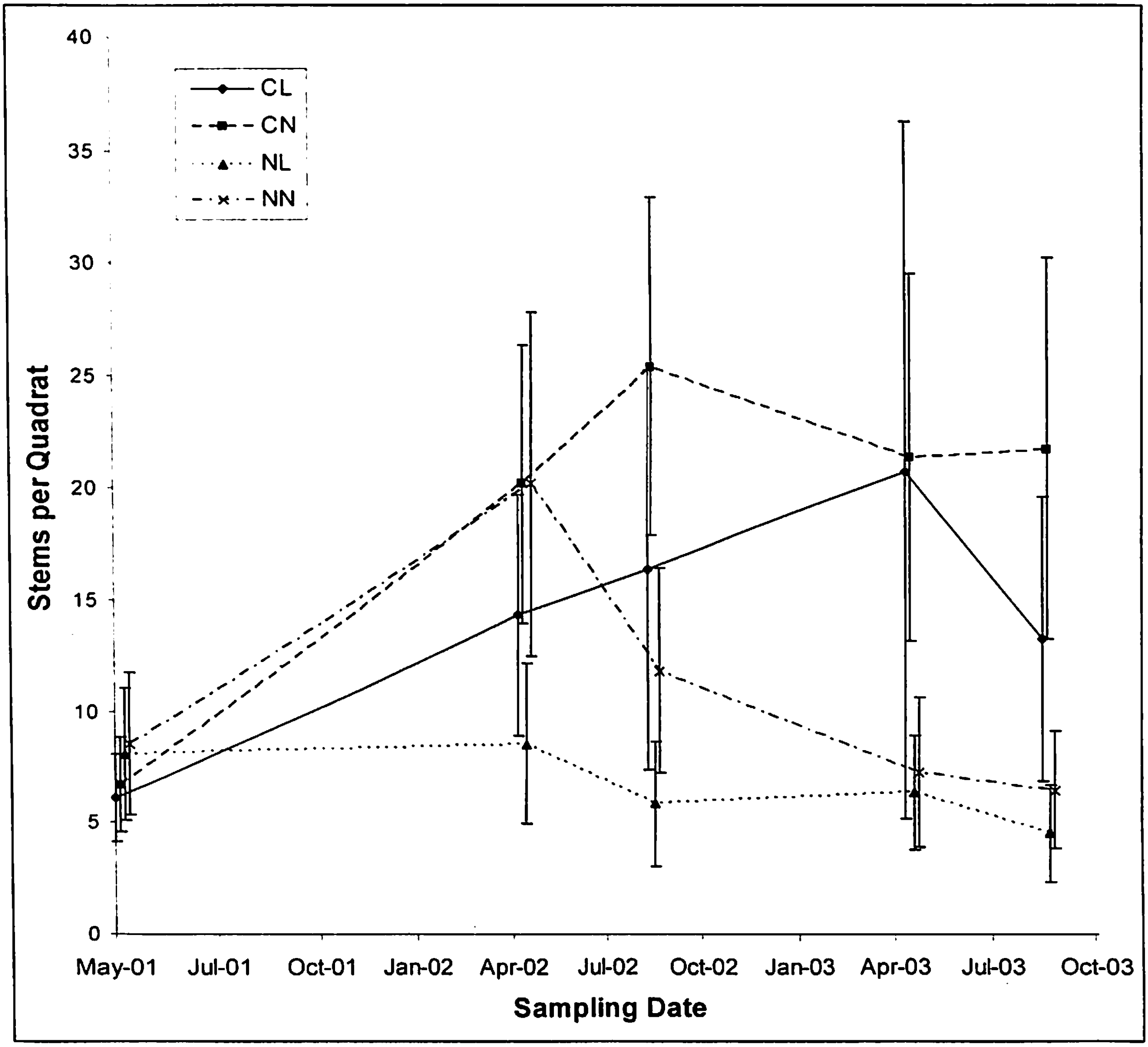

Figure 1: Mean stems per 0.25 m^2quadrat in tree removal and litter removal treatments for 2.5 years. The data points have been staggered to increase visibility of 95% confidence intervals (determined for each treatment at each sampling). CL=cut-litter, CN=cut-no litter, NL=no cut-litter, NN=no cut-no litter.

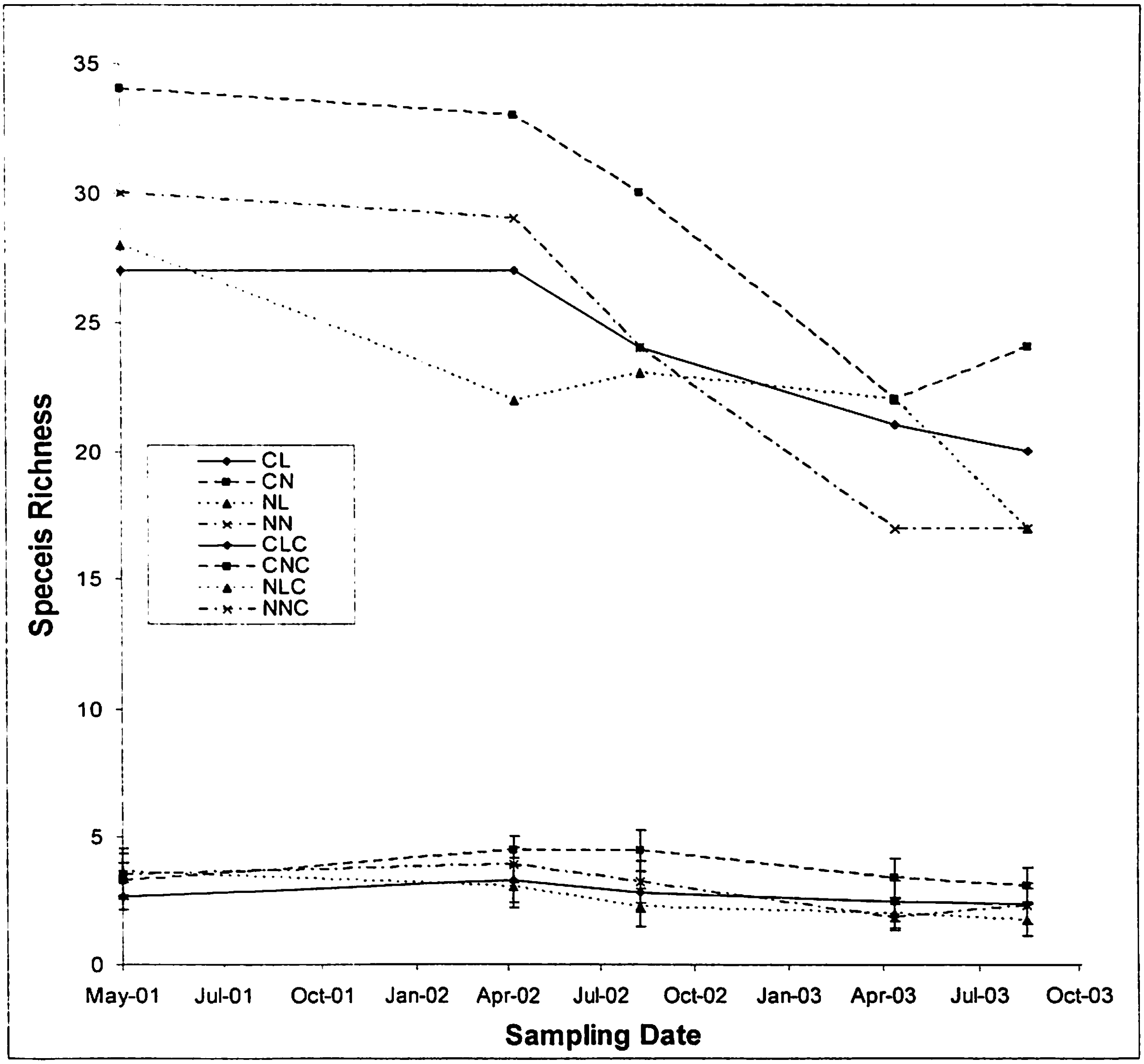

Figure 2: Mean species richness per 0.25 m^2 and cumulative species richness of tree removal and litter removal treatments for 2.5 years. The data points have been staggered to increase visibility of 95% confidence intervals (determined for each treatment at each sampling). CL=cut-litter, CLC=cumulative cut-litter, CN=cut-no litter, CNC=cumulative cut-no litter, NL=no cut-litter, CNL=cumulative no cut- litter, NN=no cut-no litter, CNN=cumulative no cut-no litter and cumulative species richness.

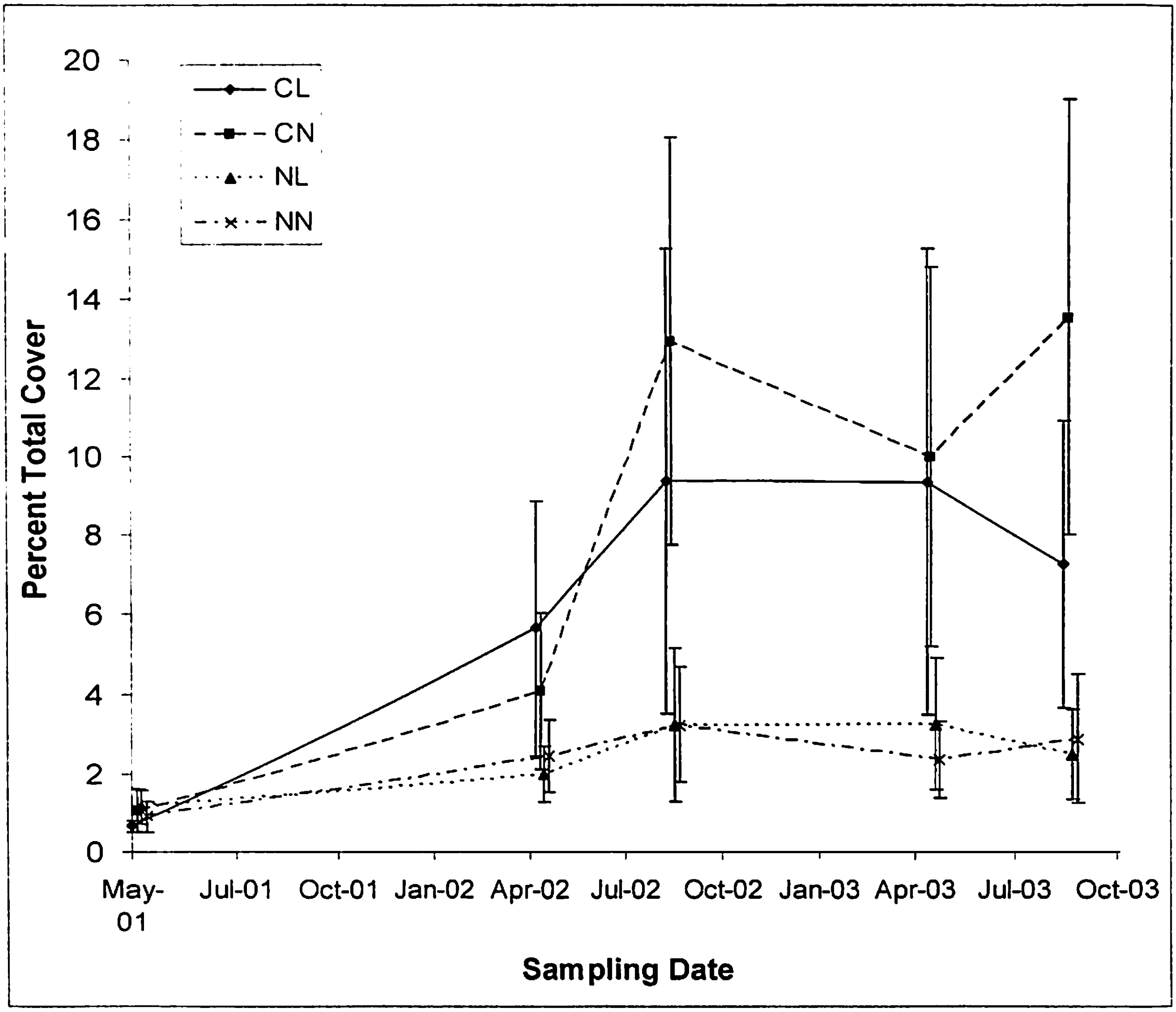

Figure 3: Mean percent total cover of tree removal and litter removal treatments for 2.5 years. The data points have been staggered to increase visibility of 95% confidence intervals (determined for each treatment at each sampling). CL=cut-litter, CN=cut-no litter, NL=no cut-litter, NN=no cut-no litter

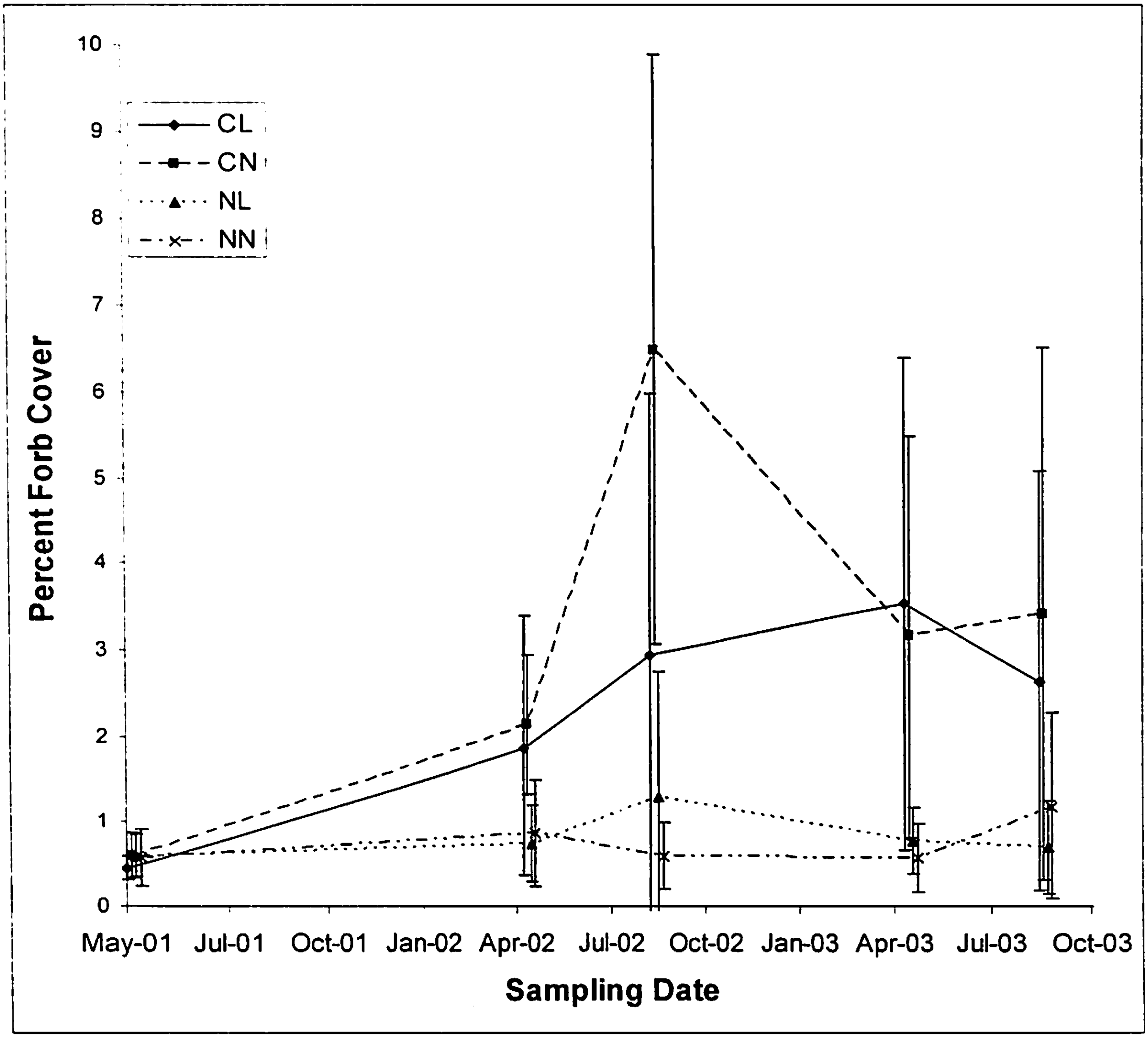

Figure 4: Mean percent forb cover of tree removal and litter removal treatments for 2.5 years. The data points have been staggered to increase visibility of 95% confidence intervals (determined for each treatment at each sampling). CL=cut-litter, CN=cut-no litter, NL=no cut-litter, NN=no cut-no litter

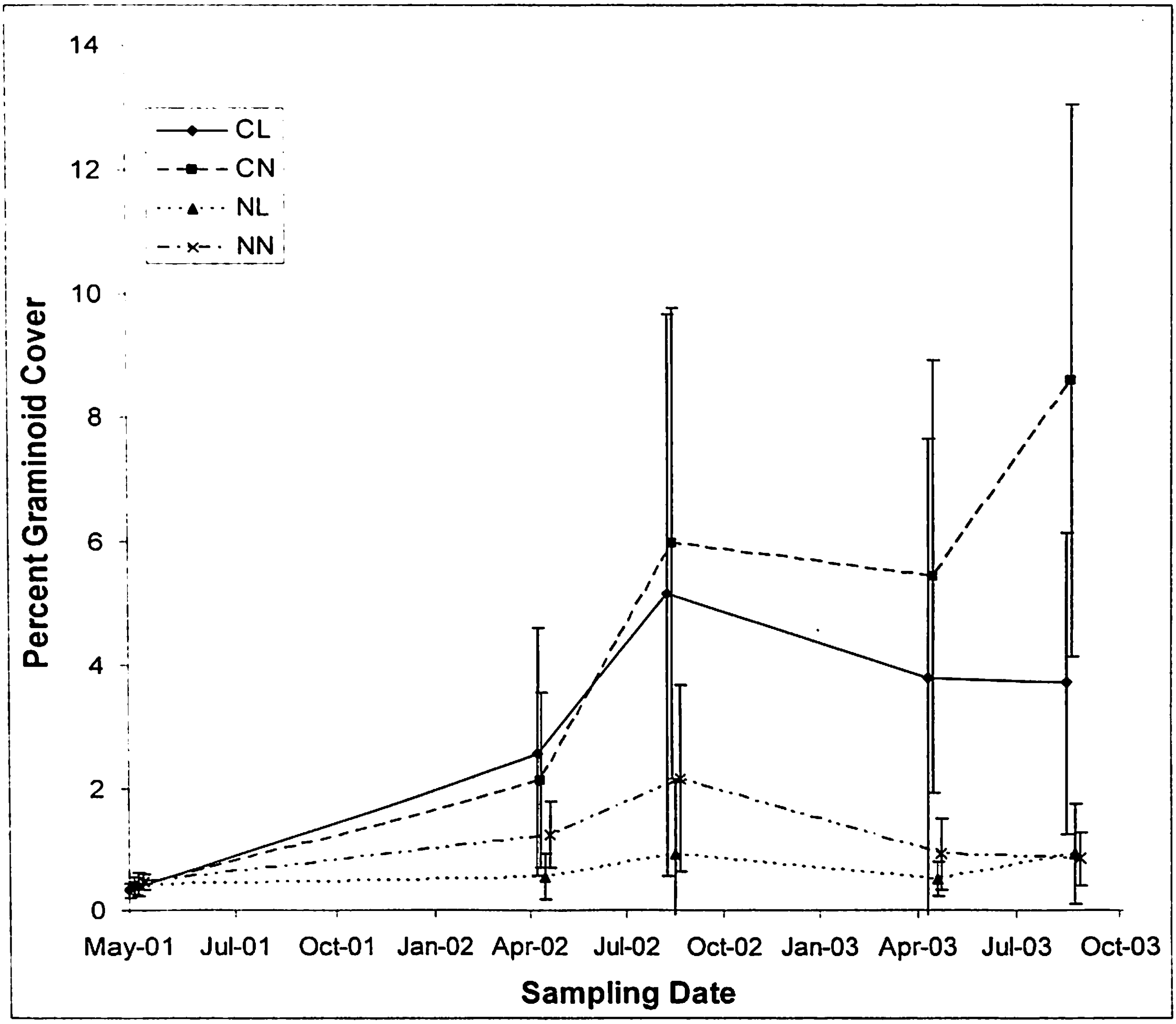

Figure 5: Mean percent graminoid cover of tree removal and litter removal treatments for 2.5 years. The data points have been staggered to increase visibility of 95% confidence intervals (determined for each treatment at each sampling). CL=cut-litter, CN=cut-no litter, NL=no cut-litter, NN=no cut-no litter

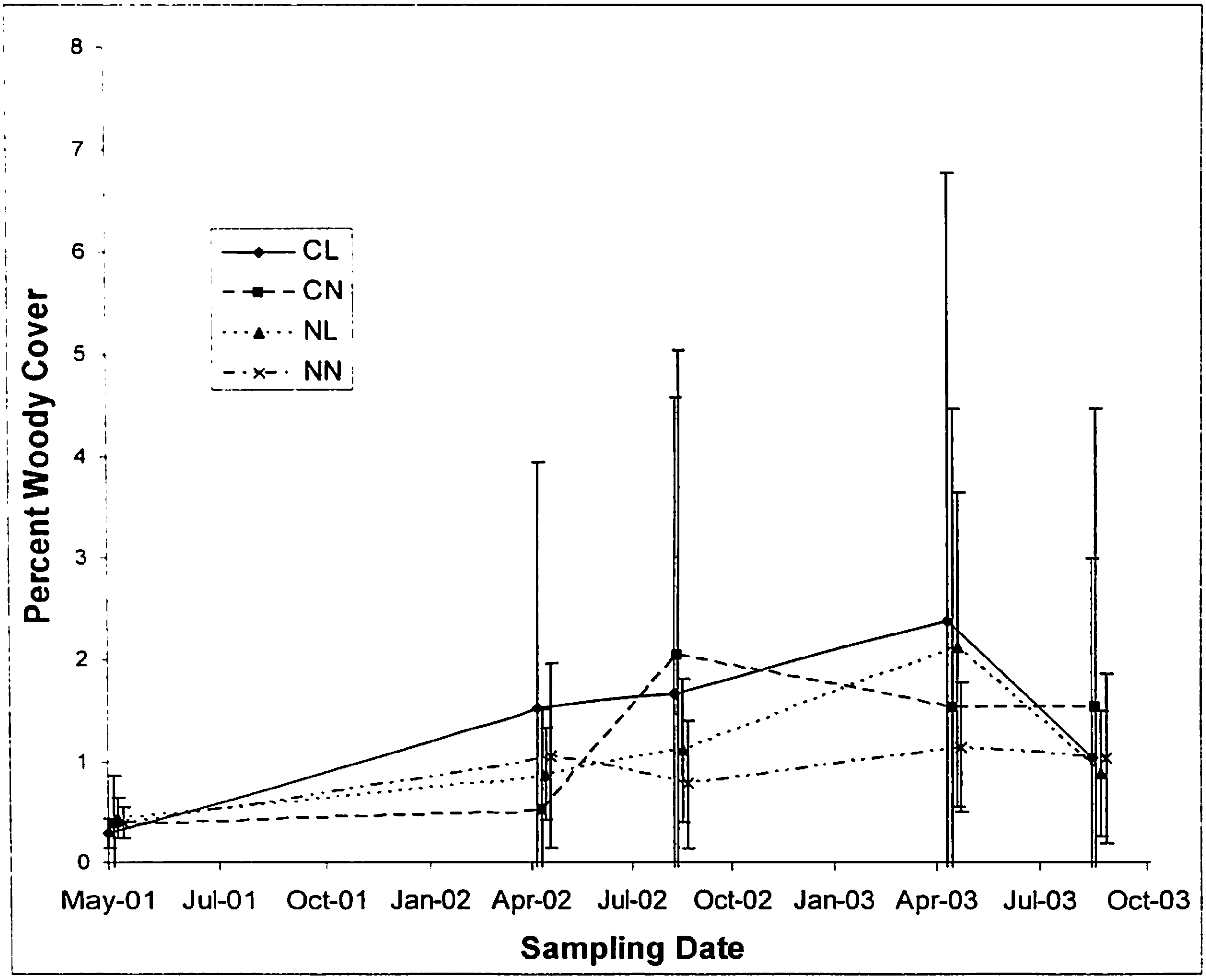

Figure 6: Mean percent woody cover of tree removal and litter removal treatments for 2.5 years. The data points have been staggered to increase visibility of 95% confidence intervals (determined for each treatment at each sampling). CL=cut-litter, CN=cut-no litter, NL=no cut-litter, NN=no cut-no litter

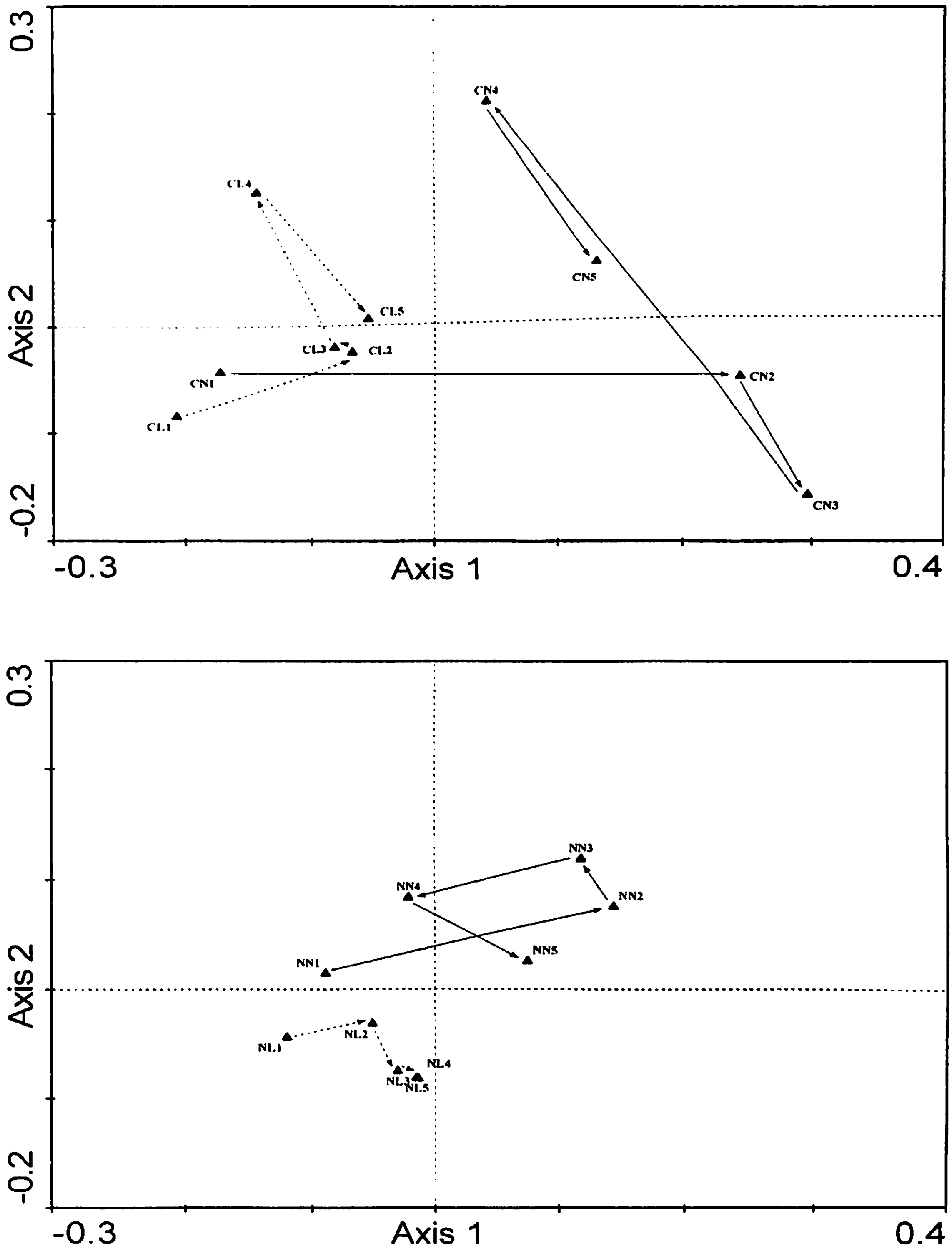

Figure 7: pRDA trajectory of tree and litter removal treatment centroids for each sampling period. The two figures are the same analysis and were separated to increased visibility. CL=cut-litter, CN=cut-no litter, NL=no cut-litter, NN=no cut-no litter. Axis 1 & 2 are displayed in both figures.

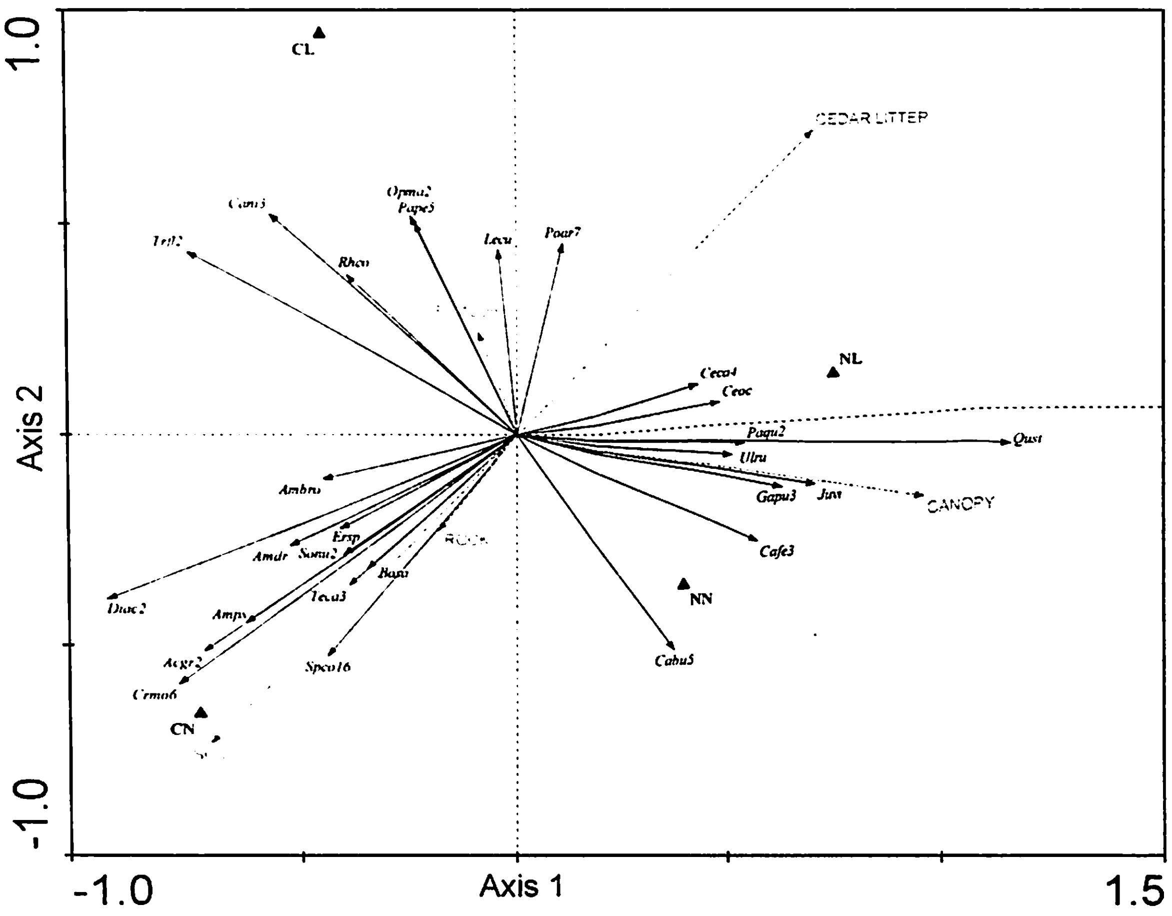

Figure 8: pRDA triplot of species codes, treatment centroids and supplemental environmental variables. All post-treatment samplings are included and axis 1 and 2 are displayed. Species codes represent the relative multi-dimensional position of each species in ordination space based on absolute cover of each species. Species codes are indexed in Appendix 1. Arrow length indicates the relative strength of supplemental variables. CL=cut-litter, CN=cut-no litter, NL=no cut-litter, NN=no cut-no litter.

Appendix 1: Species names and USDA PLANT codes.

Species	**USDA Code**
Acalypha gracilens	Acgr2
Ambrosia psilostachya	Amps
Ambrosia sp.	Ambro
Amphiachyris dracunculoides	Amdr
Bothriochloa saccharoides	Bosa
Carex bushii	Cabu5
Carex festucacea	Cafe3
Carex nigromarginata	Cani3
Celtis occidentalis	Ceoc
Cercis canadensis	Ceca4
Croton monanthogynus	Crmo6
Dichanthelium acuminatum	Diac2
Eragrostis spectabilis	Ersp
Gamochaeta purpurea	Gapu3
Juniperus virginiana	Juvi
Lespedeza cuneata	Lecu
Opuntia macrorhiza	Opma2
Oxalis stricta	Oxst
Parietaria pensylvanica	Pase5
Parthenocissus quinquefolia	Paqu2
Quercus stellata	Qust
Rhus copallinum	Rhco
Sorghastrum nutans	Sonu2
Sporobolus compositus	Spco16
Teucrium canadense	Teca3
Tridens flavus	Trfl2
Ulmus rubra	Ulru

Chapter 4

Differences in Growth and Nitrogen Uptake by *Juniperus virginiana* L. Trees Grown in a Greenhouse

By: JERAD S. LINNEMAN[1]

Oklahoma State University, Department of Botany, Stillwater, OK 74078

---

[1] Present address: Department of Botany, Oklahoma State University, Life Science East-#104, Stillwater, OK 74078. Telephone (405)744-5559; e-mail: ljerad@okstate.edu

Abstract

Two year-old eastern redcedar (*Juniperus virginiana* L.) trees were grown in a greenhouse to determine growth and N absorption characteristics at different N concentrations and ratios of NH_4^+ to $NO_3^-$to determine if redcedar preferentially absorbed NH_4^+or NO_3^-. This experiment was conducted from October 2002 to April 2003. There were no significant differences in growth characteristics until harvests six and seven, 168 and 196 days into the experiment, respectively. Differences in growth of redcedar based on N treatment ratios were significant within a harvest however; growth showed no consistent pattern related N treatment ratios over the course of the experiment. Carbon proportion was higher in the leaves than in other plant structures until the last two harvests. There were significant differences in N proportion for leaves, stems, main roots and fine roots at several harvests during this experiment. Plants given higher N concentration treatments had structures with greater N proportion. No significant differences in N proportion were found between different NH_4^+ to NO_3^- ratios at several samplings. However, nitrogen absorption was greater when NH_4^+ to NO_3^- ratios favored NH_4^+-N over NO_3^--N.

Introduction

Juniperus, as a genus, is widely recognized as including invasive species. Some examples include *Juniperus ashei* (Fuhlendorf 1992 & Fuhlendorf et al. 1997), *J. communis* (Bakker et al. 1996, Diotte and Bergeron 1989), *J. monosperma* (Jameson 1966), *J. occidentalis* (Miller and Rose 1995, Miller et al. 2000) and *J. pinchotii* (McPherson and Wright 1990). *Juniperus virginiana* has become particularly problematic within the Great Plains of the United States. Redcedar invasion into the

Great Plains has had detrimental effects on native grasslands both in terms of reduced geographic range and decreased species richness, rangeland quality and/or production (Briggs et al. 2002, Engle et al. 1987, Gehring and Bragg 1992, Hoch 2000, Holthuijzen and Sharik 1985, Smith and Stubbendieck 1990).

Several researchers and range managers have raised questions as to whether elevated soil N levels, due to previous agricultural practices and/or atmospheric deposition of N, are potentially facilitating the spread of eastern redcedar into rangelands and pasturelands in Oklahoma. Although there is extensive literature on N effects on western juniper species such as *J. occidentalis* (Bates et al. 2002, Miller et al. 1991, Miller et al. 1992, Miller et al. 1995, Tiedemann and Klemmedson 1995) and *Juniperus osteosperma* (Ehleringer et al. 1986, Klopatek and Klopatek 1997) there is relatively little information about eastern redcedar (Wright and Hinesley 1991, Henry et al. 1992a, Henry et al. 1992b). Henry et al. (1992a) discussed differences in growth rates at different N concentrations, however the N concentrations used exceed those typically found in native pastures, up to 640 ppm N

Ammonium and nitrate are the two most biological available forms of N. The release of N from organic compounds is a multiple step process and provides N to both heterotrophic and autotrophic organisms. However, plant species may preferentially utilize one form over the other (Haynes and Goh 1978 and Marschner 1995). Understanding plant species preferences may facilitate more efficient use of resources. For example, a nursery owner may want to know if ornamental species will grow faster if they are supplied with supplemental N and in a certain form (Sartain and Ingram 1984 and Hicklenton and Cairns 1992.). Although not much is known on the forms of nitrogen assimilated by *Juniperus*, study by Miller et al. (1991) has suggested that *J. occidentalis* is adapted to utilize NO_3^- and did not preferentially utilize NH_4^+.

The purpose of this study was to determine if eastern redcedar (*Juniperus virginiana* L.) preferentially utilizes N in the form of NH_4^+ or NO_3^- at concentrations characteristic of prairie soils as evidenced by both above and below ground growth rates, N accumulation in different plant structures and C and N composition of above and below ground tissues.

Methods

Experimental Design—This experiment consisted of a randomized complete block design with five replications. Each block was comprised of seven racks positioned in a row across the greenhouse, with the five blocks positioned along the length of the greenhouse. The seven treatments (one per rack) were randomly assigned to each block. Every rack contained eight PVC tubes that were spaced 10-15 cm apart. Each PVC tube measured approximately 43 cm (height) by 7.6 cm (ID) thus having approximately 2 L of growth container volume. Plants were harvested from random positions within each rack at each harvest.

Six- to seven-hundred two-year-old bareroot eastern redcedar trees were processed on October 3, 2002 at the Charles E. Bessey Nursery, U.S. Forest Service, Halsey, Nebraska, sealed in airtight bags and immediately shipped to Stillwater, Oklahoma. Upon arrival in Stillwater, 280 of the most uniformly sized trees were transplanted into the previously described PVC tubes on October 5, 2002. Prior to planting, the roots of each tree were trimmed to a length of 22 cm. The trees were planted one per PVC tube filled with sterilized sand growth medium to approximately 6 cm below the rim, thus creating a watering reservoir. The sand growth medium was autoclaved for 24 hours and stored in large bleach-sterilized plastic containers until it was used for planting.

Outside weather conditions largely dictated temperatures within the greenhouse during warmer months; however, evaporative cooling pads were used to reduce the internal temperature in hot weather. Furnaces maintained a minimum temperature of 11-12 C during the colder months. There were no supplemental growth lights used in this experiment; hence the experimental photoperiod was consistent with the seasonal photoperiod at 36°N latitude between October and April.

Nutrient Treatments—The seven nutrient treatments consisted of a N free half strength Hoagland's solution to which was added different mixtures of NH_4NO_3, KNO_3 and $(NH_4)_2SO_4$ to produce NH_4^+:NO_3^- ratios of 3:1 (1 and 3 mM), 1:1 (1, 2 and 3 mM) and 1:3 (1 and 3 mM). Reverse osmosis (RO) water from an ECOWATER Reverse Osmosis System (EPRO 6000; Quality Water, Stillwater, OK) was used to mix the nutrient solutions (refer to APPENDIX 1 for complete concentration and N ratio information). During the first month after transplanting, all trees were given approximately 200 mL of the 3 mM 1:1 N solution once a day in the morning. In addition, the tubes were flushed with ~200 mL RO water twice a week in the evening for the duration of the experiment. Following the first sampling on November 9, 2002, the seven nutrient treatments were initiated. Each plant received ~200 mL of nutrient solution every morning; in addition, each plant received an extra ~200 mL of nutrient solution twice a week in the mornings after the tubes had been flushed with RO water.

Sampling—At each harvest, one tree was randomly sampled from each rack (a total of five plants per nutrient treatment per harvest). The sand growth medium was thoroughly washed away from the roots prior to root length and shoot length measurements. The trees were then separated into roots and shoots and brought to the laboratory. In the laboratory, main roots were separated from fine roots, whereas shoots were separated into two categories: (1) stems and brown branches and (2) leaves plus young green branches. The projected area of the leaves and green branches was determined using a LI-COR Portable Area Meter (LI-3000). The area of each sample was determined twice and then averaged. If the coefficient of variation exceeded 3% of the average area, the sample was processed a third time and all three projected leaf areas were averaged. Once all fresh material was processed, the four plant structures (leaves, stems, main roots and fine roots) were dried in a convection oven for one week at 70 C. After weighing each harvest's samples, the set of samples was shipped to the U.S. Environmental Protection Agency laboratory in Ada, Oklahoma, where they were ground to a fine powder and the C and N proportions were determined by combustion using an elemental analyzer (LECO CHN2000). Harvests continued on a 28-day schedule for seven harvests.

To insure quality control in this experiment, both RO water samples and sand samples were sent to the Soil, Water and Forage Analytical Laboratory at Oklahoma State University for analysis. Water samples were collected directly from the RO supply end of the water purification system. Sand samples were flushed with RO water every morning and twice a week during the evening for one month before analysis. The N content of both the RO water and sand was negligibly small, relative to the nitrogen treatments used, and are therefore not reported herein.

Statistical Analysis—Statistical analysis was conducted with SAS (Version 8). These analyzes consisted of calculations of means and standard errors and several ANOVAs using PROC MIXED. As this is an exploratory study, I did not correct for multiple comparison (Legendre and Legendre 1998, Hallgren et al. 1999).

Results

Growth—There were no significant differences in any of the measured plant growth parameters until Harvest 6; therefore most results reported are based on Harvest 6 and 7 only (Fig. 1 A&B). For Harvests 6 and 7, shoot dry weight made up a substantial proportion, 66% and 70% respectively, of the total dry weight of all the trees. In addition, leaf dry weight accounted for 80-90% of shoot dry weight for both Harvest 6 and 7. Root dry weight accounted for only 30-35% of the total dry weight for either harvest. Fine root dry weight accounted for 75-85% of total root dry weight (Fig. 2 A&B).

Trees supplied with higher N concentrations generally weighed more than trees supplied with lower N concentrations, data not displayed; however neither root length nor shoot length were significantly affected by N concentration nor by NH_4^+:NO_3^- ratios at any time throughout the entire experiment. There were significant differences in the responses of tree dry weights to different N concentrations as well as to the different ratios of N at Harvest 6 and 7 (Table 1A&B). Although between and within harvest variation for each particular N treatment was often large, results from Harvest 6 indicated that both of the 3:1 (NH_4^+:NO_3^-) N treatments yielded lighter trees in comparison to either the 1:1 or 1:3 N treatments of the same concentration. However, this ratio preference was reversed in Harvest 7 where both 1:3 N treatments yielded lighter trees in comparison to either the 1:1 or 3:1 N treatments of the same concentration. Significant differences between N concentrations and/or NH_4^+:NO_3^- ratios were usually found in metabolically active tissues like leaves and fine roots as opposed to woody tissues like stems and main roots.

Initial root to shoot ratios ranged between 0.22-0.31 and steadily increased until Harvest 4 and 5 where they reached their maxima of 0.60-0.70. After Harvest 5, root to shoot ratios rapidly decreased to near their initial levels (Fig. 3). Leaf area ratio (LAR) was generally the inverse of root to shoot ratio, and LAR dramatically increased after Harvest 5. The large increase in LAR was due to the rapid growth of leaves after Harvest 5. Minimum LARs were observed at Harvests 4 and 5 and ranged from 9-10 $cm^2 g^{-1}$ dry weight (Fig. 4), however, by the end of the experiment LARs surpassed initial values.

Plant Structures—Not surprisingly, different plant structures contained different proportions of C and N. Carbon proportion showed only a slight treatment × structure interaction in the ANOVA. In addition, a least square means analysis showed only a slight effect of treatment. Therefore, I analyzed the main effects of treatment based on the data pooled across treatments. Percentage C ranged from 42%-48% with leaves containing the most C followed by stems, main roots and fine roots. However, C proportion in the leaves steadily decreased throughout the experiment including the last two harvests when both stems and main roots had higher C proportions than leaves (Table 2).

Total plant N content (g N g^{-1}) showed significant difference between treatments at Harvest 6 and 7. Nitrogen content was highest in plants receiving higher N concentration treatments. In general, plants receiving either the 3:1 or 1:1 NH_4^+:NO_3^- ratio contained significantly more N than plants grown at the 1:3 ratio at both the 1 mM and 3 mM N concentration. However, total plant N content increased as the study progressed regardless of N treatment concentration.

Nitrogen proportions showed a stronger treatment × structure interaction than C did. Again there appeared to be an ordered statistical structure to N proportions of the four plant structures (i.e. leaves>fine roots>stems>main roots). A larger interaction between N proportion and treatment was observed than between carbon proportion and treatment. Therefore, N proportions were not pooled across treatments. Leaves had the largest N values across all harvests 78% of the time whereas fine roots had the largest N values 22% of the time (Table 3). At all harvests, either leaves or fine roots had the highest N values. On the other hand, main roots had the least nitrogen 94% of the time and stems had the least nitrogen 6% of the time (Table 3). In addition, N proportion steadily increased in all plant structures through the first five harvests after which percent N decreased except for fine roots. By the end of the experiment, stem and main root N proportions fell to levels observed at the beginning of the experiment. Foliar and fine root N levels also decreased after Harvest 5, however both structures maintained N levels that were higher than those observed in Harvest 1 particularly for the 2 mM and 3 mM N treatments (Table 3).

Above Ground Structures—Within plant structures, N treatment concentration had a significant effect on N proportion for several harvests. Foliar N proportion ranged from 1.53% in Harvest 1 to 3.29% in Harvest 5. At both Harvests 4 and 5 the 3 mM-1:1 and 3 mM-3:1 treatments had the highest percentage of N in the leaves. In addition, the 2 mM-1:1 treatment was similar to or higher than the 3 mM-1:3 treatment. In general, higher N concentrations yielded increased foliar N proportion (Table 3).

Stem N proportion ranged from 0.82% in Harvest 1 to 1.38% in Harvest 4. Significant differences between treatments were found at Harvests 3, 4 and 7 (Table 3). As with foliar N proportion, increased N concentration usually resulted in increased stem N proportion particularly as the experiment progressed. Ammonium to nitrate ratios appeared to have no consistent effect of stem N proportion at any treatment concentration level.

Below Ground Structures—Unlike above ground plant structures, below ground plant structures had significant differences in N proportions at all harvests after the first. Main roots had the lowest N proportion of any plant structure ranging from 0.54% in Harvest 7 to 1.33% in Harvest 4 (Table 4). Main root N proportion increased as treatment concentration increased. Different NH_4:NO_3 treatment ratios also significantly influenced the N proportion within main roots. Plants receiving the 3 mM-3:1 treatment had the highest N proportion although it was not significantly different from any other 3 mM treatment except for Harvest 6. Both the 3 mM and 2 mM-1:1 treatments consistently resulted in higher main root N proportions than the 3 mM-1:3 treatment, although these differences were also not significant. At the lower 1 mM concentration treatments, NH_4:NO_3 ratio preference was not as consistent as in the 3mM treatments and most 1mM treatments were not significantly different.

Fine root N proportion ranged from 1.17% in Harvest 7 to 3.37% in Harvest 6 (Table 4). Like main roots, fine root N proportion increased as N treatment concentration increased. In addition, NH_4:NO_3 ratios also influenced N levels. Plants receiving the 3 mM-3:1 treatment had the highest N proportions for Harvests 3-7, although observed differences were rarely significantly different from any other 3 mM treatment. As with main roots, the 3 mM-1:1 treatment usually resulted in higher fine root N proportion than the 3 mM-1:3 treatment however, these differences were again not significant. Unlike N proportions observed in main roots, NH_4:NO_3 ratios had a similar effect on N proportions of fine roots at the 1 mM treatment concentration as they did at the 3 mM treatment. There were a few significant differences in fine roots between 1mM N treatments. However, in those instances, fine roots exposed to the 1mM-3:1 N treatment always had a higher N proportion compared to the 1:1 and 1:3 NH_4^+:NO_3^- treatments. The consistent pattern of NH_4^+ to NO_3^- ratio on N proportion based on the 3:1, 1:1, 1:3 NH_4^+:NO_3^- ratios in the 3 mM treatment for main roots and both the 3 mM and 1 mM treatments for fine roots should be noted.

Discussion

Growth—Growth response curves in this experiment were not similar to Henry et al. (1992a) who showed that redcedar growth responded in a continuous fashion for the duration of their experiment. My results show that only root length (Fig. 5) and root weight (Fig. 1A) continuously increased throughout the study. On the other hand, rapid increases in both shoot length and total dry weight only occurred during the last two harvest periods. These differences are likely due to the timing of each study and the corresponding seasonal influences of photoperiod. Henry et al. (1992a) observed about a two-fold increase in shoot length over 175 days for a 40 ppm N treatment. However, in this study, average shoot length increased by only 50% in the 42 ppm N treatment (i.e. 3 mM N) over 196 days.

Foliar N proportion in this experiment approached the upper limit of foliar N levels for evergreen needles reported by Larcher (1995). In addition, foliar N proportions for all treatments in this experiment were 0.4-2.2% higher at 42 ppm N than that reported by Henry et al. (1992a) at 40 ppm. Elevated foliar N proportions may be a result of reduced demand for N because of slow growth over the winter months due to relatively low solar intensity and reduced temperatures.

Nitrogen Preference—That N proportion increased as applied N treatment concentrations increased is not surprising. However, the apparent preference for NH_4^+ by eastern redcedar in this experiment is potentially of great importance in the Great Plains of the United States. Eastern redcedar typically grows in calcareous soils with rocky to sandy textures (Little 1985, Barnes and Wagner 1996). Species adapted to living in such calcareous soils, which tend to have higher pH, prefer to utilize NO_3^- as compared to NH_4^+ (Larcher 1995, Marschner 1995). In fact, Miller et al. (1991) found that *Juniperus occidentalis* grown *in situ* with supplemental NO_3^--N fertilizer had higher leaf N content and higher mean maximum carbon dioxide assimilation than plants supplied with either supplemental NH_4^+-N or no supplemental N. On the other hand, Lumme (1994) found that *Picea abies*, a species typically found in moist acidic soils, preferentially took up NH_4^+ instead of NO_3^-. However, foliar N content varied little between different NH_4^+:NO_3^- soil treatments in their study (Lumme 1994).

My results do not agree with those of Miller et al. (1991). In this study, plants grown with N treatments of 3 mM-3:1, 3 mM-1:1 and to a lesser extent 2 mM-1:1 tended to have more mass and greater N proportion than plants grown with the 3 mM-1:3 treatment. These differences, although present in all tissues, were particularly apparent in the metabolically active structures of leaves and fine roots. Since I did not analyze affluent washed out of the study containers, I am unable to determine if redcedar preference for NH_4^+ in this study was related to pH conditions within the growth container.

The preference for NH_4^+ by redcedar could directly influence its invasion potential into abandoned agricultural fields and rangelands that receive aerial N depositions in the form of NH_4^+ or elevated N levels due to previous land management practices. My results show that although redcedar shoots were not growing for the first four to five months of this experiment; roots, particularly fine roots, grew substantially. Increased root surface will likely facilitate increased N absorption as evidenced by the consistent increase in total N content over the duration of the experiment. Because analysis of organic and inorganic forms of N were not conducted on plant structures, it is impossible to determine if N present in the plant was being assimilated into organic compounds or merely stored with the plants tissue as inorganic N. However, if redcedar trees absorbed "luxury" N, it appears to have been primarily stored in the leaves with secondary storage in stems and main roots. This is evidenced by the subsequent drop in N proportion in these tissues and the translocation of N out of stems and main roots once substantial shoot growth initiated.

Because NH_4^+ is metabolically less costly to incorporate into cellular components, like amino acids, it is possible the trees in this study, particularly in the 3 mM-3:1 N treatment, used NH_4^+ for metabolic processes and NO_3^-, which is readily mobile, could have been sequestered into subcellular compartments like vacuoles until it was needed (Marschner 1995). Once substantial growth resumed prior to Harvests 6 and 7 this stored N could be readily available for rapid growth. Therefore, N acquisition during winter months, when other prairie species are dormant or relatively inactive, could provide a competitive advantage for redcedar trees and thus facilitate its invasion. Miller et al. (1995) also suggested that the ability of *J. occidentalis* to utilize NH_4^+ may account for its increased invasion into shrublands.

The advantages associated with the ability to absorb or utilize NH_4^+ during early invasion may dissipate as redcedar trees establish themselves. Previous research conducted by Spurr (1940), Arend and Collins (1949), Arend (1950) and Chapter 1 strongly suggests that as redcedar trees grow, soil conditions directly underneath the canopy become more alkaline as cedar litter accumulates. Increasingly alkaline soil conditions should allow soil bacteria to readily convert NH_4^+ to NO_3^- thus depriving redcedar of its preferred N form.

In general, I found that growth rates, plant mass, plant N content and plant N proportion was highest with the highest N concentration treatments. In addition, growth rates and N proportions were also highest when a larger amount of the supplied N was in the form of NH_4^+ as compared to NO_3^-. Several differences in N proportions based on NH_4^+ to NO_3- ratios were not significant within this study however; the repeated ordering of treatments suggests that given more time, or replications, significant differences in growth and N content based on different N ratios may occur. Additionally, if redcedar trees are preferentially absorbing NH_4^+ as compared to NO_3^- in months of little aboveground growth, this may exacerbate the competitive displacement of prairie species. This is because redcedar trees would be able to accumulate N reserves that would become available for metabolic processes once aboveground growth was initiated, unlike prairie species, which are dormant during winter months.

Acknowledgements—I thank Dr. Bjorn Martin and Dr. Dave Engle for their support and consultations regarding several facets of this study. I also thank Dr. Michael Palmer and Dr. Ron Tyrl for editorial comments. In addition, I thank Dr. Mark Payton for his help with data analysis and SAS programming. I also thank Paul Mayer and his staff, for their work processing C and N data. The efforts of Baige Zhao, José Ramón Arévalo and Kalpalatha Melmaiee in daily plant care and data collection were also greatly appreciated. This project was funded by the U.S. Environmental Protection Agency through an interagency agreement (DW-14-9390001-1) with the Biological Resources Division of the U.S. Geological Survey and was administered by the Oklahoma Cooperative Fish and Wildlife Research Unit through the Department of Plant and Soil Sciences, Oklahoma State University (1434-HQ-00-RM-0088). The research described here has not been subjected to Agency review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred.

Literature Cited

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

Arend, J.L. and R.F. Collins. 1949. A site classification for eastern redcedar in the Ozarks. *Proc. Soil Sci. Soc. Am.*, **13**:510-511.

Bakker, J.P., E.S. Bakker, E. Rosen, G.L. Verweij and R.M. Bekker. 1996. Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. *J. Vege. Sci.*, **7**:165-176.

Barnes, B.V. and W.H. Wagner. 1996. Michigan trees. University of Michigan Press. Ann Arbor, Michigan.

Bates, J.D., T.J. Svejcar and R.F. Miller. 2002. Effects of juniper cutting on N mineralization. *J. Arid Enviro.*, **51**:221-234.

Briggs, J.M., G.A. Hoch 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.

Diotte, M. and Y. Bergeron. 1989. Fire and the distribution of *Juniperus communis* L. in the boreal forest of Quebec, Canada. *J. Biogeogr.*, **16**:91-96.

Ehleringer, J.R., C.S. Cook and L.L. Tieszen. 1986. Comparative water use and N relationships in a mistletoe and its host. *Oecologia*, **68**:279-284.

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

Fuhlendorf, S.D. 1992. Influence of age/size and grazing history on understory relationships of Ashe Juniper. [Thesis]. College Station (TX): Texas A&M University.

Fuhlendorf, S.D., F.E. Smeins and C.A. Taylor. 1997. Browsing and tree size influences on Ashe juniper understory. *J. Range Manage.*, **50**:507-512.

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

Haynes, R.J. and K.M. Goh. 1978. Ammonium and nitrate nutrition of plants. *Biol. Rev.*, **53**:465-510.

Henry, P.H., F.A. Blazich, L.E. Hinesley and R.D. Wright. 1992a. Nitrogen nutrition of containerized eastern redcedar. I. Growth, mineral nutrient concentrations and carbohydrate status. *J. Am. Soc. Hort. Sci.*, **117**:563-567.

Henry, P.H., F.A. Blazich and L.E. Hinesley. 1992b. Nitrogen nutrition of containerized eastern redcedar. II. Influence of stock plant fertility on adventitious rooting of stem cuttings. *J. Am. Soc. Hort. Sci.*, **117**:568-570.

Hicklenton, P.R. and K.G. Cairns. 1992. Solubility and application rate of controlled-release fertilizer affect growth and nutrient uptake in containerized woody landscape plants. *J. Amer. Soc. Hort. Sci.*, **117**:578-583.

Hoch, G.A. 2000. Patterns and mechanisms of eastern redcedar (*Juniperus virginiana*) expansion into tallgrass prairie in the Flint Hills Kansas [Dissertation]. Manhattan (KS): Kansas State University

Holthuijzen, A.M.A. and T.L. Sharik. 1985. Colonization of abandoned pastures by eastern redcedar (*Juniperus virginiana* L.). *Can. J. For. Res.*, **15**:1065-1068.

Jameson, D.A. 1966. Pinyon-Juniper litter reduces growth of blue grama. *J. Range Manage.*, **19**:214-217.

Klopatek, C.C. and J.M. Klopatek. 1997. Nitrifiers and mycorrhizae in pristine and grazed pinyon-juniper ecosystems. *Arid Soil Res. Rehab.*, **11**:331-342.

Larcher, W. 1995. Physiological plant ecology. Springer. Berlin.

Little, E.L. 1985. Forest trees of Oklahoma. Oklahoma Forestry Division. Oklahoma City.

Marschner, H. 1995. Mineral nutrition of higher plants. Academic Press. London.

McPherson, G.R. and H.A. Wright. 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in western Texas. *Am. Midl. Nat.*, **123**:144-151.

Miller, P.M., L.E. Eddleman and J.M. Miller. 1991. The response of juvenile and small adult western juniper (*Juniperus occidentalis*) to NO3- and NH4+ fertilization. *Can. J. Bot.*, **69**:2344-2352.

Miller, P.M., L.E. Eddleman and J.M. Miller. 1992. The seasonal course of physiological processes in *Juniperus occidentalis*. *For. Ecol. Manage.*, **48**:185-215.

Miller, P.M., L.E. Eddleman and J.M. Miller. 1995. *Juniperus occidentalis* juvenile foliage: Advantages and disadvantages for a stress-tolerant, invasive conifer. *Can. J. For. Res.*, **25**:470-479.

Miller, R.F. and J.A. Rose. 1995. Historic expansion of *Juniperus occidentalis* (Western Juniper) in southeastern Oregon. *Gt. Basin Nat.*, **55**:37-45.

Miller, R.F., T.J. Svejcar and J.A. Rose. 2000. Impacts of western juniper on plant community composition and structure. *J. Range Manage.*, **53**:574-585.

Sartin, J.B. and D.L. Ingram. Influence of container medium, lime, and nitrogen source on growth of woody ornamentals. *J. Amer. Soc. Hort. Sci.*, **109**:882-886.

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

Spurr, S.H. 1940. The influence of two *Juniperus* species on soils reaction. *Soil Sci.*, **50**:289-294.

Tiedemann, A.R. and J.O. Klemmedson. 1995. The influence of western juniper development on soil nutrient availability. *Northwest Sci.*, **69**:1-8.

Wright, R.D. and L.E. Hinesley. 1991. Growth of containerized eastern redcedar amended with dolomitic limestone and micronutrients. *HortSci.*, **26**:143-145.

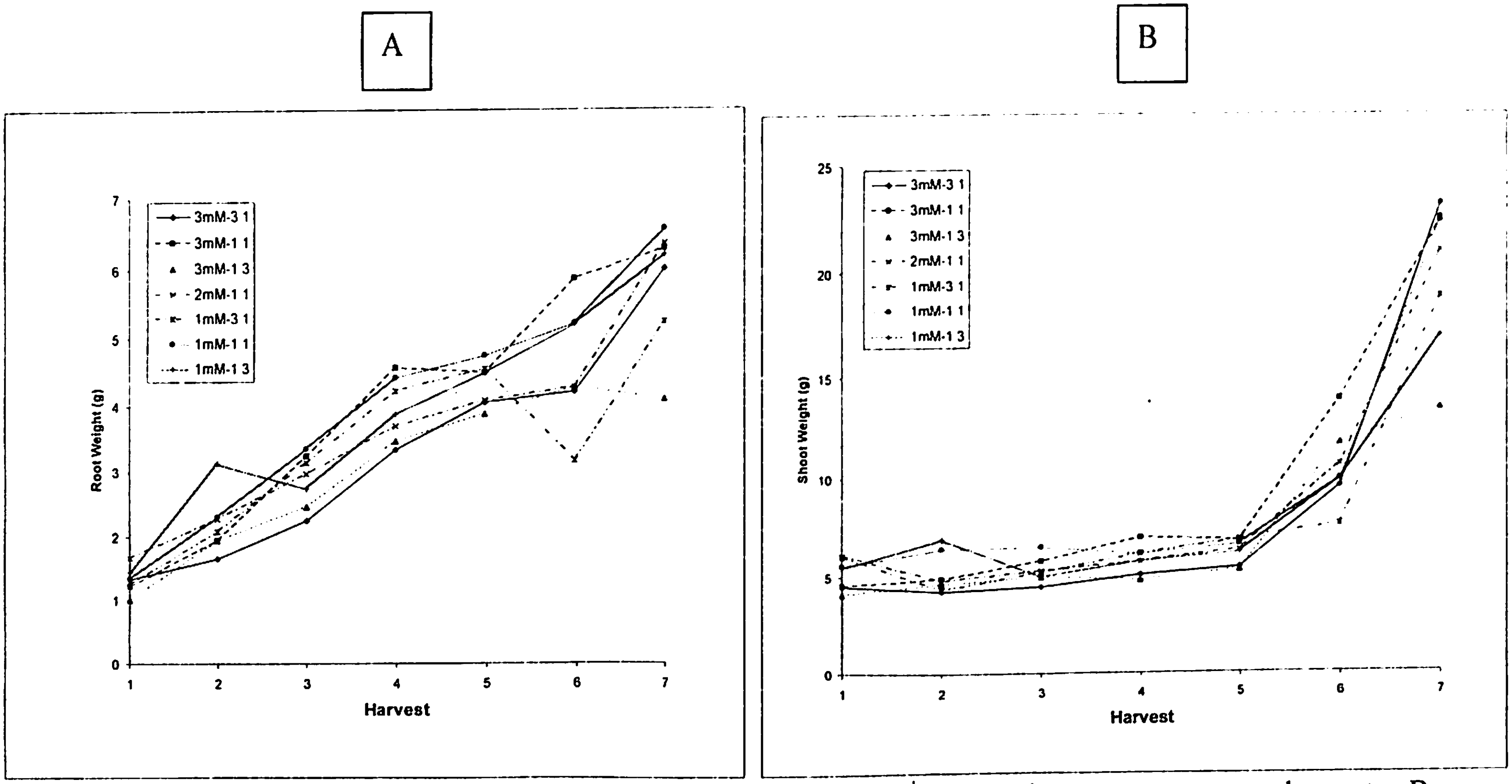

Figure 1: A—Average root dry weight of seven N concentrations and NH_4^+:NO_3^- ratios across seven tree harvests. B—Average shoot dry weight of seven N concentrations and NH_4^+:NO_3^- ratios across seven tree harvests.

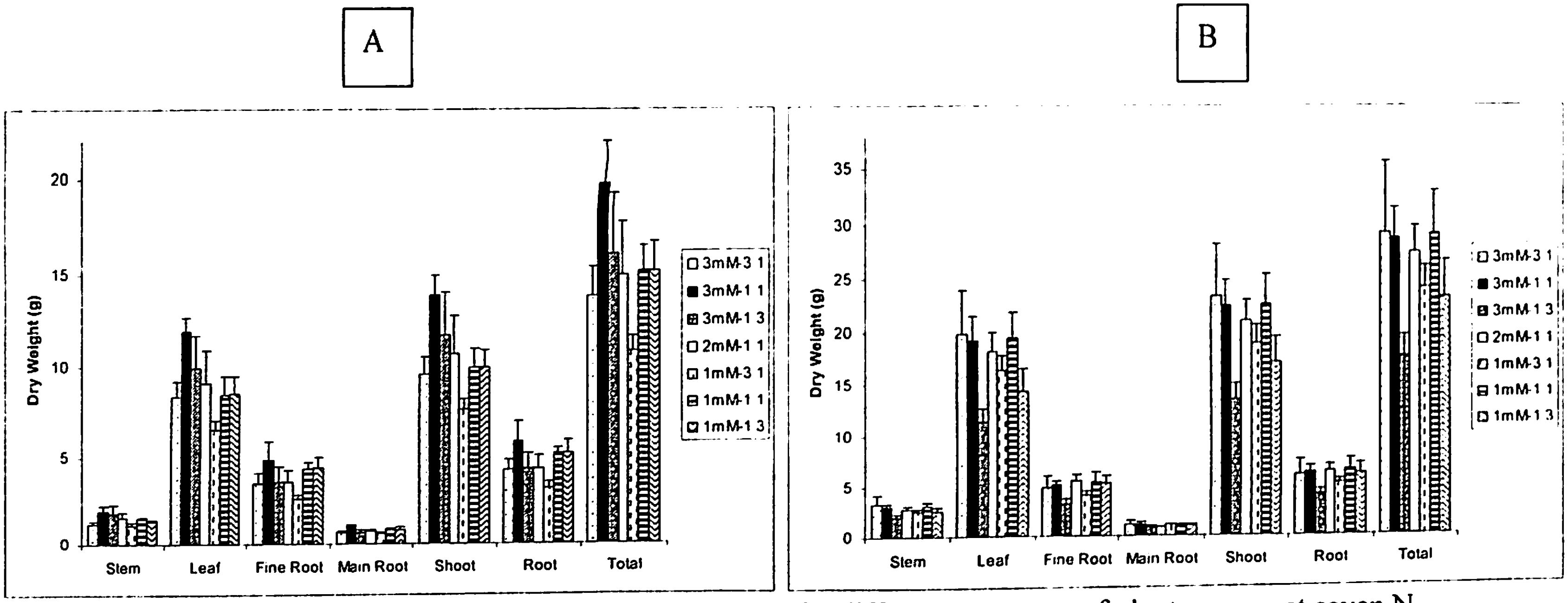

Figure 2: A—Average dry weight at Harvest 6 (29 March 2002) for different structures of plants grown at seven N concentrations and NH_4^+:NO_3^- ratios. B—Average dry weight at Harvest 7 (26 April 2002) for different structures of plants grown at seven N concentrations and NH_4^+:NO_3^- ratios.

Table 1:A—Results for several plant variables recorded at Harvest 6 (29 March 2002) including statistical differences based on $p=0.05$.

Nitrogen	Stem Dry Weight(g)	Leaf Dry Weight(g)	Fine Root Dry Weight(g)	Main Root Dry Weight(g)	Shoot Dry Weight(g)	Root Dry Weight(g)	Total Dry Weight(g)	Leaf Area Ratio	Leaf Area	Root Shoot Ratio	Leaf Weight Ratio
3mM-3:1	1.222(a)	8.362(ab)	3.518(ab)	0.690(a)	9.584(ab)	4.204(ab)	13.788(ab)	16.160(bc)	220.696(abc)	0.432(d)	0.612(abc)
3mM-1:1	1.966(a)	11.942(c)	4.820(b)	1.030(a)	13.908(c)	5.852(c)	19.760(c)	15.294(b)	293.940(c)	0.410(d)	0.612(c)
3mM-1:3	1.774(a)	9.990(bc)	3.592(ab)	0.680(a)	11.764(bc)	4.276(ab)	16.040(bc)	17.004(c)	264.012(bc)	0.360(a)	0.632(bc)
2mM-1:1	1.562(a)	9.120(abc)	3.538(ab)	0.750(a)	10.682(abc)	4.286(ab)	14.968(abc)	15.906(bc)	238.072(abc)	0.406(cd)	0.606(abc)
1mM-3:1	1.132(a)	6.530(a)	2.584(a)	0.590(a)	7.662(a)	3.172(a)	10.834(a)	16.210(bc)	174.220(a)	0.416(bc)	0.604(a)
1mM-1:1	1.480(a)	8.492(ab)	4.342(b)	0.870(a)	9.972(ab)	5.212(bc)	15.184(abc)	13.092(a)	204.130(ab)	0.542(d)	0.550(ab)
1mM-1:3	1.370(a)	8.582(ab)	4.358(b)	0.850(a)	9.952(ab)	5.204(bc)	15.156(abc)	13.468(a)	204.422(ab)	0.524(ab)	0.566(ab)

Table 1: B—Results for several plant variables recorded at Harvest 7 (26 April 2002) including statistical differences based on $p=0.05$.

Nitrogen	Stem Dry Weight(g)	Leaf Dry Weight(g)	Fine Root Dry Weight(g)	Main Root Dry Weight(g)	Shoot Dry Weight(g)	Root Dry Weight(g)	Total Dry Weight(g)	Leaf Area Ratio	Leaf Area	Root Shoot Ratio	Leaf Weight Ratio
3mM-3:1	3.382(d)	19.842(d)	4.806(bc)	1.190(a)	23.224(d)	5.996(b)	29.220(d)	17.514(b)	500.308(d)	0.254(a)	0.688(a)
3mM-1:1	3.132(cd)	19.25(cd)	5.110(bc)	1.160(a)	22.382(cd)	6.274(b)	28.656(cd)	16.766(b)	486.132(d)	0.284(a)	0.668(a)
3mM-1:3	2.108(a)	11.378(a)	3.242(a)	0.860(a)	13.486(a)	4.100(a)	17.586(a)	16.514(b)	292.250(a)	0.302(a)	0.648(a)
2mM-1:1	2.784(bcd)	18.210(cd)	5.472(c)	0.870(a)	20.994(cd)	6.346(b)	27.340(bcd)	17.494(b)	474.650(cd)	0.302(a)	0.666(a)
1mM-3:1	2.504(ab)	16.328(bc)	4.084(ab)	1.140(a)	18.832(bc)	5.228(ab)	24.060(bc)	16.748(b)	401.736(bc)	0.278(a)	0.678(a)
1mM-1:1	3.080(bcd)	19.432(cd)	5.408(c)	1.150(a)	22.512(d)	6.554(b)	29.066(d)	16.596(b)	483.232(d)	0.286(a)	0.670(a)
1mM-1:3	2.568(abc)	14.392(ab)	5.190(bc)	1.010(a)	16.96(ab)	6.198(b)	23.158(b)	14.730(a)	341.020(ab)	0.370(a)	0.620(a)

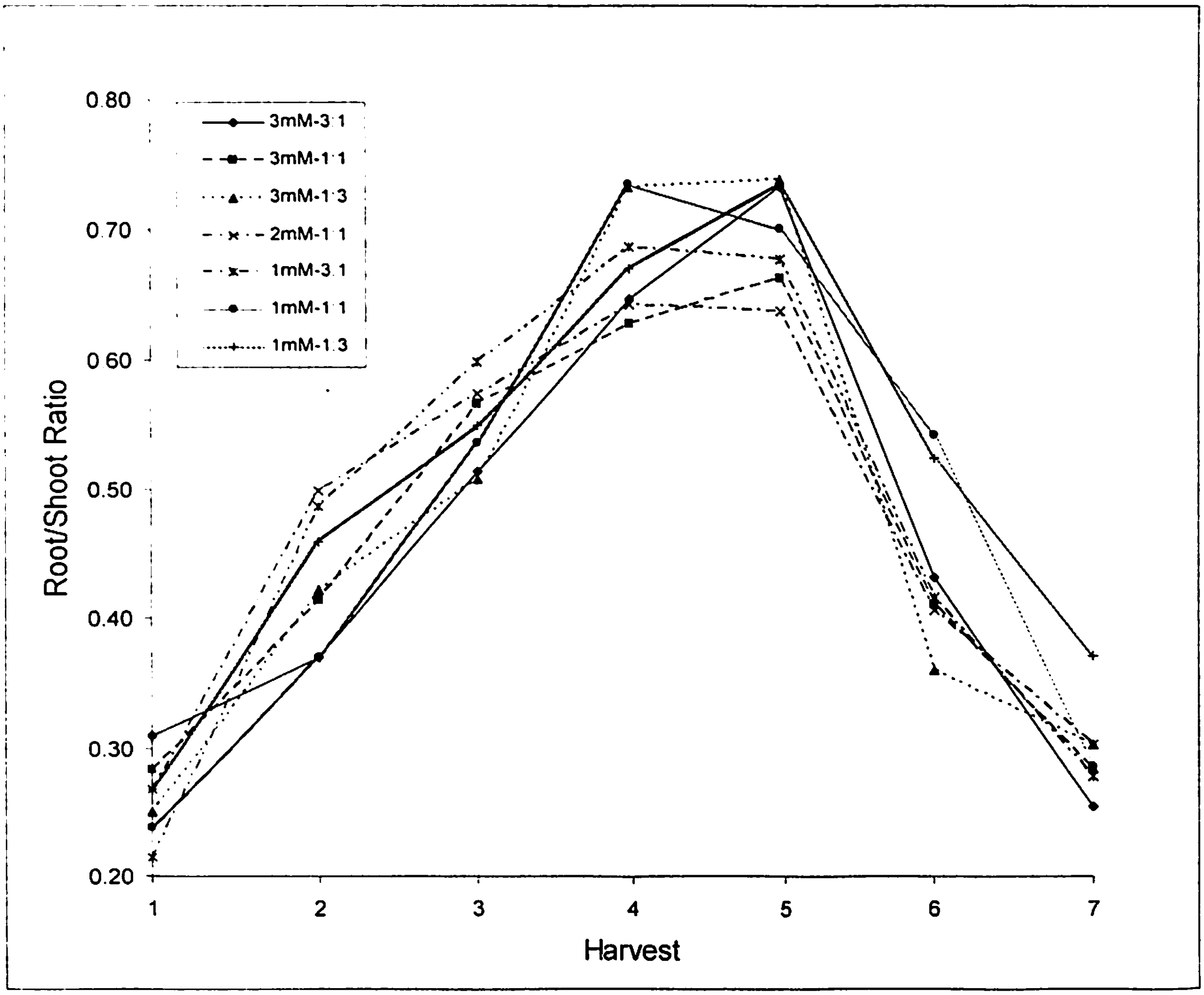

Figure 3: Root to shoot ratio of seven combinations of N concentrations and NH_4^+:NO_3^- ratios for seven harvests.

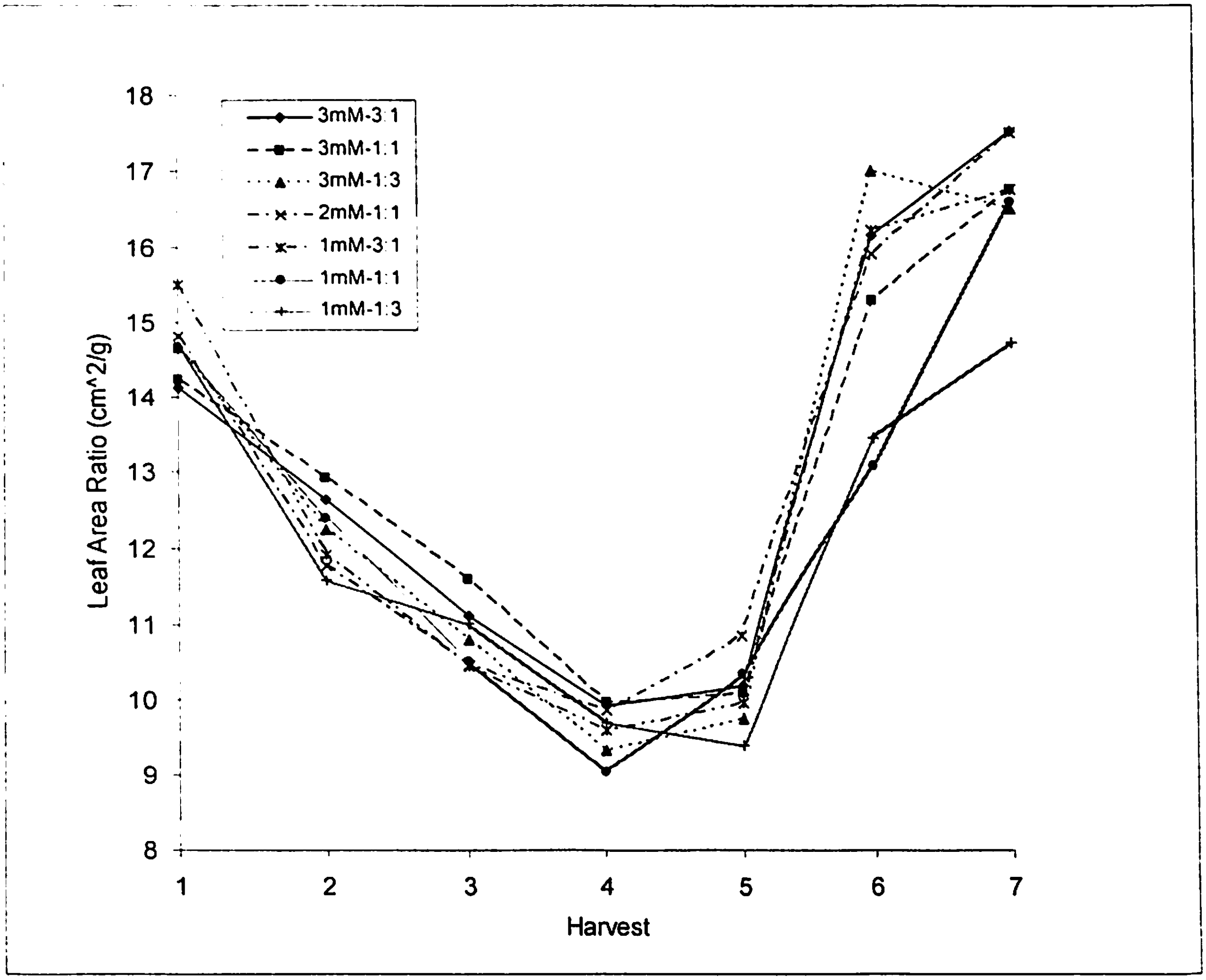

Figure 4: Leaf area ratio of seven combinations of N concentrations and NH_4^+:NO_3^- ratios for seven harvests.

Table 2: Proportion of carbon pooled across treatments for each plant structure. Letters represent difference in significance within a harvest as determined by LSD at p=0.05

Harvest **Date (2002)**	**1** **9 Nov.**	**2** **7 Dec.**	**3** **4 Jan.**	**4** **1 Feb.**	**5** **1 Mar.**	**6** **29 Mar.**	**7** **26 Apr.**
Leaves	48.158(d)	48.499(d)	47.674(d)	47.867(d)	46.049(d)	44.687(c)	44.366(b)
Stems	46.253(c)	45.189(c)	45.604(c)	45.186(c)	45.419(c)	44.703(d)	44.868(d)
Main Roots	44.772(b)	44.459(b)	44.728(b)	44.600(b)	44.593(b)	44.093(b)	44.824(c)
Fine Roots	43.260(a)	42.134(a)	43.038(a)	42.943(a)	43.072(a)	42.788(a)	43.883(a)

Table 3: Comparison of proportion nitrogen within each nitrogen treatment for all four plant structures. Letters represent difference in significance as determined by LSD at p=0.05 within a row per harvest. Lower case letters indicate significance within a plant structure across all nutrient treatments within a harvest. Upper case letters represent significance between plant structures within a nutrient treatment within a harvest.

Harvest 1 (9 Nov. 2002)

Treatment	Leaves	Stems	Main Roots	Fine Roots
3mM—3:1	1.778(a)(D)	1.023(a)(B)	0.664(a)(A)	1.536(a)(C)
3mM—1:1	1.887(a)(B)	0.857(a)(A)	0.701(a)(A)	1.680(a)(B)
3mM—1:3	1.752(a)(C)	0.947(a)(B)	0.613(a)(A)	1.489(a)(C)
2mM—1:1	1.772(a)(C)	0.847(a)(B)	0.571(a)(A)	1.547(a)(C)
1mM—3:1	1.865(a)(C)	0.821(a)(A)	0.626(a)(A)	1.572(a)(B)
1mM—1:1	1.777(a)(C)	0.881(a)(A)	0.672(a)(A)	1.431(a)(B)
1mM—1:3	1.767(a)(B)	0.900(a)(A)	0.789(a)(A)	1.596(a)(B)

Harvest 2 (7 Dec. 2002)

Treatment	Leaves	Stems	Main Roots	Fine Roots
3mM—3:1	2.133(abc)(C)	1.040(a)(A)	0.851(ab)(A)	1.861(bc)(B)
3mM—1:1	2.358(bc)(B)	0.911(a)(A)	0.931(ab)(A)	2.127(c)(B)
3mM—1:3	2.171(abc)(B)	0.987(a)(A)	0.784(a)(A)	2.059(c)(B)
2mM—1:1	2.359(c)(C)	1.210(a)(A)	1.183(b)(A)	1.749(abc)(B)
1mM—3:1	2.100(abc)(C)	1.044(a)(A)	0.795(a)(A)	1.711(ab)(B)
1mM—1:1	1.986(ab)(D)	1.015(a)(B)	0.631(a)(A)	1.498(a)(C)
1mM—1:3	1.918(a)(C)	0.889(a)(A)	0.698(a)(A)	1.499(a)(B)

Harvest 3 (4 Jan. 2002)

Treatment	Leaves	Stems	Main Roots	Fine Roots
3mM—3:1	2.800(c)(B)	1.293(b)(A)	1.065(ab)(A)	2.773(c)(B)
3mM—1:1	2.556(c)(B)	1.057(ab)(A)	1.169(b)(A)	2.577(bc)(B)
3mM—1:3	2.316(b)(B)	1.050(ab)(A)	0.987(ab)(A)	2.437(b)(B)
2mM—1:1	2.722(c)(B)	1.188(ab)(A)	1.141(b)(A)	2.495(bc)(B)
1mM—3:1	2.229(ab)(C)	1.013(ab)(A)	0.959(ab)(A)	1.671(a)(B)
1mM—1:1	2.066(ab)(C)	0.937(a)(A)	0.823(a)(A)	1.645(a)(B)
1mM—1:3	1.986(a)(C)	0.929(a)(A)	0.824(a)(A)	1.467(a)(B)

Harvest 4 (1 Feb. 2002)

Treatment	Leaves	Stems	Main Roots	Fine Roots
3mM—3:1	3.142(d)(B)	1.384(b)(A)	1.332(c)(A)	3.231(c)(B)
3mM—1:1	2.989(d)(B)	1.236(ab)(A)	1.229(bc)(A)	3.049(c)(B)
3mM—1:3	2.741(c)(B)	1.172(ab)(A)	1.158(abc)(A)	2.939(c)(C)
2mM—1:1	2.705(bc)(C)	1.172(ab)(A)	1.073(abc)(A)	2.349(b)(B)
1mM—3:1	2.576(abc)(C)	1.042(a)(A)	1.032(abc)(A)	2.135(b)(B)
1mM—1:1	2.391(ab)(C)	0.926(a)(A)	0.914(ab)(A)	1.681(a)(B)
1mM—1:3	2.354(a)(C)	1.052(a)(A)	0.890(a)(A)	1.609(a)(B)

Harvest 5 (1 Mar. 2002)

Treatment	Leaves	Stems	Main Roots	Fine Roots
3mM—3:1	3.140(d)(A)	1.241(a)(A)	1.221(b)(A)	3.311(b)(B)
3mM—1:1	2.968(cd)(B)	1.216(a)(A)	1.053(ab)(A)	3.230(b)(C)
3mM—1:3	2.591(ab)(B)	1.214(a)(A)	0.992(ab)(A)	3.193(b)(C)
2mM—1:1	2.807(bc)(B)	1.156(a)(A)	1.015(ab)(A)	3.088(b)(C)
1mM—3:1	2.511(ab)(C)	1.043(a)(A)	0.888(a)(A)	2.209(a)(B)
1mM—1:1	2.385(a)(C)	1.029(a)(A)	0.825(a)(A)	1.977(a)(B)
1mM—1:3	2.493(ab)(C)	1.035(a)(A)	0.847(a)(A)	1.997(a)(B)

Harvest 6 (29 Mar. 2002)

Treatment	Leaves	Stems	Main Roots	Fine Roots
3mM—3:1	2.955(b)(B)	0.988(a)(A)	0.883(a)(A)	3.369(c)(C)
3mM—1:1	2.754(b)(B)	1.050(a)(A)	0.901(b)(A)	3.158(c)(C)
3mM—1:3	2.855(b)(C)	1.003(a)(A)	0.766(a)(A)	2.478(b)(B)
2mM—1:1	2.814(b)(C)	1.007(a)(A)	0.830(a)(A)	2.483(b)(B)
1mM—3:1	2.618(ab)(C)	0.917(a)(A)	0.665(a)(A)	2.232(b)(B)
1mM—1:1	2.376(a)(C)	0.842(a)(A)	0.653(a)(A)	1.674(a)(B)
1mM—1:3	2.320(a)(C)	0.724(a)(A)	0.551(a)(A)	1.458(a)(B)

Table 3: Continued

Harvest 7 (26 Apr. 2002)

Treatment	Leaves	Stems	Main Roots	Fine Roots
3mM—3:1	2.460(b)(B)	1.018(ab)(A)	0.844(a)(A)	2.410(e)(B)
3mM—1:1	2.457(b)(D)	1.088(b)(B)	0.829(a)(A)	2.042(cd)(C)
3mM—1:3	2.258(b)(C)	0.996(ab)(B)	0.751(a)(A)	2.159(de)(C)
2mM—1:1	2.235(b)(C)	0.979(ab)(A)	0.801(a)(A)	1.736(bc)(B)
1mM—3:1	1.775(a)(C)	0.766(a)(A)	0.596(a)(A)	1.370(a)(B)
1mM—1:1	1.678(a)(C)	0.730(a)(A)	0.543(a)(A)	1.170(a)(B)
1mM—1:3	1.878(a)(C)	0.854(ab)(A)	0.623(a)(A)	1.427(ab)(B)

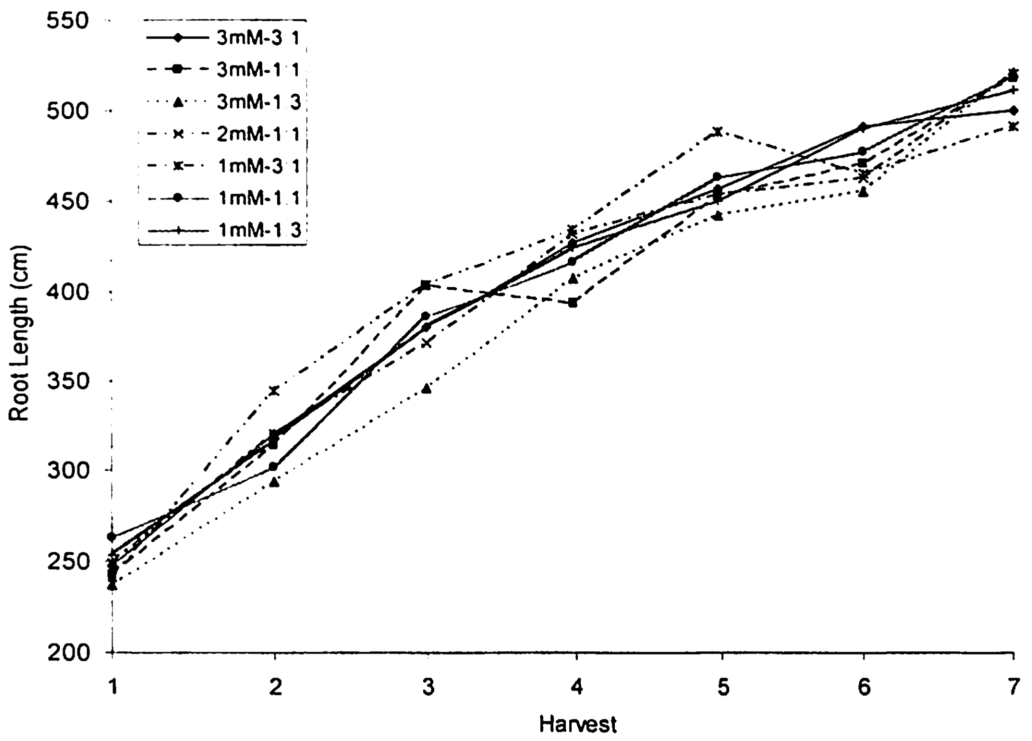

Figure 5: Root length of plants grown at of seven combinations of N concentrations and NH_4^+:NO_3^- ratios.

Macronutrients (for 150 L final solution).

Chemical	mol wt	mM	mol/150 L	g/150 L
KH_2PO_4	136.09	1	0.15	20.41
K_2SO_4	174.27	2	0.3	52.28
$MgSO_4x7H_2O$	246.47	1.5	0.225	55.46
$CaCl_2x2H_2O$	147.02	3	0.45	66.16

Micronutrients (for 1 L stock solution). Add 150 mL micronutrient stock solution to 150 L final nutrient solution.

Chemical	mol wt	M	g/L of stock
$MnSO_4x1H_2O$	169.1	0.01	1.69
$ZnSO_4x7H_2O$	287.54	0.001	0.29
$CuSO_4x5H_2O$	249.68	0.001	0.25
H_3BO_3	61.83	0.05	3.09
$(NH_4)_6Mo_7O_{24}x4H_2O$	1235.86	0.00036	0.044
$CoCl_2x6H_2O$	237.93	0.00016	0.04

Appendix 1: Continued

Ferric sulfate – EDTA (for 1 L stock solution). Add 150 mL micronutrient stock solution to 150 L final nutrient solution.

Chemical	**mol wt**	**M**	**g/L of stock**
$FeSO_4x7H_2O$	278.03	0.025	7.45
EDTA	372.24	0.025	9.21

Nitrogen – Amounts and forms that should be added to 20 L of Macronutrients.

Concentration (mM) N	**mM NH_4^+**	**mM NO_3^-**	**NH_4^+:NO_3^-**	**NH_4NO_3**	**NH_4Cl**	**$NaNO_3$**
3	2.25	0.75	3:1	1.20	1.61	0.00
3	1.50	1.50	1:1	2.40	0.00	0.00
3	0.75	2.25	1:3	1.20	0.00	2.55
2	1.00	1.00	1:1	1.60	0.00	0.00
1	0.75	0.25	3:1	0.40	0.53	0.00
1	0.50	0.50	1:1	0.80	0.00	0.00
1	0.25	0.75	1:3	0.40	0.00	0.85

VITA #✓

Jerad S. Linneman
311 East Third Avenue
Stillwater, OK 74074
405-533-5379

Education:

Oklahoma State University
Master of Science in Botany (May 2004)
University of Wisconsin-Green Bay GPA 3.36 / 4.0
Bachelor of Science in Environmental Science and Philosophy (May 1999)

Skills:

Computer Literacy: Canoco for Windows, Deskscan II/Epson Twain 4, Microsoft Office XP, Nero 6 Ultra, Norton Systemworks 2003, SPSS 11.0 for Windows

Completed FISTA (Forestry Industry Safety & Training Alliance, Inc.) course in chainsaw and brushsaw safety. Course included training on tree felling, limbing, bucking, and proper approaches to brush removal and springpole cutting techniques.

Organizations:

Founder and Member of OSUBS, Oklahoma State University Botanical Society (Fall 2000-Present)

Member of the Graduate and Professional Students Association (September, 2000-May, 2001)

Member of the NAS, Natural and Applied Science, Search and Screen Student Advisory Committee (January, 1999-Febuary, 1999)

Member of the Institute for Philosophical Studies at Green Bay (September, 1996-Present)

Member of the Student Philosophy Forum (September, 1995-May, 1997)

Honors:

President of the Oklahoma State University Botanical Society (Fall 2000-May, 2001 & August, 2003-May, 2004)

President of the Student Philosophy Forum (September, 1996-December, 1996)

Vice-President of the Student Philosophy Forum (January, 1995-May, 1995)

Field Work and Experience:

Prescribed Fire Crew
Oklahoma State University
Stillwater, OK 74078
January, 2002-May, 2002 & January, 2004-May, 2004

Participated in a course where classroom theory regarding prescribed fire was supplemented with prescribed fire field experience. I was a crew member on approximately 30 prescribed fires where my duties included head/back fire ignition, spot ignition, fire break clean-up, and spot fire patrol. I have been a crew boss several times and I was also fire boss of a 40 acre prescribed fire where my duties included planning the prescribed fire, notifying landowners and public safety agencies, supervising ignition, fire suppression, and mop-up, and crew safety.

Master's Thesis
Oklahoma State University
Stillwater, OK 74078-3013
May, 2001-May, 2004

I conducted vegetation sampling on two groups of twenty trees. The first group was used to define how invasion of eastern redcedar affects community vegetation patterns, structure, and understory composition within grasslands. Sampling parameters included: plant species identification, light intensity, soil pH, soil temperature, litter accumulation/decomposition rates, and rainfall accumulations. The second group of trees was used to disentangle the particular effects of the overstory trees versus litter accumulations on plant species underneath eastern redcedar in a manipulative design. Additionally, eastern redcedar was also grown in a greenhouse to determine both total nitrogen uptake and if eastern redcedar prefers a particular form of nitrogen (ammonium versus nitrate).

Teaching Assistant
Oklahoma State University
Stillwater, OK 74078-3013
September, 2000-May, 2003 & January, 2004-May, 2004

I have taught four semesters of General Ecology Lab. In these labs, we tried to communicate principles involved ecological theory and its application in the field. Principles included were not strictly limited to ecology, but also included statistical methods/analysis and ethical approaches to land management questions. I composed weekly lab quizzes for twenty students per lab and co-composed midterm/final examinations for approximately 100 students. Additionally, I have also taught two semesters of Plant Physiology Lab. Duties include laboratory and experiment set-up, chemical preparation, lab management, and facilitating student learning.

Nutrient Cycling Field Technician
Oklahoma State University & University of New Mexico
Stillwater, OK 74078-3013
May, 2001-June, 2001
Assisted nutrient cycling researcher collect and process soil samples collected from the Sevilleta National Wildlife Refuge (LTER). I collected data for several ongoing experiments related to nutrient cycling, particularly nitrogen and carbon. Duties included locating study sites, soil sampling, preparation of soil samples, injection of radiolabel nitrogen into soil surrounding vegetation patches, and above and below ground biomass sampling.

Vegetation Sampling Field Technician
Oklahoma State University
Stillwater, OK 74078-3013
June, 2000 & July, 2001
Assisted with vegetation sampling at the Tallgrass Prairie Preserve (Pawhuska, OK). Duties included locating study sites, site set-up, recording environmental parameters, and plant species identification.

Field Forestry Technician
Wisconsin Department of Natural Resources
Eagle, WI 53119
May, 1999-December, 1999
Aided in timber stand improvement on state as well as private lands including, but not limited to: brush control, timber stand marking for thinning purposes, exotic species removal, and insect/disease identification. Conducted forest reconnaissance where observation included plant species identification, estimating basal area, and measuring cords of timber at all sample plots. I assisted with timber sale management particularly related to background information regarding sale contracts. Additionally, I participated in conducting several prescribed fires and pre-burn fire suppression activities including fire break preparation and tree/vegetation removal.

International Environmental Consultant
University of Wisconsin-Green Bay
Green Bay, WI 54311-7001
March, 1999
Contracted by the Tobagian government to perform an environmental assessment of the island of Tobago. The assessment team was comprised of University of Wisconsin-Green Bay professors, faculty, and invited students. Collected data consisted of personal observations and notes which were then revised into categorical ecological issues. An ecological impact statement was written and submitted to the country of Tobago.

Ornithological Mortality Surveyor
University of Wisconsin-Green Bay
Green Bay, WI 54311-7001
November, 1998-January, 1999
This study attempted to find if any linkage existed between electricity production with wind turbines was related to migratory bird mortality. Field duties consisted of walking transects searching for pre-placed and non-placed dead bird specimens. Collected data included specimen description, specimen location, and environmental conditions.

Land Snail Community Ecology Researcher
University of Wisconsin-Green Bay
Green Bay, WI 54311-7001
September-December 1998
Assisted in conducting a study of land snail community composition of the Niagara Escarpment. Duties included sample preparation and specimen extraction. This study involved the archiving of more than 300 sites throughout the upper Midwest.

Environmental Quality Incentives Program (EQIP) Workshop Coordinator
Natural Resource Conservation Service and Glacierland RC&D
Manitowoc, WI 54221
August-October 1998
Coordinated Town of Winchester (WI) wetland informational workshop. The workshop was intended to facilitate the interaction of private landowners and representatives of several government agencies including the United States Fish and Wildlife Service, Wisconsin Department of Natural Resources, and the Natural Resource Conservation Service. Duties included coordination of workshop speakers, composing press releases/public service announcements, advertising, and tracking grant expenditures. Composed final evaluation of several wetland workshops based on an analysis of participants responses to a workshop survey. A cost-effectiveness analysis was also included within the report.

Field Administrative Intern to EQIP Grant Proposer
Natural Resource Conservation Service and Glacierland RC&D
Manitowoc, WI 54221
February-June 1998
I assisted in coordinating wetland workshops (see description above). I also conducted research to obtain necessary background information about wetlands including: definitions of wetlands, soil vegetation types/characteristics, formation, and functional values. Compiled informational folders that were distributed to workshop participants. Field work consisted of plant, animal, and soil identifications using socially accepted common names. Administrative duties included confirming workshop speakers, sign construction, and staffing registration area.

Presentations:

Linneman, J.S. 2004. Environmental conditions and litter production underneath *Juniperus virginiana* trees in a central Oklahoma grassland. Proceedings of the Oklahoma Academy of Science. Chickasaw, Oklahoma.

Manuscripts:

Linneman, J.S. October, 1998. Evaluative Workshop Report on: "The Economic and Environmental Values of a Wetland". USDA-NRCS Manitowoc, WI.

Linneman, J.S. 2004. Environmental conditions and litter production underneath *Juniperus virginiana* trees in a central Oklahoma grassland. (Abstract) Proceedings of the Oklahoma Academy of Science. (In Press)

Linneman, J.S. 2004. Chapter 1: Environmental Conditions and Litter Production Underneath Juniperus virginiana L. Trees in Central Oklahoma. (In progress)

Linneman, J.S. 2004. Chapter 2: The Effect of Juniperus virginiana L. Trees on Plant Species Composition in a Central Oklahoma Grassland. (In progress)

Linneman, J.S. 2004. Chapter 3: The Effects of Removal of Juniperus Virginiana L. Trees and Litter from a Central Oklahoma Grassland. (In progress)

Linneman, J.S. 2004. Chapter 4: Differences in growth and nitrogen uptake by eastern redcedar trees grown in a greenhouse. (In Progress)