JUNIPER EXPANSION IN A PRAIRIE-FOREST TRANSITION REGION

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled:

JUNIPER EXPANSION IN A PRAIRIE-FOREST TRANSITION REGION

presented by Lyndia D. Hammer a candidate for the degree of Master of Science, and hereby certify that, in their opinion, it is worthy of acceptance.

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CHAPTER 1

INTRODUCTION

In North America, an extended period of tree and shrub expansion in grasslands and open woodlands has followed major changes to forest structure, fire regimes and grazing regimes caused by Euro-American exploration and settlement (Auken, 2000; Nowacki and Abrams, 2008). Climate modes and changes in anthropogenic land use patterns may be considered the greatest drivers of broad scale vegetation community composition and distribution over time (Miller and Wigand, 1994; Guyette et al., 2002; Abrams and Nowacki, 2008). These broad-scale changes are subject to significant fine-scale variation as population distributions and disturbance regimes vary with topography and micro-climatic conditions, creating diversity in vegetation communities across the landscape (Bradley and Fleishman, 2008; Stambaugh and Guyette, 2008; Elliott, 2012). In xeric ecosystems of North America, woody species of the genus *Juniperus* have increased in density and extent on the landscape coincident with Euro-American settlement, causing changes to vegetation community dynamics, fire regimes and ecosystem services (Bragg and Hulbert, 1976; Burkhardt and Tisdale, 1976; DeSantis et al., 2011; Tausch et al., 1981). Despite the general consensus that juniper populations have increased throughout North America, the historic population dynamics of native juniper species remain poorly understood and are a major focus of this study.

Juniper Expansion

Western juniper species have expanded and receded across landscape positions with major shifts in moisture and temperature patterns throughout the Holocene, though the rate of juniper expansion attributed to anthropogenic causes over the past 120 years appears to be unprecedented (Miller and Wigand, 1994). Several studies have implicated changes to fire and grazing regimes as proximate causes of juniper expansion throughout much of the US during the past 150 years.

In a study modeling Ashe juniper (*Juniperus ashei*) response to varied fire regimes on the Edwards plateau of Texas, simulations of fire intervals of varying lengths led to differential rates of woody community expansion and corresponding decreases in herbaceous biomass that either maintained "steady state" communities or led to threshold changes in the vegetation community. Positive feedback between decreasing herbaceous biomass and decreased fire severity favored juniper density increase, eventually leading to a "threshold change" from fire-maintained grassy woodland to closed canopy juniper woodland (Fuhlendorf et al., 1996). In the tallgrass prairie ecosystem of Kansas, conversion from grassland to juniper forest was documented over a 40 year period in absence of fire (Briggs et al., 2002). Following this transition from herbaceous to woody canopy, return to grassland requires intensive land management (manual tree removal and or herbicide use) or high severity fire, both of which mark a departure from the prior "stable state" in which the plant community structure and composition was maintained by relatively frequent, low to moderate severity fire (Fuhlendorf et al., 1996).

In unburned Texas grasslands, the increase in juniper on grazed vs. un-grazed land was partially attributed to ground disturbance and an increase in percent bare ground due to grazing (McPherson et al., 1988). In the Flint Hills tallgrass prairie ecosystem of Kansas during a 30 year period from 1937- 1969, Bragg and Hulbert (1976) reported a 34% increase in woody plant density in unburned prairie, compared to a 1% increase in burned prairie. The invasion rate was highest on lowlands and steep, rocky ground and lowest on upland clay-dominated soils. In pinyon-juniper woodlands of the western US Great Basin, the largest increase in tree density during a 600 year period of record occurred during the Euro-American settlement period (last half of the 19^{th} century), when logging, mining, grazing, fire suppression and a warmer, wetter climate were all implicated in the expansion of woody species (Tausch et al., 1981).

The Cross Timbers Region

The Cross Timbers, mapped by Kuchler (1964), is a region distinguished by a vegetation mosaic of oak woodland and mixed grass prairie that serves as a broad transition zone between eastern deciduous forest and the southern Great Plains. The region has a rich cultural and natural history, having been named and used as a landmark by Native Americans, early European explorers, and Euro-American settlers (Hoagland et al., 1999). Early exploratory accounts of the region suggest the Cross Timbers' name may have been derived from the heavy bands of vegetation that had to be "crossed" as explorers and settlers traveled east to west through forests and prairie, or perhaps for the cross shaped leaf of the ubiquitous "cross oak" or post oak tree (Francaviglia, 2000). The dominant trees of the region are post oak (*Quercus stellata)* and blackjack oak (*Quercus marilandica*), with black hickory (*Carya texana*) an important species in the east, and eastern redcedar (*Juniperus virginiana*), hereafter referred to as ERC, a now important species throughout the region (Figure 1.1). Common understory species include: gum bumelia (*Bumelia languinosa*), winged elm (*Ulmus alata*), buckbrush (*Symphoricarpos orbiculatus*), and sumac (*Rhus sp.*). Dominant grasses include little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), hairy grama (*Boutela hirsuta*) and Indian grass (*Sorghastrum nutans*) (Hoagland et al., 1999).

The Cross Timbers span an ecotone from forest to prairie and thus span gradients in temperature and precipitation. Ranging from southeastern Kansas to central Texas, and across Oklahoma from Arkansas to the Texas border, annual average temperatures range from 15 °C in the north to 18.8 °C in the south, and average annual precipitation varies from 102 cm in the east to 71 cm in the west (Hoagland et al., 1999). The region is part of a major North American bird and butterfly migration route, and is home to at least one endangered avian species, the black capped vireo (*Vireo atricapilla*). American bison (*Bison bison*) were once common and the largest remaining herd in the region survives today on the Wichita Mountains Wildlife Refuge in Indiahoma, OK. The Cross Timbers have been called home to some of the largest tracts of old growth oak forest in North America, but the region's conservation status is not well known (Therrell and Stahle, 1998; Clark and Hallgren, 2003). Possible threats to the characteristic vegetation of the region include the expansion of eastern redcedar (ERC) (Stambaugh et al., 2009) and possible changes in the composition and character of prairies and woodlands due to increasing woody species density, decreasing herbaceous biomass, and decreasing fire severity (DeSantis et al., 2011).

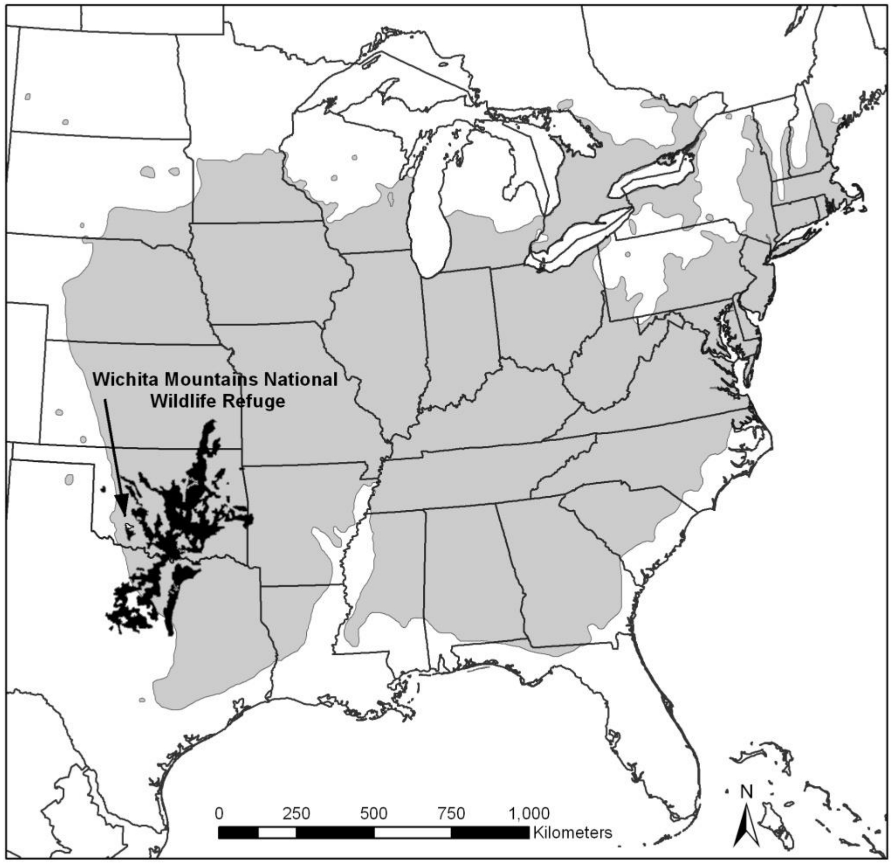

Figure 1.1. Map of eastern North America (http://nationalatlas.gov) showing the range of Eastern redcedar (*Juniperus virginiana*) in grey (Little, 1971) and the location of WMWR. The black polygon represents the Cross Timbers forest region (Kuchler, 1964).

In a repeat-measurement, dendro-ecological study examining vegetation change over a 50 year period in the Oklahoma Cross Timbers, DeSantis et al., (2011) found a major increase in ERC density and dominance throughout much of the region and concluded that fire suppression was the major proximate cause. In addition to increasing in density, ERC appeared to successfully compete with the dominant post oak and blackjack oak by rapidly recruiting and expanding into the canopy in absence of fire and following drought (DeSantis et al., 2011). Without frequent fire to stimulate root sprouting, oak regeneration decreased while ERC regeneration continued to increase (DeSantis et al., 2011). Physiologically, ERC can adapt to a wide range of light and moisture conditions and is both a sun obligate (Ormsbee et al., 1976) and shade tolerant, possessing the ability to photosynthesize under the canopy of dormant deciduous trees (Lassoie et al., 1983). These adaptations, among others, are perhaps key characteristics that have helped make it the most widespread conifer in eastern North America (Figure 1.1).

ERC is a long-lived species with a slow growth rate (Guyette et al., 1980). It has the capacity to reproduce and colonize areas rapidly in large numbers partly due to the widespread consumption and distribution of its cones by avian species (Holthuijzen et al., 1987). ERC is readily killed by fire when small (less than 1.5 m tall), but can resist low and even moderate intensity fire with increasing size (Engle and Stritzke, 1995). Drought is also a major control on ERC longevity in the xeric portion of its range where it is periodically killed by severe droughts (Rice and Penfound, 1959; Stambaugh, unpublished data).

This study represents an opportunity to examine changes in an eastern juniper species over time in a relatively intact landscape. The portion of the Cross Timbers within the WMWR is unique in its land use history in that it transitioned from Native American reservation land to a National Forest Reserve without undergoing the typical period of Euro-American settlement, logging, and cropping (Buck, 1964; Griffin et al., 2005; USFWS, 1985). Historic conditions or reference studies in intact ecosystems provide important information for understanding future land management in a changing environment (Hobbs and Harris, 2001; Whitlock et al., 2003). Specifically, the presence of native grazers (American bison, Rocky Mountain elk (*Cervus elaphus*), White-tailed deer (*Odocoileus virginianus*) and black-tailed prairie dogs (*Cynomys ludovicianus*)), and the maintenance of a prescribed fire regime on an un-plowed and largely un-logged landscape, represent conditions that are assumed to be more representative of historic structure and function of this ecosystem.

Two main hypotheses were investigated in this study:

Hypothesis 1: ERC density has increased on the landscape coincident with Euro-American settlement and refuge establishment.

Hypothesis 2: ERC age and spatial distribution are significantly correlated with topographic and vegetation variables.

CHAPTER 2

METHODS

Study Area Description

The study site is located in the Wichita Mountains Wildlife Refuge (WMWR) at the western edge of the Cross Timbers region of southwestern Oklahoma, Comanche County, USA (Fig. 2.1). In an ecotone spanning the dry, western prairie and humid, eastern deciduous forest, much of the woody vegetation in the Wichita Mountains occurs at the edge of its range. The WMWR serves as an important crossroads for eastern and western plant and animal species. Eastern deciduous species including sugar maple (*Acer saccharum*) and red mulberry (*Morus rubra*) occur here in small areas of mesic forest and riparian zones along with other minor refuge species including walnut (*Juglans microcarpa*), pecan (*Carya illinoinensis*), chinquapin oak (*Quercus muehlenbergii*), bur oak (*Quercus macrocarpa*), and Shumard oak (*Quercus shumardii*). Dominant trees are post oak, blackjack oak and eastern redcedar, and dominant grasses include little bluestem, big bluestem and hairy grama (Buck, 1964). The Endangered Black-capped vireo has a large breeding population in the scrub oak matrix, and the refuge is home to a managed herd of bison (*Bison bison*) and Rocky Mountain elk (*Cervus elaphus*).

Southwestern Oklahoma, encompassing the Wichita Mountains, is characterized by a continental, temperate climate with a mean annual temperature of 16.1 degrees Celsius (Period: 1895-2011; National Climatic Data Center, NCDC, Division 7, SW Oklahoma) and 78 cm average annual rainfall (period: 1914-2008; NCDC, 1999).

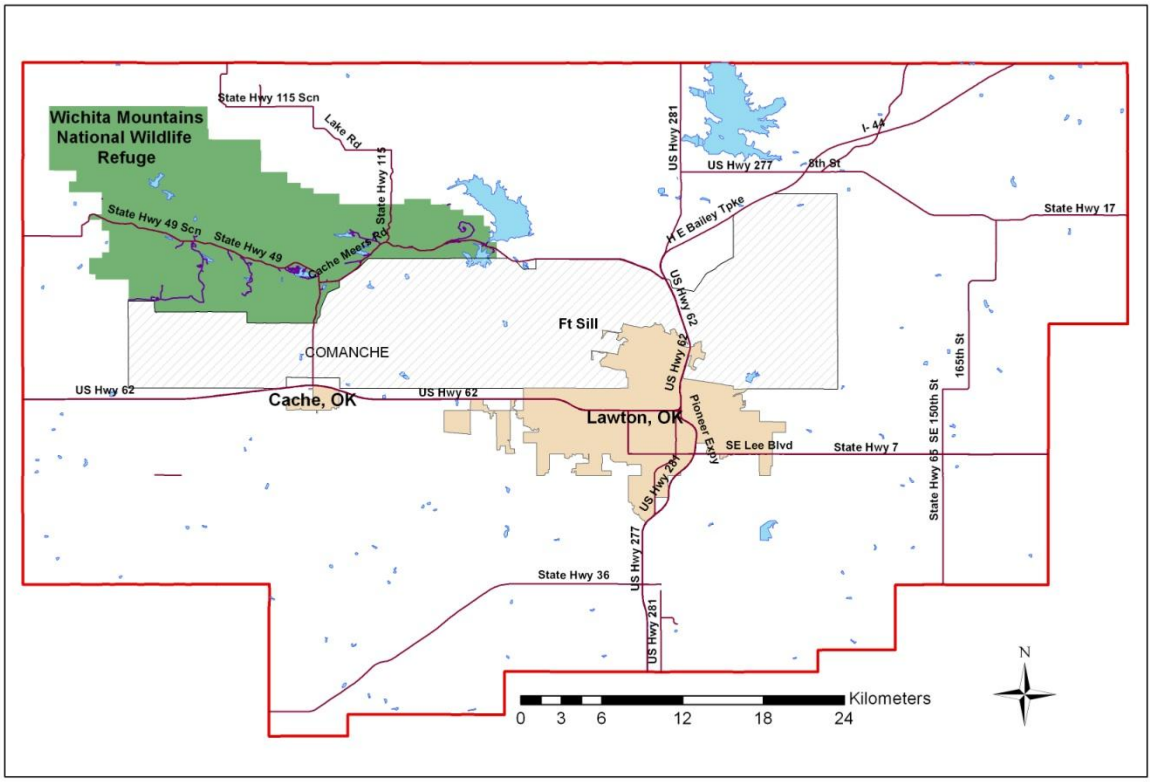

Figure 2.1 Map of Comanche County, Oklahoma showing the location of the Wichita Mountains Wildlife Refuge in proximity to nearby municipal areas and major highways.

Most precipitation occurs during the growing season (April- September), with the greatest rainfall quantities occurring in the spring (Dooley, 1983). Winter is typically the driest season, though 20th century winter precipitation means included an annual range of 12.7 to 17.8 cm of snow with periodic heavy wind and ice storms. Tornados can occur in spring, and severe hail storms occur near annually in spring (from 1945 – 1985) (USFWS, 1985).

The region is characterized by highly variable weather and consequently mean precipitation values may not be as descriptive or important to the vegetation as minimums and maximums. The refuge's weather records reveal a 107 cm difference in annual precipitation during the 20th century, recording 146.1 cm of precipitation in 1908, and only 38.3 cm in 1910 (USFWS, 1985). Though the 20th century mean annual rainfall is 78 cm (period: 1914-2008; NCDC 1999), refuge records include the following extremely dry years as receiving only 39.7 to 49.8 total cm of precipitation: 1939, 1948, 1954, 1963, 1970 (USFWS, 1985).

The Wichita Mountain chain is 97 kilometers long and 40 kilometers wide, and 30 by 15 kilometers of the range are encompassed by the wildlife refuge. The ancient, Paleozoic Era Wichita Mountains once stood more than 3,350 meters high. The boulders and decomposed soils present today are the remnant igneous core of these mountains, comprised primarily of granite, rhyolite, and gabbro (Buck, 1964). The mountains are characterized by a gradient of rocky soil conditions, from bare, rocky peaks to rough, stony soils and loams in the valley bottoms. Major vertical joints in rocks cause variation in water availability, which has influenced the distribution of vegetation with trees appearing to grow along "fault lines" generally of a NW/ SE orientation (Buck, 1964) (See inset photo, Figure 2.3).

Granite rock outcrop and granite rock derived soils comprise most of the refuge substrate. A1960 soil survey of the refuge by the Soil Conservation Service described 95% of the refuge as classified in the "Stoney rock land-Granite cobbly land" association, with 5% classified as "clay loam within the Foard-Tillman and Zaneis-Lawton-Lucien" soil association (USFWS, 1985). The "Stoney rock – Granite cobbly land" soil association is characterized by shallow to deep loamy soils with gravel and cobblestones, sustaining both mixed-grass prairie and oak woodlands. The mountain peaks and ridges are generally oriented in an east/west direction (Fig. 2.2). Elevations range from 411 m asl near the base of Mt. Scott in the SE to 756 m asl on Mt. Pinchot in the NW portion of the refuge (USFWS, 1985). Mountain peaks are surrounded by a matrix of mixed grass prairie with wooded lower slopes and creeks forming an intermediate zone between the relatively flat valley floor and the steep, rocky mountain peaks. Three land types: grassland, woodland, and rock outcrops, occupy 98.5% of the land cover of the refuge. The remaining 1.5% of the land area is occupied by roads, buildings, lakes and ponds (USFWS, 1985). What is today known as WMWR became a US National Forest Reserve in 1901 and in 1935 became part of the US Fish and Wildlife Refuge system (USFWS, 1985).

A Brief History of the Refuge, Summarized from the Wichita Mountains Wildlife Refuge Grassland Management Report (USFWS, 1985):

Exploration by Spanish and French explorers began as early as the mid 16th century, though earliest written accounts of the region date to the US Military "Marcy Expedition" of 1852. The Medicine Lodge Treaty was signed in 1867 delineating the Comanche and Kiowa Indian Reservation that encompassed the Wichita Mountains. Bison were eliminated from the area in 1870, and the refuge area was fenced for domestic livestock following the extirpation of bison. Both Native American tribes and Texas cattle ranchers grazed large numbers of domestic livestock on the refuge during this period. Refuge records indicated that some firewood tree cutting occurred, though the specific locations and extent were not documented: "…no less than 1200 cords of wood per year were being removed from the present day refuge for use on Fort Sill. In fact, so much timber had been cut from the area that the military had to cease its cutting and go far to the east to get sufficient firewood" (USFWS, 1985).

The refuge was designated the Wichita Forest Reserve in 1901 by President William McKinley, and the primary activity on the reserve was mining until the forest reserve was designated a National Game Preserve in 1905 when a plan to bring buffalo to the preserve was initiated. In 1907, 15 buffalo were brought to the refuge by rail, and the descendants of these animals comprise the present herd, which ranges between 450 – 900 animals. Intentionally heavy grazing by domestic cattle was used between 1906 and 1920 to reduce fire danger in areas surrounding the fenced, central pasture containing the buffalo.

ERC plantations were initiated for fence posts beginning in 1912 at 5 locations on the refuge. Historic accounts of "several hundred thousand robins and blackbirds" flying in and out of the mature ERC plantations during winter and early spring ostensibly consuming and then later spreading (via defecation) hundreds of thousands of juniper seeds across the landscape, may have influenced the local ERC population (USFWS, 1985).

In 1927 a small herd of Texas Longhorn Cattle (*Bos taurus*) was brought to the refuge to prevent the extinction of this breed. In the 1930's Civilian Conservation Corps (CCC) and Works Progress Administration (WPA) projects including roads, dams, and buildings were initiated throughout the refuge. In 1935 the Wichita Forest and Game Preserve was renamed the Wichita Mountains Wildlife Refuge and management was transferred from the Department of Agriculture to the Bureau of Biological Survey, which later came under the administration of the Department of the Interior and finally the US Fish and Wildlife Service. Domestic grazing was eliminated on the refuge by 1937 due in part to overgrazing and range degradation. From this point forward refuge management has been focused on the maintenance of buffalo, elk, deer, a Texas longhorn herd, and other wildlife species.

Frequent fire was observed by early explorers and settlers to the region, and was maintained by early settlers and miners during the refuge establishment period. Refuge records document a large fire in 1904, but little to no fire between 1904 and 1935 due to an intentional policy of overgrazing and active suppression on the Forest Reserve. Subsequent to the reserve transfer to a wildlife refuge, multiple wildfires of varying sizes burned annually some portion of the refuge between 1938 and 1976. From 1976 to the present, a combination of wildfire and prescribed fires has occurred near annually at some location on the refuge.

Plot Design

To address the major hypotheses of this study concerning the spatio-temporal expansion of ERC across the landscape, a randomized, fixed-radius plot design was used for quantifying topographic and biotic (e.g., plant community) variables and ERC ages. At the plots, an "oldest tree" sample method was used to identify the ERC establishment date at each site. Age sampling of the oldest trees per plot identifies the earliest ERC cohorts per plot location, though previous occupation and removal by disturbance of trees in the more distant past cannot be excluded from consideration of initial species establishment date (Tausch et al., 1981). In some cases, standing dead trees may have pre-dated the live trees in the plot, but they were not age sampled due to extreme difficulty in dating ERC lacking a known death date at the study site. Instead, standing dead trees were tallied by tree form/ age class (e.g., seedling, sapling, tree, strip bark), which provided a gross correlation with age and thus duration of ERC occupancy on the site.

Plot locations were randomly generated in a GIS (ArcView 3.2; ESRI) and allocated to three land types within the Special Use Area of the refuge: "rocky", "riparian" and "all". Once plot locations were randomly generated, point locations were realigned to the center of the associated 30m grid cell of the digital elevation model (DEM) used for mapping the refuge (USGS National Elevation Dataset; Gesch et. al., 2009). This position adjustment was made to align plot data with remotely sensed data so the circular sample plot (706 m^2) would cover the majority of a single, 30 x 30 m pixel (900 m^2).

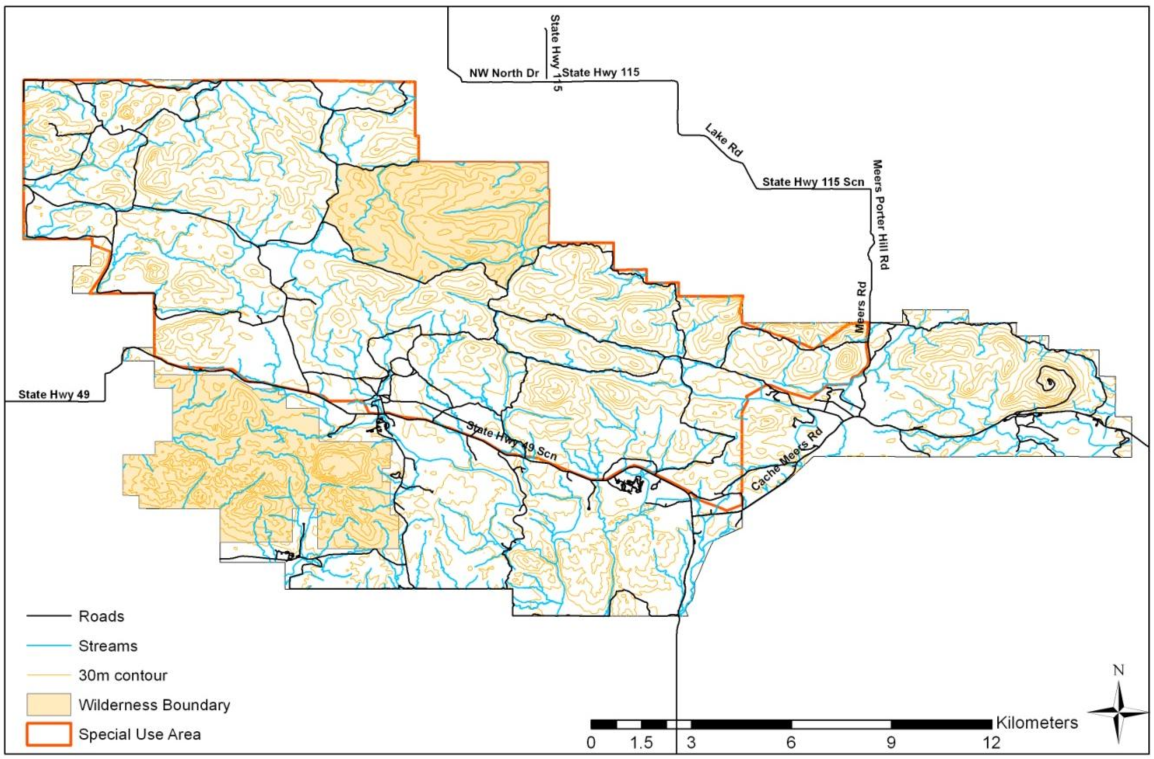

Figure 2.2 Map of the Wichita Mountains Wildlife Refuge showing the Special Use Area Boundary, road network, streams, and 30m contour intervals

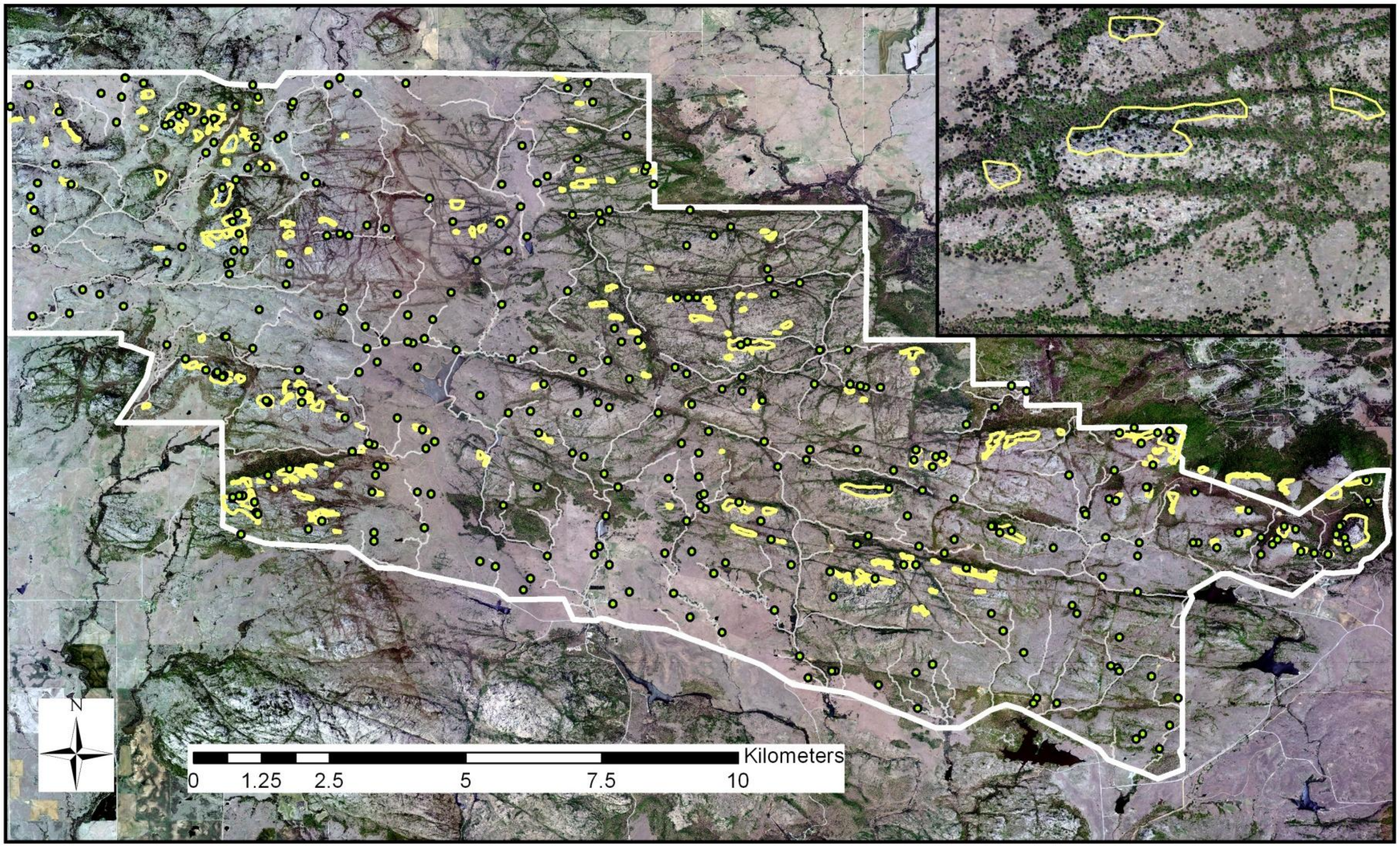

Figure 2.3 Aerial photo showing the Special Use Area with all sampled plots, creeks, and outlined rocky areas. Inset photo shows outlined rock outcrop area in yellow and the visible landscape pattern of vegetation establishing along "fault lines".

In the field, plot center points were located using a handheld Garmin GPS 60 Map CSX unit (3m accuracy) and verified using aerial photographs showing plot locations.

"Rocky" plots (n=100) were randomly located within polygons of rock outcrops that were visually digitized in a GIS using a 1m resolution aerial photo of the Special Use Area (Fig. 2.3). These areas were delineated because eastern redcedar is known to survive for centuries in rock outcrops, and these rocky areas occupy only 6% of the refuge land (USFWS, 1985). Similarly, multi-century aged ERC have been described in riparian zones or rocky creeks, so mapped riparian areas within the Special Use Area were obtained from the refuge. "Riparian" plots (n=100) were randomly located within one meter of a mapped riparian corridor in the GIS. "All" plots (n=200) were randomly distributed throughout the entire Special Use Area, across all land types.

For analysis, plots sampled in each of the target landscapes (rocky, riparian and all) were re-classified based on the vegetative cover measured at each plot. Dominant land-cover type thresholds were established for sampled plot areas using a modification of Hoagland's (2000) Oklahoma vegetation community type definitions, where:

1) Woodland plots were defined by having $\geq 25\%$ deciduous tree cover;
2) Grassland plots were defined by >25% combined grass and forb cover, and < 25% deciduous tree cover;
3) Rocky areas were defined by > 25% rock cover and < 25% deciduous or grassland cover.

Fig. 2.4 Photographs from the study area showing the mosaic of grassland, woodland and rocky areas characteristic of the Wichita Mountains.

Deciduous tree cover was used rather than total tree cover (including ERC) as part of the vegetation type definitions in an attempt to identify historic grassland and woodland land types independent of vegetation community changes resulting from recent juniper expansion.

Riparian plots, while having the common feature of a seasonal or permanent channel, did not have other unifying characteristics measured by this study and were best broadly described by the riparian area substrate or dominant land type of either rock, grassland or woodland. Of the total number of sampled plots initially located in rocky, riparian and random plot locations (n=343), 42% were woodland, 42% were grassland, and 16% were rocky.

Data Collected

Oldest ERC Age

Each of the three oldest live ERC trees on the plot was identified for age sampling based on visually detected tree characteristics. Three trees were sampled instead of one to increase the probability of capturing the oldest tree per plot and to increase the total sample size of ERC age by tree form. Older trees have morphological characteristics which enable their identification in the field including: crown dieback, twisted formation of tree stem and branches, partial cambial dieback (hereafter referred to as "strip-bark"), scarring, and stem rot (Stahle, 1996). Trees estimated to be older than 80 years were sampled with an increment borer, while trees estimated to be younger than 80 years were cut and a basal cross section was collected. The age threshold of 80 years was established by the WMWR out of stakeholder interest in protecting the oldest trees on the refuge. For each sample tree, the diameter (cm) at sample height, diameter (cm) at breast height, height (cm) of sample location above ground, total tree height (m), tree form class, tree sex, and nurse tree relationship (yes/ no) were recorded.

Tree forms were classified as follows:

Seedlings: <0.5 meter tall, and tallied into frequency classes per plot as follows: 0, 1-10, 11-100, 101-500, and 501-1,000.

Saplings; ≥0.5 meters tall and with a diameter at breast height (dbh) of < 5cm;

Trees; ≥5 cm dbh, and if ERC, not in the strip bark class;

Bush (ERC only); <1.37m tall, mature leaves/ cones, not of tree form/ poor apical dominance, low lying vegetation, diameter at base ≥7 cm;

Strip bark tree (ERC only); >1.37 meters tall, tree form, strip bark growth habit of tree bole;

All trees were recorded individually with the exception of seedlings.

"Nurse tree" refers to the tendency of ERC to grow in clusters around post oak trees in the Cross Timbers (Rykiel and Cook, 1986) and was recorded as a part of the overall objective to identify ERC establishment patterns on the landscape. This "nurse tree" or "pioneer tree" growth pattern has been documented in numerous plant community types, including in nearby mesquite-acacia savannah in Texas where expanding mesquite trees facilitate the establishment of other woody species in grasslands (Archer, 1988; Archer et al., 1989).

Tree Density Data

All live and dead stems of rooted tree species were tallied in the tree form classes described above. A basal area estimate by tree species was measured from plot center using a 10 factor prism. There was no diameter limit for tree inclusion in the basal area estimate. Tree species were defined as those woody plants listed as trees rather than shrubs or vines in the Field Guide to Oklahoma Plants (Tyrl et.al, 2008).

Topographic Relative Moisture Index (TRMI)

Plot slope was measured from plot center in degrees using a clinometer. Aspect was recorded from plot center using a standard, non-declination corrected compass and was transformed from a non-linear to a linear index using a cosine transformation (aspects convert from 0-359 degrees to a numeric index from 0 to 2) for use in multiple regression models (Beers, 1966). The topographic relative moisture index (TRMI) was developed for mountainous, mid-latitude areas of the Northern hemisphere and used to describe landform shape and plot-scale hydrologic dynamics based on a combination of slope position, slope shape, slope (in degrees) and aspect (Parker, 1982). Following Parker's (1982) methods, values of slope, aspect, topographic position and slope shape were assigned a numeric value with the lowest numbers representing the driest conditions, and progressively higher numbers representing wetter landscape locations. The TRMI ranges from 0 – 60 (Parker, 1982). For this study, 25 degrees or NNE represented the wettest landscape position (transformed aspect value=2), and 205 degrees or SSW represented the driest landscape position (transformed aspect value=0) (Parker, 1982).

Vegetation and Ground Cover

To describe the vegetation and ground cover composition in each plot, an estimate of percent ground cover was made for the entire plot area using standard area estimates as a guide (e.g., 1 x 7 meter coverage equals 1% of the plot, or 5 x 7 m coverage is equal to 5% of the plot, etc.). Dominant ground cover categories and definitions were:

- <u>Grass</u>: live and standing dead grasses or thatch covering the ground
- <u>Forb</u>: live and standing dead forb species covering the ground
- <u>Shrub</u>: woody, non-tree species covering the ground by rooted stem or live foliage
- <u>Litter</u>: detached, dead leaves and twigs from woody species covering the ground
- <u>Wood</u>: detached, dead woody stems and branches in contact with the ground
- <u>Tree</u>: area of live or dead rooted tree stem covering the ground (e.g., ground-level basal area)
- <u>Soil</u>: exposed bare soil not otherwise covered
- <u>Rock</u>: exposed bare rock not otherwise covered
- <u>Moss</u>: surface moss (generally growing on rock or bare soil)

In addition to the ground cover measurements, a separate measurement of aerial cover was made. This measurement reflects vegetation coverage of the plot as would be viewed from above and seen in an aerial photograph during leaf-on conditions. The purpose of this measurement was to match aerial photos or remotely sensed data with plot vegetation coverage. Coverage estimates included the previously defined ground cover classes and two additional cover classes:

- Deciduous cover: deciduous woody tree or shrub coverage; includes seedling, sapling and shrub cover
- Evergreen cover: evergreen woody tree or shrub coverage, primarily represented by ERC seedlings, saplings and trees

Additional Plot Measurements

Canopy cover was recorded using a concave spherical densiometer. An average canopy closure value was generated per plot by taking four measurements from plot center while facing: 0, 90, 180, and 270 degrees. Charcoal occurrence was noted within the plot and age of charcoal was not determined. From plot center, one photograph facing each cardinal direction was taken beginning with north and proceeding clockwise (N, E, S, W).

The majority of plots (n = 280) were sampled during leaf-on conditions (May-November), but due to fieldwork logistics, some plots (n=63) were sampled during leaf-off conditions. To ensure consistent data collection, measurements of aerial cover and canopy openness were recorded as if leaves were on by visually estimating leaf area of live trees when conducting crown openness measurements and cover estimates.

Topographic Roughness Index (TRI)

Variation in surface topography or "topographic roughness" can influence fire frequency and effect fire propagation (Stambaugh and Guyette, 2008). Topographic or surface roughness can be quantified using a topographic roughness index, calculated as a ratio of the measured landform shape to a flat surface of the same area (Stambaugh and Guyette, 2008). The Wichita Mountains topography consists of large areas of boulders, cliffs and cracks, which likely exert a strong influence on vegetation distribution (Buck, 1964). To quantify topographic variability within the plot area, slope measurements were collected along four transects from plot center in each cardinal direction: 0, 90, 180, 270 degrees. Looking down each transect, angles to three points were measured: 1) slope to transect end, 2) slope to the highest point on transect, 3) slope to the lowest point on transect. Slopes were recorded in degrees using a clinometer and distances to each point were recorded in meters using an OptiLogic Model 100LH laser rangefinder. An index of topographic roughness was created by calculating the slope distances for each transect and dividing the total transect slope distance by the flat transect distance (15m). This produced an index of deviation from horizontal with values that ranged from 0 (perfectly level or flat) to 2.15 at 80 degrees (maximum value observed). Indices of each transect were averaged to the plot level.

Solar Radiation

Solar radiation (exposure) was hypothesized to be a limiting factor for woody vegetation in this dry, forest-prairie ecotone, so solar radiation values were calculated for each 30 meter pixel in the study area. The Solar Radiation tool in the Spatial Analyst tool box was used in ArcMap 10 (ESRI) to generate a grid layer of solar insolation for the Special Use Area of the WMWR. The tool uses an algorithm to calculate direct and diffuse solar radiation for a given location based on the estimated "viewshed" as would be detected by an upward-facing hemispherical view from the given point or cell on a digital elevation model (DEM). Default settings and the latitude of the WMWR Headquarters were used to produce a map of average predicted annual solar radiation watt hours per square meter (wh/m^2) for each 30 meter grid cell.

Data Processing

Dendrochronological techniques

ERC samples were sanded to a polish using progressively finer sandpaper and dated using binocular magnification (40x) and standard dendrochronological techniques (Stokes and Smiley, 1996). An existing Wichita Mountains master ERC ring-width chronology served as the dating reference for ring-width pattern matching (Stambaugh et. al., unpublished data). Due to the profusion of intra-annual bands (false rings) (Edmondson, 2010), missing rings, highly irregular, lobed growth, and the short ring-width series available on most samples, the ERC samples for this study were not cross-dated but ring counted with a margin of error not estimated to exceed 5 years. Dating error was estimated to be less than 5 years due to the presence of marker years during the 20th century that aided with dating accuracy including: damage to rings from false spring events (known as "frost rings") (Stahle, 1990) and signature years identified using the master chronology (Stambaugh, unpublished data). Though not present in all samples frequently encountered false spring years were 1926, 1931 and 1987. In addition to use of the master chronology and frost rings, the following criteria were used for distinguishing true rings from intra-annual banding: abrupt transition in cell size at the ring boundary; uniformity of final band of latewood cells; relative size in relation to 3 preceding and succeeding rings; uniformity of cell wall circumference and thickness during transition from earlywood to latewood and at the ring boundary (Stokes and Smiley, 1996).

Age-Height Adjustment Methods

To enable adjustment from the age at sampling height to the age at the ground level, an age-height linear model was constructed by plotting the change in height versus the change in years, measured as the number of annual rings between sample heights, to get a linear model of age at height in centimeters above the ground. To construct this model, cross sections of ERC stems were obtained at ground level, and at several centimeters up the stem from 1 to 90 centimeters above the ground level. Both surfaces of the stem were prepared so that annual rings could be counted both at ground level, and at a known height above ground level. The resulting linear regression equation represented a model of height growth per year for young ERC trees, and was used to adjust sample pith dates to the pith date at the ground level, or true germination date (Fig. 2.5).

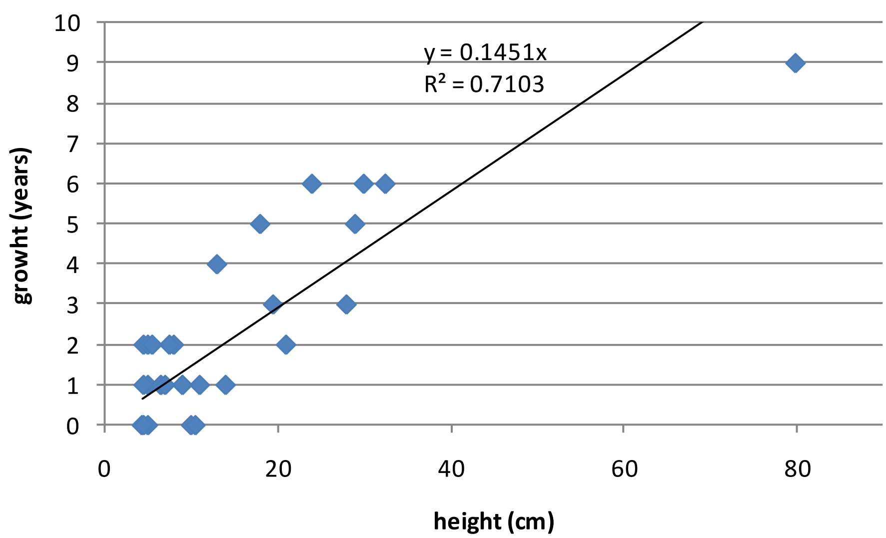

Figure 2.5. Age-height regression model constructed from 30 ERC samples.

Analysis Procedures

ERC Age distributions

To address Hypothesis 1, the ERC max age per plot frequency distribution was compiled for the entire study area and by dominant land type. A log-transformed linear model was fit to the oldest tree age frequency data to compare the frequency of establishment dates to an exponential model. Model fit was assessed by comparing the actual distribution to the model curve with 95% confidence intervals.

Tree Species Composition Summary Statistics

Density, basal area, relative density, dominance and importance value for each species was calculated for all plots and by land type. Sapling and tree density were calculated by expanding the tally of stems per plot in each size class to stems per hectare, and then calculating the mean number of stems per hectare per size class for each species and by land type. Basal area was converted from square feet per acre to square meters per hectare and then averaged per species and grouped by land type. Occurrence was calculated as the number of plots in which the species occurred divided by the total number of plots sampled, so the number represents the percent of plots in which the species occurred in any life form (seedling through mature or strip-bark live tree).

Tree species relative density and dominance were calculated as the ratio of one species total density (density) or basal area (dominance) to the total density or basal area of all species (Cottam and Curtis, 1956). Statistics were calculated for trees in mature tree growth form (e.g., not seedlings or saplings) as: density = total number of trees of one species / # trees of all species (*100); and, dominance = one species total basal area / all species total basal area (*100). The importance value for each species was calculated as the sum of density and dominance divided by two (Dooley, 1983). Data were presented for the study area as a whole, and grouped by dominant land type.

Eastern Redcedar Max Age Model

Environmental variables measured for each plot were evaluated as predictors of ERC maximum age (max age) in multiple regression models (Table 2.1). Scatter plots and Pearson correlation coefficients were used to assess the prediction capacity of each independent variable and its relationship with the response variable. Significantly correlated predictors ($p < 0.05$) were combined and the interaction variables were re-examined for correlation with the response variable. Log transformations of significant independent variables were tested in models to improve linearity between individual predictors and the response variable. Stepwise linear regression was used on all significantly correlated predictors to develop models. Models resulting from forward and backward procedures were compared. Significant ($p < 0.05$) predictors resulting from the stepwise analysis were further analyzed using generalized linear and multiple regression models. Multicollinearity was addressed by combining highly correlated variables and assessment of the Variance Inflation Factor (VIF) of each predictor. Final model selections were made by judging the model R-square values, significance of predictors and intercept, model stability through 31 re-sampling iterations, parsimony and biological relevance.

Table 2.1 Environmental variables measured or calculated at each plot

Variable name	Variable definition
Slope	Slope measured from plot center in degrees
Aspect	Cosine transformed aspect (Beers, 1966) 0 = 25° or SSW, 2 = 205° or NNE
Openness	Percent canopy openness, densiometer measurement from plot center
Elevation	Elevation in meters, measured using handheld GPS (Garmin)
TRMI	Topographic Relative Moisture Index (Parker, 1982); 0 = dry, 60 = wet
Solarrad	Solar radiation in watt hours/ m^2 (ArcMap 10, Spatial Analyst)
Percent Ground Cover	Plot coverage of major ground cover types
Prairie	Percent cover of grass + forb
Rock	Percent cover of bare rock
Wooded	Percent cover of litter + wood + tree
Rockprairie	Percent rock - percent prairie (< 0 = prairie, > 0 = rock)
Percent Aerial Cover	Plot coverage estimate as if viewing from the air
Aircovdecid	Percent of area covered by deciduous crown
Aircovevergreen	Percent of area covered by evergreen crown
TRI	Topographic Roughness Index (Stambaugh and Guyette, 2008)
Basal Area	Basal area estimate from plot center, 10 factor prism
Nonjuviba	Live basal area excluding *Juniperus virginiana* (JUVI)
Trees per Hectare	Stem count of all live trees in plot
Totalnonjuvitph	Stem count of all live trees excluding JUVI

Models were developed using the PROC REG, PROC GLM, PROC STEPWISE, PROC CORR procedures in SAS software version [9.2] (SAS Institute Inc., Cary, NC USA).

Eastern Redcedar Presence/ Absence Model

All topographic and biotic predictors were assessed in a classification and regression tree and logistic regression model to predict probability of ERC occurrence across the landscape. The CART analysis was used to identify predictor variables most strongly related to the binary response variable (ERC presence or absence), and the logistic model enabled modeling and mapping of predictive relationships. The classification and regression tree (CART) was created in the Party package (Hothorn et. al., 2006) in the R statistical environment (R Core Development Team, 2008) to identify statistically significant environmental variables and associated thresholds most strongly associated with ERC occurrence. The recursive partitioning algorithm in the 'ctree' package (Hothorn et. al., 2006) tests for independence between the covariates and the response variable and recursively selects the covariate most strongly associated with the response variable until the global null hypothesis of independence between the response variable and remaining covariates cannot be rejected at the specified alpha level (0.05). For each selected covariate, the best binary split is determined through linear modeling of the conditional distributions of each predictor and the response variable in a permutation test framework (Hothorn et .al, 2006).

To develop a model with quantitative, predictive power Spearman's rank correlation coefficients were used to identify significant ($p < 0.05$) relationships and to eliminate highly correlated predictor variables. Logistic models were attempted using all variables significantly correlated with the binary response variable and evaluated using the Akaike Information Criterion (AIC). Final model selection included evaluation of AIC scores, biological significance, and to a lesser degree, variable utility for predictive modeling. Logistic models were developed using PROC LOGISTIC using the descending option (ERC present = 1) and PROC CORR procedures in SAS software version [9.2] (SAS Institute Inc., Cary, NC USA).

Mapping ERC Max-Age and Presence Models

Layers of significant predictor variables of ERC presence and max age identified through regression modeling were organized within a Geographic Information System (GIS, ESRI) environment for use in developing a predictive map. To differentiate between rock, tree cover and grassland on the refuge, a supervised classification tool (ArcMap 10, ESRI) was used to identify and classify pixels of each land cover from a 1m resolution aerial photograph. To do this the user "trains" the classification tool on the ranges in each color band that represent the land cover of interest. From the training, pixel values are then classified into specified cover types (rock, tree or grassland) based on maximum likelihood classification methods within Spatial Analyst. Spatial Analyst (ArcMap 10) was used to reclassify the raster so each cell had a binary code for the land cover type of interest (e.g., 1 = rock cover and 0 = no rock cover). This process was repeated resulting in a rock cover raster, a prairie cover raster, and a tree cover raster. Data was then aggregated from one meter resolution to 30 meter resolution using the

Aggregate tool in Spatial Analyst (ArcMap 10, ESRI), to enable comparison between the calculated values and the plot data. To verify accuracy of classified rasters, the resulting raster values for each layer (rock, prairie and tree cover) were compared to actual measured values at a subset of plots using Pearson correlations and a paired t-test to determine the level of similarity between measured values and predicted values from the classified layer. This step increased confidence in the computer-classified images by determining they were not significantly different from the plot vegetation classifications.

Raster Calculator in the Spatial Analyst tool box was used to map the probability of ERC occurrence and the maximum age of ERC on the landscape. (ESRI, ArcMap 10, 2011). Both the linear and logistic regression models were mathematically applied to raster data layers to produce spatially explicit models of probability of ERC presence or predicted ERC age across the Special Use Area of the refuge.

CHAPTER 3

RESULTS

Summary Statistics of Environmental Variables

Means of environmental variables describe an open, oak woodland landscape (Table 3.1). Frequency distributions of landscape values measured were generally normally distributed with a few exceptions. For example, the mean value of percent canopy openness was 80; indicating that many plots had no overstory trees and that the measured landscape was generally open (Table 3.1). Steep slopes of up to 41 degrees occurred on the landscape, but the mean landscape slope value of 9 degrees described the relative dominance of gentler sloping hills and bottomlands across the landscape. Aspects were evenly sampled, as were landscape positions described by the topographic relative moisture index (TRMI) and solar radiation values (Table 3.1). Basal area averaged 8 square meters per hectare and reached a maximum of 46 square meters per hectare. Total stem densities averaged 2,389 stems per hectare with a maximum of 17,882 stems per hectare. Excluding seedlings, stem densities were much lower at 1,242 stems per hectare (average) and 10,554 stems per hectare (maximum) (Table 3.1).

The grassland land-cover type generally occurred on gentle slopes (mean slope = 6.4 degrees) at lower elevations and across all aspects (Table 3.2). The largest grassland expanses occurred in the bottomlands; though grasslands also stretched up hills and onto ridges. The mean TRMI value for grassland plots was slightly wetter than other

Table 3.1 Summary statistics for topographic and plant community features of all plots, n=343.

Variable name	Mean value	Std. Dev.	Min	Max
Slope (degrees)	9.9	8.2	0	41
Transformed Aspect	1.08	0.73	0	2
% Openness	80.6	28	1.3	99.8
Elevation (meters)	577.8	51.3	459	722
TRMI	34.7	10.5	6	59
Solar Radiation (watt hours/m^2)	53,819	10,306	16,957	78,594
% Ground Cover				
% Prairie	43.3	31	0	100
% Rock	37.5	29.1	0	98
% Wooded	10.2	15.6	0	86
Rock-Prairie	-5.8	56.9	-100	97.6
% Aerial Cover				
% Deciduous Cover	24.4	25.6	0	96
% Evergreen Cover	4.7	10.4	0	80
Max TRI	1.058	0.110	1.000	2.145
Mean TRI	1.027	0.047	1	1.524
Basal Area (m^2/hectare)	8.06	9.82	0	45.92
non-ERC Basal Area (m^2/hectare)	6.3	8.12	0	43.62
Stem Density (trees/hectare - TPH)	2,389	2,610	0	17,882
Non-ERC Stem Density (TPH)	2,049	2,341	0	17,641
Stem Density (TPH - excluding seedlings)	1,242	1,387	0	10,554
Non-ERC Stem Density (TPH - excluding seedlings)	1,092	1,301	0	10,554

Table 3.2 Summary statistics for topographic and plant community features of Grassland plots, n=145.

Variable name	Mean value	Std. Dev.	Min	Max
Slope (degrees)	6.4	5.3	0	25
Transformed Aspect	1	0.7	0	2
% Openness	97.3	9.2	21.6	99.8
Elevation (meters)	573.1	49.3	463	722
TRMI	36	10.3	7	57
Solar Radiation (watt hours/m^2)	56,015	6,653	35,744	72,587
% Ground Cover				
% Prairie	68.2	23.1	25	100
% Rock	23.2	21.9	0	67
% Wooded	1.4	2.7	0	16
Rock-Prairie	-45	43.9	-100	38
% Aerial Cover				
% Deciduous Cover	4.5	6.4	0	24
% Evergreen Cover	1.4	4.7	0	35
Max TRI	1.022	0.036	1.000	1.218
Mean TRI	1.01	0.015	1	1.084
Basal Area (m^2/hectare)	1.77	3.3	0	22.96
non-ERC Basal Area (m^2/hectare)	1.38	2.62	0	13.78
Stem Density (trees/hectare - TPH)	934	1,233	0	7,088
Non-ERC Stem Density (TPH)	816	1,077	0	7,088
Stem Density (TPH - excluding seedlings)	490	611	0	3,551
Non-ERC Stem Density (TPH - excluding seedlings)	450	593	0	3,551

land types, including generally more bottomland and concave slope positions. Mean solar radiation (watt hours per square meter) was higher for this land type than others due to the open, exposed nature of the grasslands. As expected, grassland areas were characterized by a high percent cover of grass and forbs, low to moderate rock cover, and very low woody plant cover.

Woodlands occurred on all aspects and varied slope positions, with the majority of woodlands occurring on low to moderate slopes (mean slope of 9.9 degrees) at generally lower elevations (Table 3.3). Woodlands occurred from bottomland positions to extreme rocky slopes characterized by the highest recorded TRI values on the landscape. Woodlands were characterized by a mean value of 55% tree cover, 30% grass ground cover, and 20% shrub, vine, litter and downed wood ground cover. Calculated solar radiation was moderate at woodland locations (mean of 53,964 watt hours/m^2) at an intermediate level between grassland (higher solar radiation) and rocky locations (lower solar radiation).

The rocky land type was characterized by the steepest slopes, least vegetative cover, highest rock cover and occurred at the highest elevations on the refuge (Table 3.4). Interestingly, some of these rocky positions receive the least solar radiation of all land types, likely due to the steepness and shading effect created by rock walls. Mean overstory tree and grassy understory cover were less than 12%, and mean rock cover was high at more than 74%. Within-plot topographic roughness was highest for this land type, as was overall plot slope (Table 3.4).

Table 3.3 Mean and summary topographic and plant community features for Woodland plots, n=144.

Variable name	Mean value	Std. Dev.	Min	Max
Slope (degrees)	9.9	8.2	0	41
Transformed Aspect	1.1	0.7	0	2
% Openness	64	30.1	1.3	99.8
Elevation (meters)	569.6	50.4	459	703
TRMI	36.1	9.7	14	58
Solar Radiation (watt hours/m^2)	53,964	10,279	17,116	76,353
% Ground Cover				
% Prairie	30.3	23.6	0	90
% Rock	38.1	26.9	0	89
% Wooded	20.6	18.9	0	86
Rock-Prairie	7.8	45.9	-90	87.8
% Aerial Cover				
% Deciduous Cover	49	19.1	25	96
% Evergreen Cover	5.9	10.1	0	65
Max TRI	1.063	0.139	1.000	2.145
Mean TRI	1.028	0.057	1	1.524
Basal Area (m^2/hectare)	15.19	10	0	45.92
non-ERC Basal Area (m^2/hectare)	12.81	8.57	0	43.62
Stem Density (trees/hectare - TPH)	4,240	2,765	0	17,882
Non-ERC Stem Density (TPH)	3,709	2,599	0	17,641
Stem Density (TPH - excluding seedlings)	2,230	1,543	0	10,554
Non-ERC Stem Density (TPH - excluding seedlings)	1,967	1,511	0	10,554

Table 3.4 Mean and summary topographic and plant community features for Rocky plots, n=54.

Variable name	Mean value	Std. Dev.	Min	Max
Slope (degrees)	18.8	7.9	0	37
Transformed Aspect	1.2	0.8	0	2
% Openness	80	30.6	1.3	99.8
Elevation (meters)	611.9	45.5	509	698
TRMI (0 - 60)	26.9	9.7	6	59
Solar Radiation (watt hours/m^2)	50,050	15,822	20,788	78,594
% Ground Cover				
% Prairie	11.5	7.5	0.2	25.2
% Rock	74.2	16.7	25	98
% Wooded	6	7.9	0	35
Rock-Prairie	62.7	21.5	10	97
% Aerial Cover				
% Deciduous Cover	7.2	6.3	0	20
% Evergreen Cover	10.9	18	0	80
Max TRI	1.144	0.108	1.004	1.417
Mean TRI	1.068	0.049	1.002	1.188
Basal Area (m^2/hectare)	6.08	8.6	0	41.33
non-ERC Basal Area (m^2/hectare)	2.3	3.43	0	11.48
Stem Density (trees/hectare - TPH)	1,358	1,741	0	8,262
Non-ERC Stem Density (TPH)	932	1,037	0	4,768
Stem Density (TPH - excluding seedlings)	627	617	0	2,759
Non-ERC Stem Density (TPH - excluding seedlings)	482	471	0	1,811

Tree Summary Statistics

Tree species composition was dominated by post oak, blackjack oak and eastern redcedar, which occurred on 59% - 67% of all surveyed plots (Table 3.5). Eastern redcedar (ERC) was the most ubiquitous tree species occurring at 67% of all plots, though its relative dominance was less than half that of post oak, due to its smaller average diameter. Blackjack oak occurred at the highest density but was low in dominance due to small tree sizes and resulting low basal area. Post oak dominated the tree species composition with the largest relative basal area and a similar density to the other dominant species, resulting in the highest importance percentage (Table 3.5). Many other deciduous forest species occurred at low densities throughout the study area, with all tree species outside of the dominant post oak, blackjack oak and eastern redcedar occurring at a relative density of 2% or less. All tree species detected were represented both as trees and saplings suggesting that all tree species present were actively reproducing. Two woody species, hackberry (*Celtis laevigata*) and gum bumelia (*Sideroxylon languinosum*), were widely represented at plots as saplings, but were uncommon as trees. Other minor trees detected at 5% or more of sampled plots included: elm (*Ulmus spp.*), ash (*Fraxinus spp.*), walnut (*Juglans spp.*), maple (*Acer spp.*) and Shumard oak (*Quercus shumardii*).

In woodland plots, ERC and blackjack oak occurred in 88% of plots, and post oak occurred in 85% of plots. Additional genera/ species occurring mostly as saplings in woodland plots included (with percent occurrence in parentheses): hackberry (*Celtis spp.*) (74%), gum bumelia (*Sideroxylon languinosum*) (40%), elm (38%), ash (10%), walnut (12%), and Shumard oak (16%) (Table 3.6).

Table 3.5 . Woody species importance, density, dominance and occurrence for all plots surveyed (n=343). Summary values are reported for trees unless noted as saplings. Percent species occurrence describes the presence or absence of the species in all life forms (e.g., seedling, sapling, tree etc). Other minor tree species occurring on less than 1% of all plots included: hawthorn (*Crataegus spp*)., persimmon (*Diospyros virginiana*), honey locust (*Gleditsia triacanthos*) and red mulberry (*Morus rubra*).

Genus/ Species	Common Name	Importance Percentage	Relative Density	Relative Dominance	Percent Occurrence	Saplings ha^{-1} mean (range)	Trees ha^{-1} mean (range)	Basal Area (m^2 ha^{-1}) mean (range)
Quercus stellata	Post oak	39	30	47	59	115 (0 - 2,971)	92 (0 - 863)	4 (0 - 44)
Quercus marilandica	Blackjack oak	27	36	19	64	474 (0 - 9,493)	110 (0 - 1,174)	2 (0 - 23)
Juniperus virginiana	Eastern redcedar	22	21	22	67	84 (0 - 1,217)	66 (0 - 1,103)	2 (0 - 37)
Ulmus spp.	Elm	3	2	4	25	23 (0 - 679)	6 (0 - 325)	<1 (0 - 16)
Acer spp.	Maple	2	2	1	5	23 (0 - 1,938)	8 (0 - 891)	<1 (0 - 14)
Juglans spp.	Walnut	2	1	2	9	11 (0 - 1,259)	4 (0 - 113)	<1 (0 - 9)
Celtis spp.	Hackberry	1	2	1	56	80 (0 - 2,122)	7 (0 - 170)	<1 (0 - 2)
Fraxinus spp.	Ash	1	2	1	8	14 (0 - 1,415)	5 (0 - 297)	<1 (0 - 14)
Quercus muehlenbergii	Chinquapin oak	1	1	1	2	2 (0 - 283)	2 (0 - 283)	<1 (0 - 14)
Carya illinoinensis	Pecan	1	1	1	1	4 (0 - 821)	2 (0 - 424)	<1 (0 - 9)
Quercus shumardii	Shumard oak	1	1	<1	9	12 (0 - 707)	3 (0 - 142)	<1 (0 - 5)
Quercus macrocarpa	Bur oak	<1	<1	1	1	1 (0 - 227)	1 (0 - 184)	<1 (0 - 9)
Sapindus saponaria	Soapberry	<1	<1	<1	2	11 (0 - 2,829)	2 (0 - 283)	<1 (0 - 7)
Sideroxylon lanuginosum	Gum bumelia	<1	1	<1	24	24 (0 - 1,556)	2 (0 - 156)	<1 (0 - 2)

Post oak was the dominant tree in woodland stands, as described by its basal area, relative dominance and importance percentage (Table 3.6). Blackjack oak and ERC followed in order of importance, with blackjack oak having a high stem density but low basal area. Blackjack oak saplings were particularly dense, at a rate of more than four times the density of blackjack trees. The majority of blackjack saplings apparently originated as stump sprouts, appearing in clusters around mature or dead trees, rather than appearing singly as individuals of apparent seed origin. ERC was present in nearly all plots, but was least important in terms of density and basal area, and was represented largely by seedlings, saplings and small trees. All woodland tree species (listed in Table 3.6) were represented by a higher density of saplings than mature trees.

Woody composition in the grasslands was relatively sparse. Trees occurred at 41% or fewer plots at a mean density not exceeding 98 trees per hectare (excluding seedlings and saplings). Due to the generally small stature of the woody stems present in grasslands, the average basal area across all grassland plots was low at two square meters per hectare or less (Table 3.7). Post oak was the most important woody species in terms of density and dominance though blackjack oak was more numerous in terms of sapling and tree stem density. ERC was the most widely distributed tree occurring at 40% of plots, though was the lowest in density of the three dominants. Blackjack oak and ERC were more numerous as saplings than trees, with an average sapling density of 23 saplings per hectare for ERC and 153 saplings per hectare for blackjack oak. Hackberry, elm and gum bumelia were the only non-dominant woody species detected at more than 10% of woodland plots, and were largely present as saplings.

Table 3.6 . Woody species importance, density, dominance and occurrence for woodland plots (n=144). Summary values are reported for trees unless noted as saplings. Percent species occurrence describes the presence or absence of the species in all life forms (e.g. seedling, sapling, tree etc). Other minor tree species occurring on less than 1% of all plots included: hawthorn (*Crataegus spp*)., persimmon (*Diospyros virginiana*), honey locust (*Gleditsia triacanthos*) and red mulberry (*Morus rubra*).

Genus/ Species	Common Name	Importance Percentage	Relative Density	Relative Dominance	Percent Occurrence	Saplings ha^{-1} mean (range)	Trees ha^{-1} mean (range)	Basal Area (m^2 ha^{-1}) mean (range)
Quercus stellata	Post oak	42	31	52	85	228 (0 - 2,971)	172 (0 - 863)	8 (0 - 44)
Quercus marilandica	Blackjack oak	26	36	16	88	900 (0 - 9,493)	199 (0 - 1,174)	3 (0 - 23)
Juniperus virginiana	Eastern redcedar	10	19	1	88	159 (0 - 1,217)	101 (0 - 1,103)	2 (0 - 30)
Ulmus spp.	Elm	3	2	3	38	38 (0 - 679)	10 (0 - 325)	1 (0 - 16)
Acer spp.	Maple	2	3	2	7	52 (0 - 1,938)	16 (0 - 891)	<1 (0 - 14)
Juglans spp.	Walnut	2	1	2	12	17 (0 - 1,259)	5 (0 - 113)	<1 (0 - 9)
Celtis spp.	Hackberry	1	2	<1	74	112 (0 - 2,122)	12 (0 - 170)	<1 (0 - 2)
Fraxinus spp.	Ash	1	1	1	10	16 (0 - 665)	8 (0 - 297)	<1 (0 - 14)
Quercus muehlenbergii	Chinquapin oak	1	1	1	3	5 (0 - 283)	5 (0 - 283)	<1 (0 - 14)
Carya illinoinensis	Pecan	1	1	1	3	9 (0 - 821)	5 (0 - 424)	<1 (0 - 9)
Quercus shumardii	Shumard oak	1	1	0	16	26 (0 - 707)	6 (0 - 142)	<1 (0 - 5)
Quercus macrocarpa	Bur oak	1	<1	1	2	3 (0 - 226)	3 (0 - 184)	<1 (0 - 9)
Sapindus saponaria	Soapberry	<1	1	<1	3	26 (0 - 2,829)	3 (0 - 283)	<1 (0 - 7)
Sideroxylon lanuginosum	Gum bumelia	<1	1	<1	40	48 (0 - 1,556)	4 (0 - 156)	<1 (0 - 2)

Table 3.7. Woody species importance, density, dominance and occurrence for grassland plots (n=145). Summary values are reported for trees unless noted as saplings. Percent species occurrence describes the presence or absence of the species in all life forms (e.g. seedling, sapling, tree etc). Other minor tree species occurring on less than 1% of all plots included: hawthorn (*Crataegus spp*)., persimmon (*Diospyros virginiana*), honey locust (*Gleditsia triacanthos*) and red mulberry (*Morus rubra*).

Genus/ Species	Common Name	Importance Percentage	Relative Density	Relative Dominance	Percent Occurrence	Saplings ha^{-1} mean	(range)	Trees ha^{-1} mean	(range)	Basal Area (m^2 ha^{-1}) mean	(range)
Quercus stellata	Post oak	38	33	42	37	33	(0 - 523)	33	(0 - 354)	1	(0 - 9)
Quercus marilandica	Blackjack oak	27	40	13	37	156	(0 - 2,193)	39	(0 - 566)	<1	(0 - 5)
Juniperus virginiana	Eastern redcedar	19	15	23	40	23	(0 - 538)	15	(0 - 382)	<1	(0 - 9)
Ulmus spp.	Elm	7	3	11	20	15	(0 - 424)	3	(0 - 113)	<1	(0 - 7)
Acer spp.	Maple	<1	0	0	<1	0		0		0	
Juglans spp.	Walnut	4	2	6	6	6	(0 - 707)	2	(0 - 85)	<1	(0 - 5)
Celtis spp.	Hackberry	2	2	1	41	53	(0 - 806)	2	(0 - 71)	<1	(0 - 2)
Fraxinus spp.	Ash	3	2	3	7	7	(0 - 283)	2	(0 - 141)	<1	(0 - 5)
Quercus muehlenbergii	Chinquapin oak	0	0	0	0	0		0		0	
Carya illinoinensis	Pecan	0	0	0	0	0		0		0	
Quercus shumardii	Shumard oak	1	<1	1	3	1	(0 - 113)	<1	(0 - 14)	<1	(0 - 2)
Quercus macrocarpa	Bur oak	0	0	0	0	0		0		0	
Sapindus saponaria	Soapberry	<1	<1	0	1	<1	(0 - 42)	<1	(0 - 42)	0	
Sideroxylon lanuginosum	Gum bumelia	<1	<1	0	11	5	(0 - 170)	<1	(0 - 14)	0	

Table 3.8. Woody species importance, density, dominance and occurrence for rocky plots (n=54). Summary values are reported for trees unless noted as saplings. Percent species occurrence describes the presence or absence of the species in all life forms (e.g. seedling, sapling, tree etc). Other minor tree species occurring on less than 1% of all plots included: hawthorn (*Crataegus spp*)., persimmon (*Diospyros virginiana*), honey locust (*Gleditsia triacanthos*) and red mulberry (*Morus rubra*).

Genus/ Species	Common Name	Importance Percentage	Relative Density	Relative Dominance	Percent Occurrence	Saplings ha^{-1} mean (range)	Trees ha^{-1} mean (range)	Basal Area ($m^2\ ha^{-1}$) mean (range)
Quercus stellata	Post oak	18	17	20	46	35 (0 - 538)	36 (0 - 269)	1 (0 - 12)
Quercus marilandica	Blackjack oak	20	28	13	74	189 (0 - 140)	6 (0 - 608)	1 (0 - 12)
Juniperus virginiana	Eastern redcedar	54	46	62	80	45 (0 - 439)	86 (0 - 736)	4 (0 - 37)
Ulmus spp.	Elm	<1	0	0	7	5 (0 - 226)	<1 (0 - 28)	0
Acer spp.	Maple	1	2	0	9	6 (0 - 255)	5 (0 - 241)	0
Juglans spp.	Walnut	2	2	1	11	12 (0 - 410)	5 (0 - 71)	<1 (0 - 2)
Celtis spp.	Hackberry	2	3	1	52	67 (0 - 707)	7 (0 - 99)	<1 (0 - 2)
Fraxinus spp.	Ash	1	1	1	6	29 (0 - 142)	3 (0 - 142)	<1 (0 - 2)
Quercus muehlenbergii	Chinquapin oak	0	0	0	0	0	0	0
Carya illinoinensis	Pecan	0	0	0	0	0	0	0
Quercus shumardii	Shumard oak	<1	<1	0	7	5 (0 - 113)	1 (0 - 57)	0
Quercus macrocarpa	Bur oak	0	0	0	0	0	0	0
Sapindus saponaria	Soapberry	<1	<1	1	2	0	0	<1 (0 - 2)
Sideroxylon lanuginosum	Gum bumelia	<1	<1	0	17	13 (0 - 467)	<1 (0 - 14)	0

Trees in rocky land types were dominated by ERC in terms of relative dominance, density and importance values (Table 3.8). ERC occurred at 80% of rocky plots, with an average basal area of four square meters per hectare and a density of 86 trees per hectare (excluding seedlings and saplings). Departing from the trend for all woody species in all other land types, ERC trees in rocky areas outnumbered ERC saplings. Post oak saplings and trees occurred at a similar density as in grasslands, and post oak occurred at only 1/5th of its woodland density in the rocky land type. Blackjack oak was the second most important species following ERC at a greater density of saplings than the density of all other species in the sapling class. Other frequently encountered minor species included hackberry and gum bumelia.

ERC Max Age Distributions

The age distribution of oldest ERC samples across the study area was heavily dominated by 20th century trees (Figure 3.1). While trees dated back into the late 15th century, only 3% of sampled trees pre-dated 1800 CE. The exponential-like increase in cohort size during the past two centuries displays step-up increases during three distinct time periods (Figure 3.2). A relatively stable population over time of few, long-lived individuals occurs in the record from the late 15th century to the mid 19th century. Beginning in approximately 1840 CE, ERC cohort sizes approximately doubled in 30 to 50 year intervals: from 1840 to 1870; 1900 to 1930; and 1950 to 2000 (Figure 3.1). The first major cohort showing an increase from the observed background frequency occurred in the 1840's, and the 1850 and 1860 cohorts continued to retain more individuals than

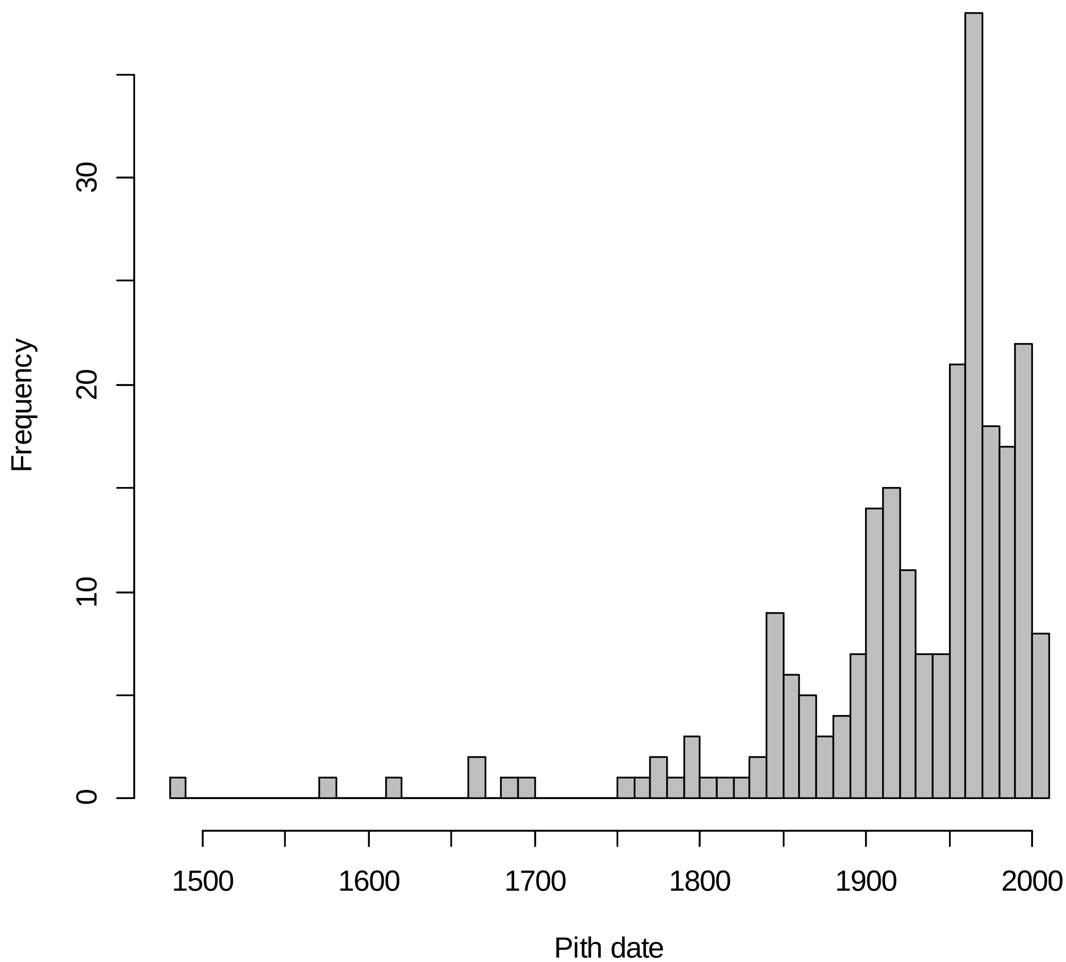

Figure 3.1 Frequency histogram of maximum ERC age per plot, n=232 trees, in 10 year age bins

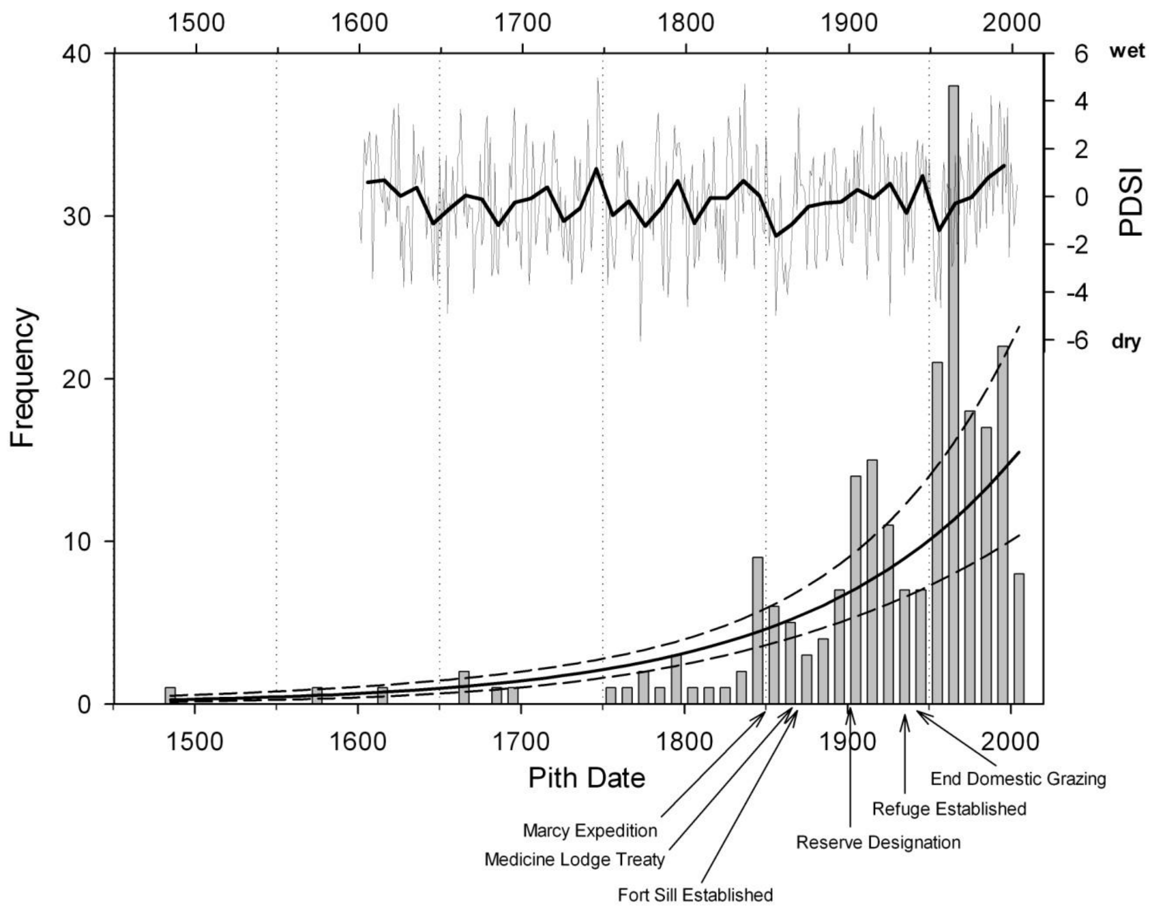

Figure 3.2 Frequency histogram of ERC pith dates showing an exponential growth model (solid line) with 95% confidence intervals (dotted lines); annual reconstructed Palmer Drought Severity Index (PDSI) (grey line) in the upper right with an 11 year centered average (dark line); and arrows to important anthropogenic events.

existed in the three centuries prior to 1840. The period from 1750 to 1850 was marked by tribal displacement and movement and increasing conflict between Native Americans and the US military. By the time of the Marcy Expedition in 1852 bison numbers had been severely reduced regionally (Marcy, 1854), and Fort Sill, bordering the present day refuge, was established in 1870. Climatically, the 1840's follow a wetter than average period from approximately 1825-1840 (Figure 3.2). Annual mean precipitation declined in the late 1840's and was followed by the severe Civil War drought from 1855 – 1862 (PDSI, Cook et.al., 2004; Stambaugh et. al., 2009) (Figure 3.2).

Following the Civil War drought in the 1850's and 1860's, cohort sizes increased again in the 1890's and through the first two decades of the 20th century. This increase in cohort sizes from the 1890's into the 1920's corresponded with a period of wetter conditions following the Civil War drought which persisted through several decades (notwithstanding a severely dry year in the mid 1920's) up until the severe droughts of the mid 1930's and mid 1950's. Cohort frequencies appeared to broadly fit these climatic trends in precipitation and drought, with cohort sizes increasing during wetter decades, and stabilizing during drought periods (Fig. 3.2). Anthropogenic events coinciding with changes in the ERC cohort frequency include: movement and displacement of tribes, conflict with Euro-American settlers and removal of native grazers, addition of cattle and domestic grazers, and changes in the historic fire frequency. Based on a fire history site analyzed in the central portion of the refuge (Stambaugh et al., 2009), changes to the fire regime included a period of increased fire frequency from a mean fire interval (MFI) of 4.4 years for the period from the 1750's to 1901, to an MFI of 1.7 years from 1855 to 1880. Following refuge establishment in 1901, the MFI lengthened to 5.2 years and fire severity, based on percentage of trees scarred, decreased. During the 250 year long period of record, the interval between fires ranged from 1 to 17 years, with the longest fire free intervals occurring during the 20th century (Stambaugh et al., 2009).

Patterns of cohort frequency distributions for grasslands, woodlands and rocky areas showed a similar overall pattern of 20th century increase in ERC abundance, though, the rocky land type appeared to host the most even distribution of age classes approximating what might be described as an uneven or old growth age distribution in which the rates of reproduction and mortality appear relatively constant over time (Figure 3.3). The rocky land type hosted trees defined as old growth for this region (exceeding 250-300 years of age) by Therrell and Stahle (1998) whereas grassland and woodland age distribution curves were more heavily dominated by younger trees and tree ages that did not extend back in time much beyond 200 years. The mean rocky land-type ERC age was 145 years, while the mean woodland ERC age was 79, and the mean grassland ERC age was 48 (Table 3.9). Twenty percent of the rocky plots visited had no ERC present.

Table 3.9. Mean ERC ages by land type (n=232)

Land Type	Mean	Std. Dev.	Min	Max	N
Grassland	48	36	6	170	57
Woodland	79	57	7	311	130
Rocky	145	117	5	522	45
All Plots	84	76	5	522	232

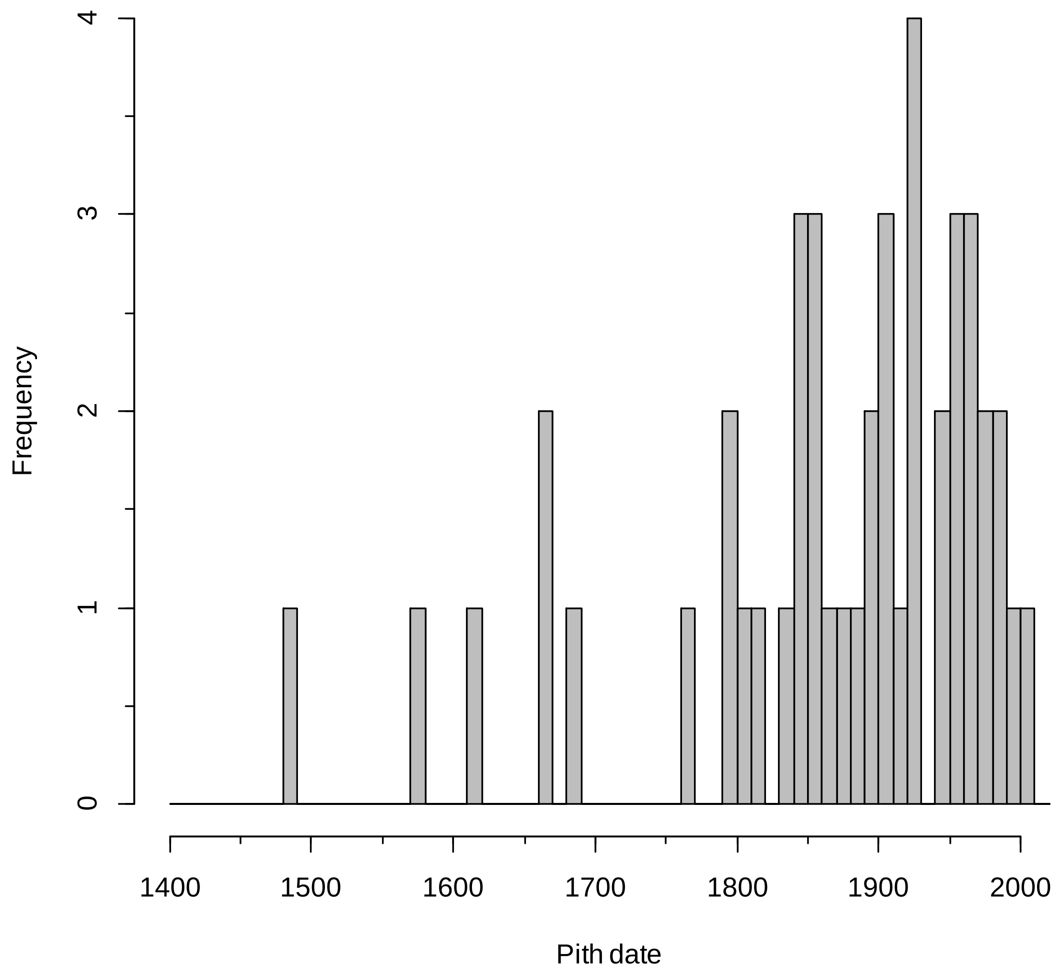

Figure 3.3. Frequency histogram of maximum ERC age per plot in rocky plots in 10 year age bins

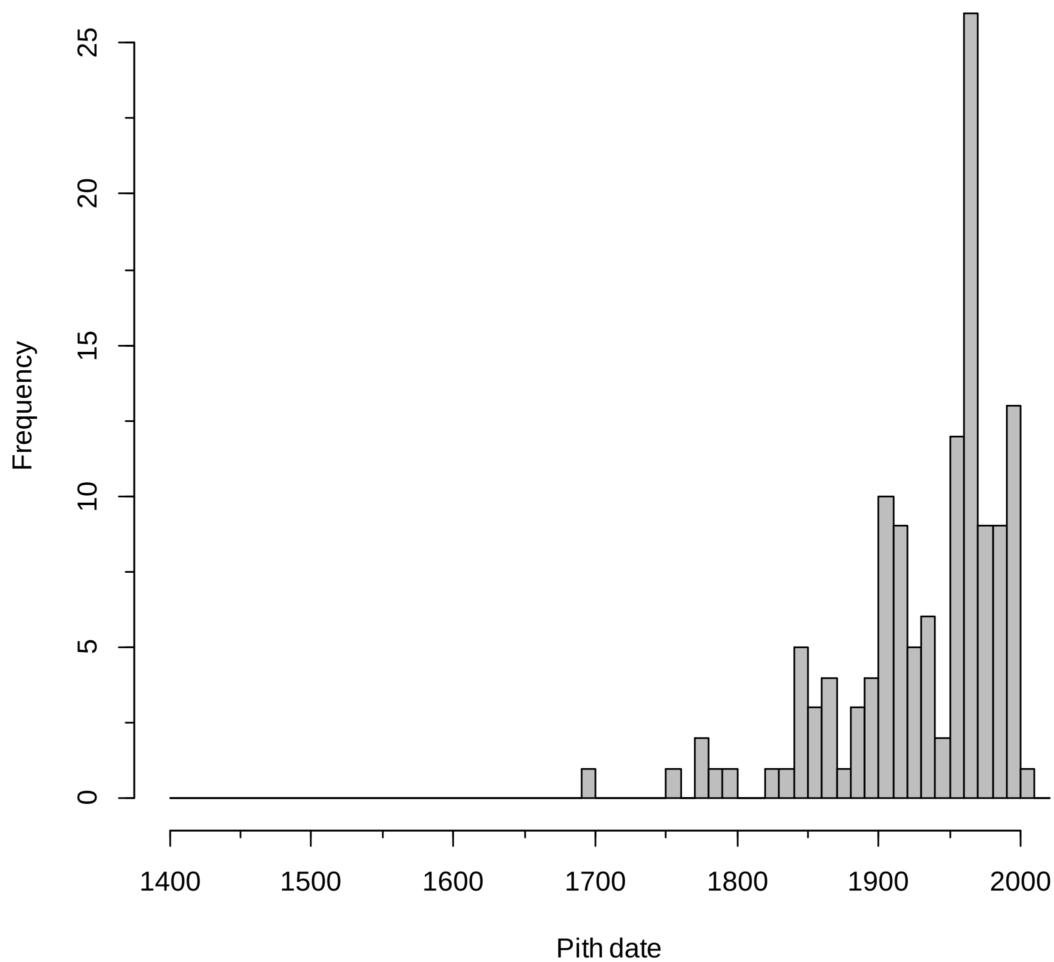

Figure 3.4. Frequency histogram of maximum ERC age per plot in Woodland plots in 10 year age bins

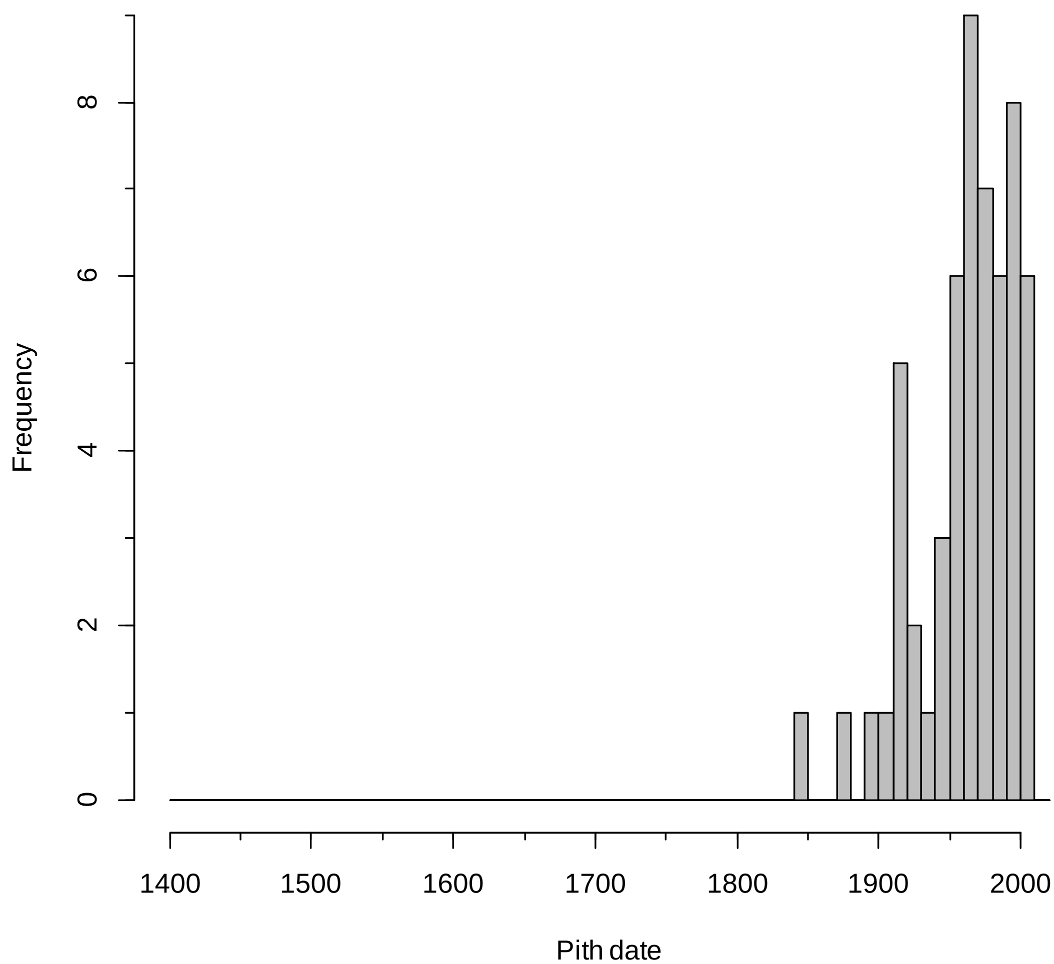

Figure 3.5 Frequency histogram of maximum ERC age per plot in Grassland plots in 10 year age bins

The woodland land type does host some older trees, but those individuals with pith dates prior to 1799 occurred in areas of high percent rock ground cover (51-84%) that were classified as wooded due to the tree cover present. Of all woodland plots sampled, 88% had some ERC present. Mean age in the woodland land type was 79 years, with a youngest age of 7 years and oldest of 311 years (Table 3.9). In the woodland, similar to the overall age distribution, ERC cohort frequencies increased in the 1840's, again at the turn of the 20th century, decreased in the 1940's, and increased again in the 1950's and dramatically increased in the 1960's, before leveling off in the late 20th century (Figure 3.4).

ERC was absent from 60% of the grassland plots visited, and of the 40% of grassland plots with ERC present, trees originated almost entirely from the 20th century with only 3 individual trees pre-dating 1900 CE (Figure 3.5). The mean age in the grassland land-type was 48 years, with a min of 6 years and a max of 170 years (Table 3.9). ERC recruitment increased between 1910 and 1920, but the largest recruitment period occurred between 1950 and the present. Recruitment and persistence appears relatively even and constant during the past 50 years. As was true in the woodland land-type, the 1960's cohort was the largest.

Table 3.10. Mean and summary statistics for ERC age per growth form, n = 606

Tree Form	Mean	Std. Dev.	Min	Max	N
Seedling	5	2	1	7	14
Sapling	21	9	6	50	151
Tree	73	37	14	233	368
Bush	44	17	24	78	8
Strip Bark	174	98	51	522	65

ERC Max Age Model

Results of a correlation analysis of maximum ERC age and the measured environmental variables identified significant ($p < 0.05$) positive correlations between ERC maximum age (max age) and: slope, aspect, elevation, percent rock, rockprairie, aircovevergreen, and mean TRI. Significant negative correlations were identified between max age and solar radiation, prairie, TRMI, and total trees per hectare excluding ERC (totalnonjuvitph) (Table 3.11; for variable definitions see Table 2.2). Due to the strong, negative correlation between percent prairie and percent rock ground cover, those variables were differenced, resulting in the rockprairie variable, which was highly correlated and significant with ERC max age (Table 3.11, Fig.3.6). The variable rockprairie showed a positive, linear increase with maximum ERC ages as higher numbers described increasing percent rock ground cover (and decreased prairie ground cover) (Fig 3.6). Similarly, max age increased with increasing slope (degrees)

Table 3.11. Pearson correlations between environmental variables and ERC maximum age.

Variable	r	Pr > t	n
Slope	0.48	<0.0001	231
Aspect	0.21	0.001	232
Elevation	0.27	<0.0001	233
TRMI	-0.19	0.0034	231
Solarrad	-0.35	<0.0001	232
Prairie	-0.46	<0.0001	232
Rock	0.47	<0.0001	232
Rockprairie	0.5	<0.0001	232
Aircovevergreen	0.24	<0.0001	223
Mean TRI	0.38	<0.0001	233
Totalnonjuvitph	-0.13	0.0437	233

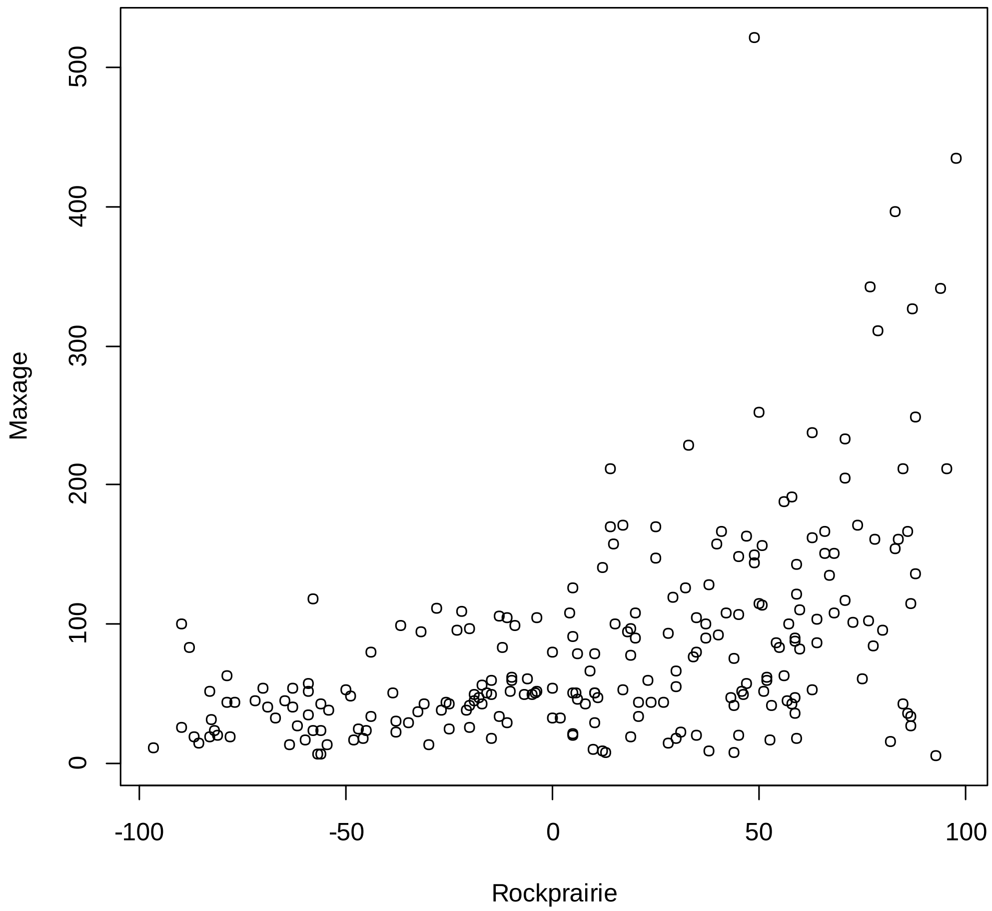

Fig 3.6. Scatterplot of percent [rock]-[prairie] cover with maximum ERC age per plot (n = 232).

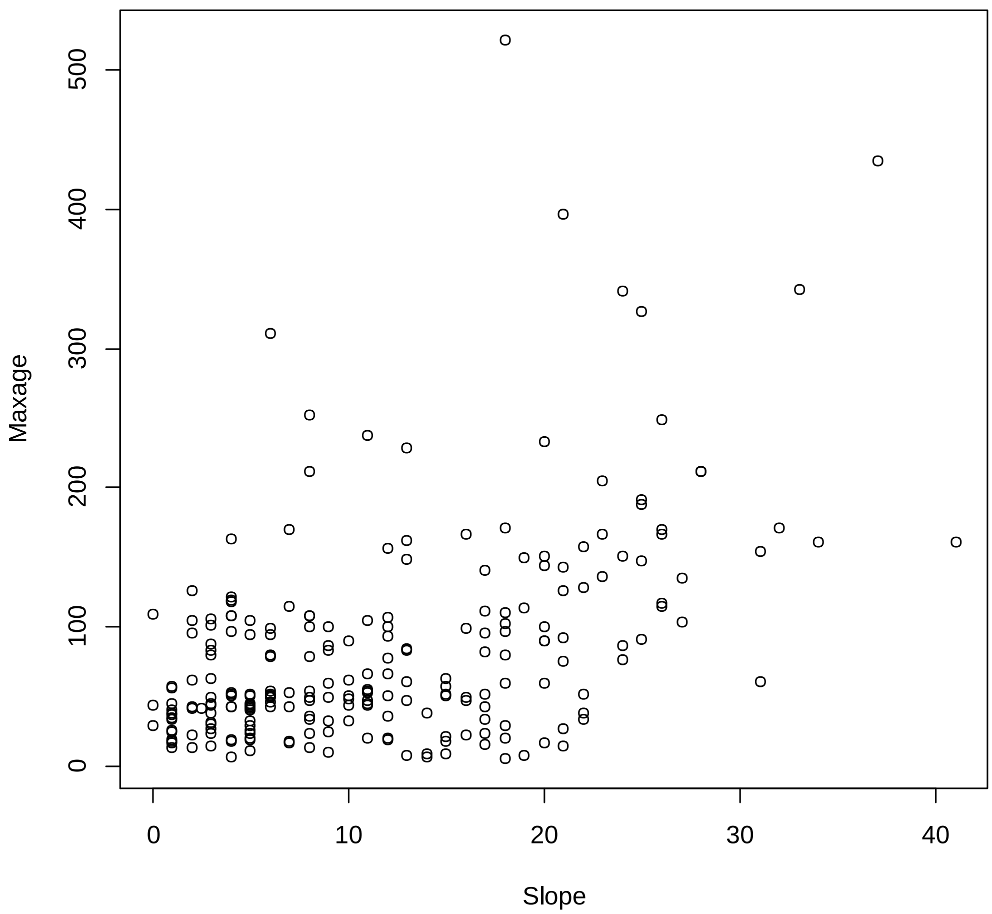

Fig 3.7. Scatterplot of percent slope (degrees) with maximum ERC age per plot (n = 232).

(Fig.3.7). Max ERC age and solar radiation were significantly, negatively correlated, and this relationship was not strongly linear but showed a peak in the mid-range of values, suggesting the oldest trees were found not at the highest or lowest solar radiation values, but between a maximum and minimum threshold (Fig. 3.8)

Stepwise linear regression, both forward and backward, was used on all significantly correlated variables to identify significant predictors of ERC max age. Visual assessment of scatterplots was used to verify the assumption of linearity between the predictor and response variables. When non-linear relationships were suspected, log transformations were attempted, though none significantly improved the model r-square value. There was a positive, significant relationship between older trees and decreasing evergreen cover (Fig. 3.9), though evergreen cover was excluded from further analysis because the relationship between max age and percent evergreen cover was not independent. Significant predictors identified by the stepwise regression were analyzed in a linear regression framework with ERC max age and the selected model was described by the following regression equation (Table 3.12):

$$\text{Maxage} = 106.1 + (0.45*\text{rockprairie}) + (1.87*\text{slope}) - (0.00096*\text{solarrad}) \quad (1)$$

Several linear regression models were attempted and selection was based on model significance, parsimony and biological explanation. The selected model worked well under the range of conditions observed but not beyond measured data parameters (Table 3.1).

Table 3.12. Max age multiple regression model results

Regression results

Response variable	n	r^2	*F* -value	*pr* > *F*	Coefficient of variation
maxage	229	0.3083	33.42	<0.0001	74.4431

Regression coefficients

Predictor	B	SE of B	*pr* > *t*	VIF
intercept	106.0952	26.1755	<0.0001	0
rockprairie	0.45409	0.01054	<0.0001	1.6903
slope	1.87098	0.6813	0.0065	2.0027
solarrad	-0.0009608	-0.0004188	0.0227	1.3118

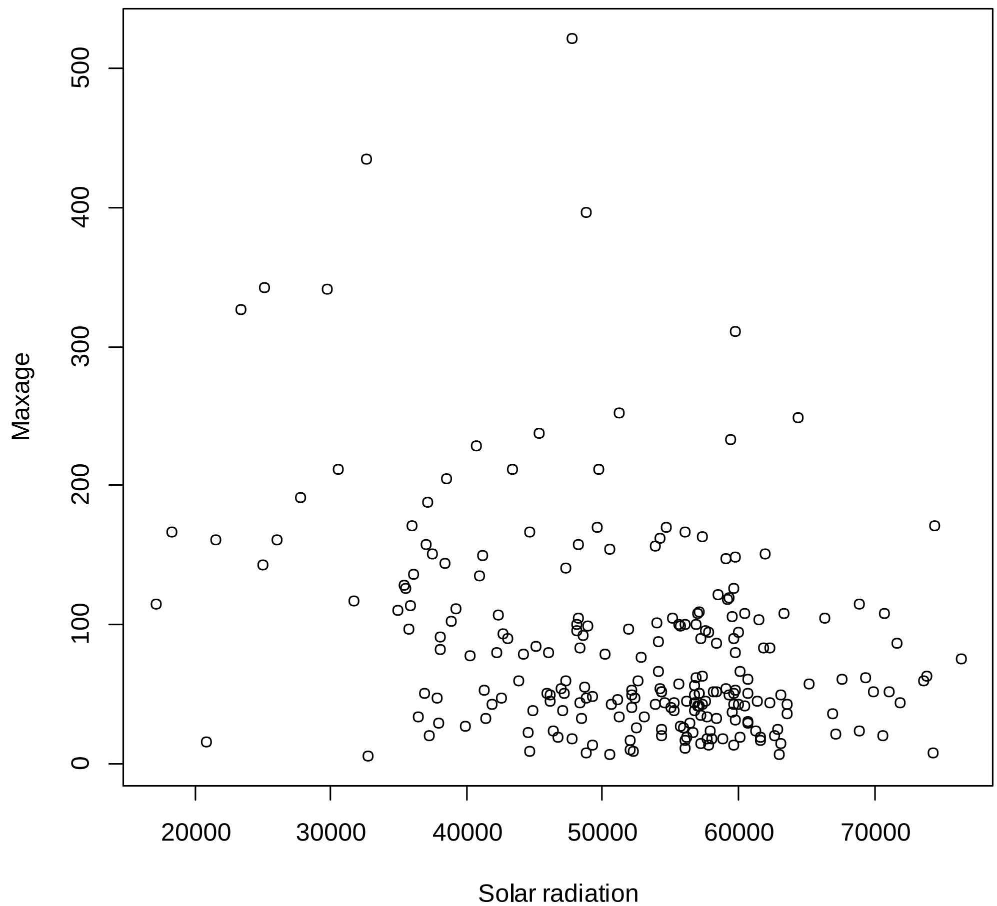

Fig 3.8. Scatterplot of solar radiation (watt hours/m^2) with maximum ERC age per plot (n = 232).

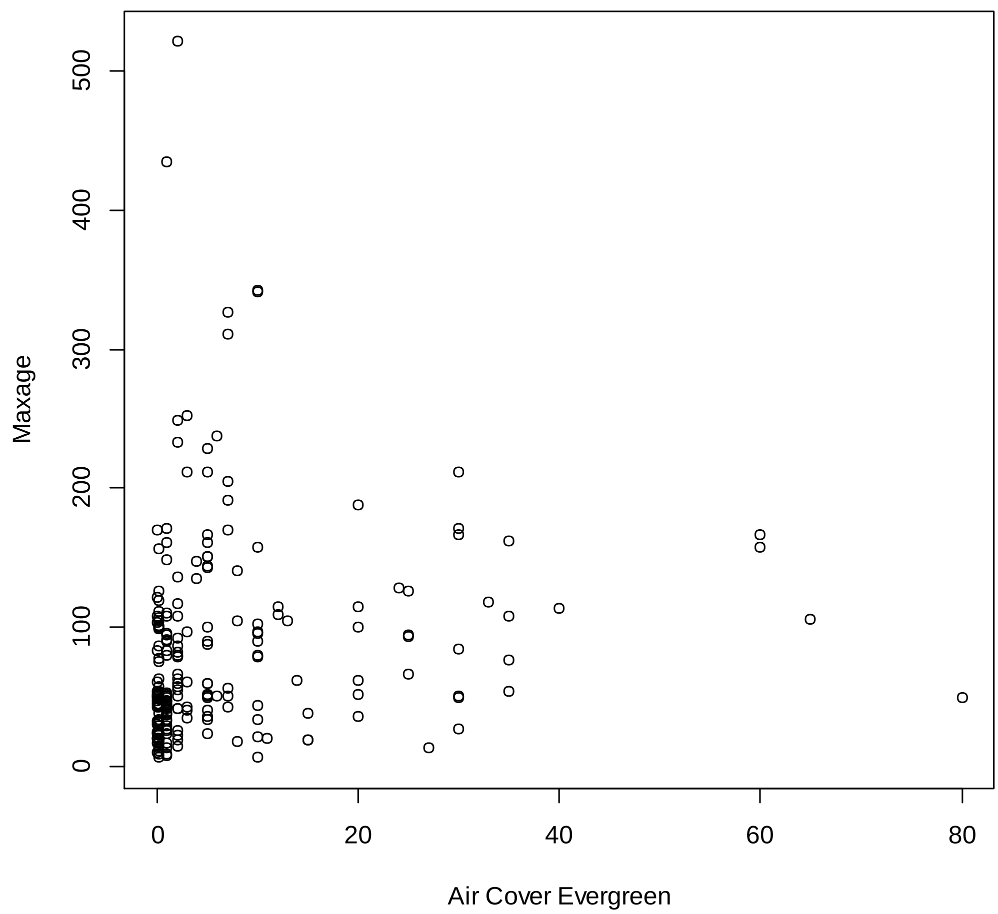

Fig 3.9. Scatterplot of evergreen aerial cover with maximum ERC age per plot (n = 232).

Testing the model, with rockprairie and slope at maximum measured values and solar radiation at its minimum measured value, the maximum age prediction was 227 years. When slope was increased to its theoretical maximum of 90 degrees (with the other variables held constant), the predicted ERC max age was 302 years old (the maximum age predicted by this model). With predictor values at mean measured values, the modeled max age prediction was 70 years. With slope and rockprairie at minimum measured values and solar radiation at mean value, the predicted age was 9 years. When the solar radiation maximum value was used with minimum slope and rockprairie values (which describe a perfectly flat, rock-less grassland), the max predicted age was -7. This result reveals that model predictions may not be accurate beyond the range of observed environmental parameter distributions.

Resample methods were used for the purpose of assessing model and variable stability. An average of 115 observations (range from 101 to 133) of 233 possible was used in each of the resample iterations. Results varied significantly based on the random inclusion or exclusion of the limited number of oldest samples (> 200 years) in the data set. In general the same or similar predictors were selected each time, the mean model R square value for all resample events was 0.31, and the intercept and predictors were statistically significant ($p < 0.10$) for most of the model iterations. Specifically, the mean R square value was 0.31 with a range from 0.22 to 0.41 and a standard deviation of 0.05. The intercept was significant for 87% of resample iterations at $p < 0.10$, and 77% at $p < 0.05$. Rockprairie was significant in all resample events at $p < 0.10$, and 94% at $p < 0.05$. Slope was significant in 74% of resample iterations at $p < 0.10$ and 55% at $p < 0.05$.

Solarrad was significant in only 58% of resample iterations at $p < 0.10$ and 13% at $p < 0$ .05.

Spatial Modeling of Max ERC Age

The max age model (Table 3.12) was applied in a GIS to produce a spatial depiction of the historic ERC distribution (Fig. 3.10). Modeled spatial locations of ERC greater than 110 years of age appeared to closely match those locations where trees pre-dating the refuge were actually found (Fig. 3.11). These locations generally occurred on rocky outcrops located on upper, northerly slopes. In contrast, spatial locations of trees established following reserve establishment appear much more widely distributed across the landscape (Fig. 3.12). Significant variables correlated with the spatial distribution of younger ERC were assessed in logistic regression models.

ERC Presence / Absence Model

All measured environmental variables (Table 2.2) were considered in a binary model framework where ERC presence (all growth forms) = 1 and ERC absence = 0. Both logistic regression (Proc Logistic, SAS 9.3) and a classification and regression tree (PARTY package, R statistical environment) selected generally the same environmental predictors of ERC presence. Significant variables selected by both models included percent prairie ground cover, percent deciduous cover, solar radiation (watt hours/square meter) and slope (degrees). Mean TRI was also significant and performed slightly better than slope in attempted logistic regression models, but mean TRI was not independent

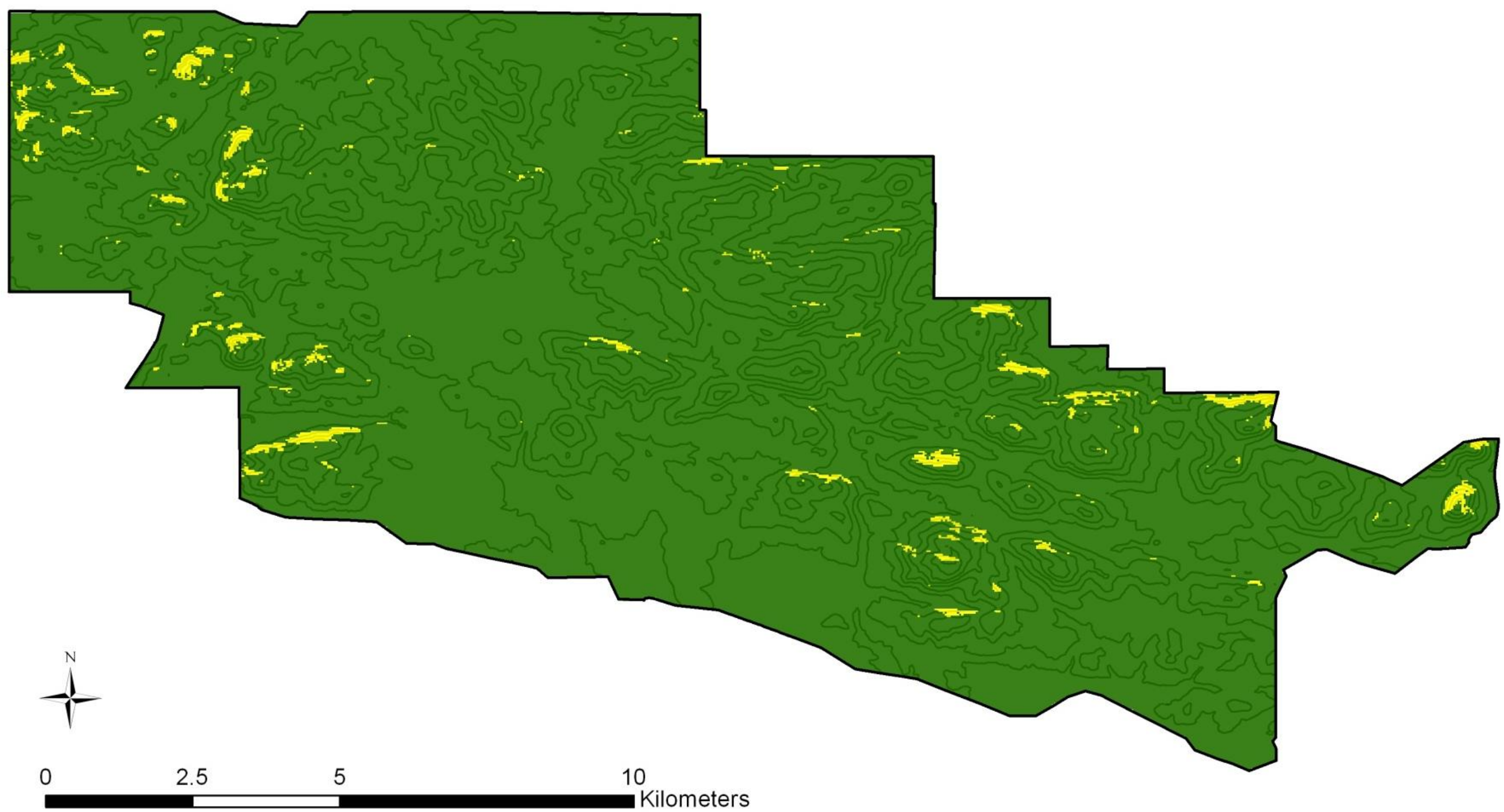

Figure 3.10. Spatial depiction of historic ERC distribution with 30 m contour intervals; yellow polygons represent expected locations of ERC > 110 years old, derived from the max age model.

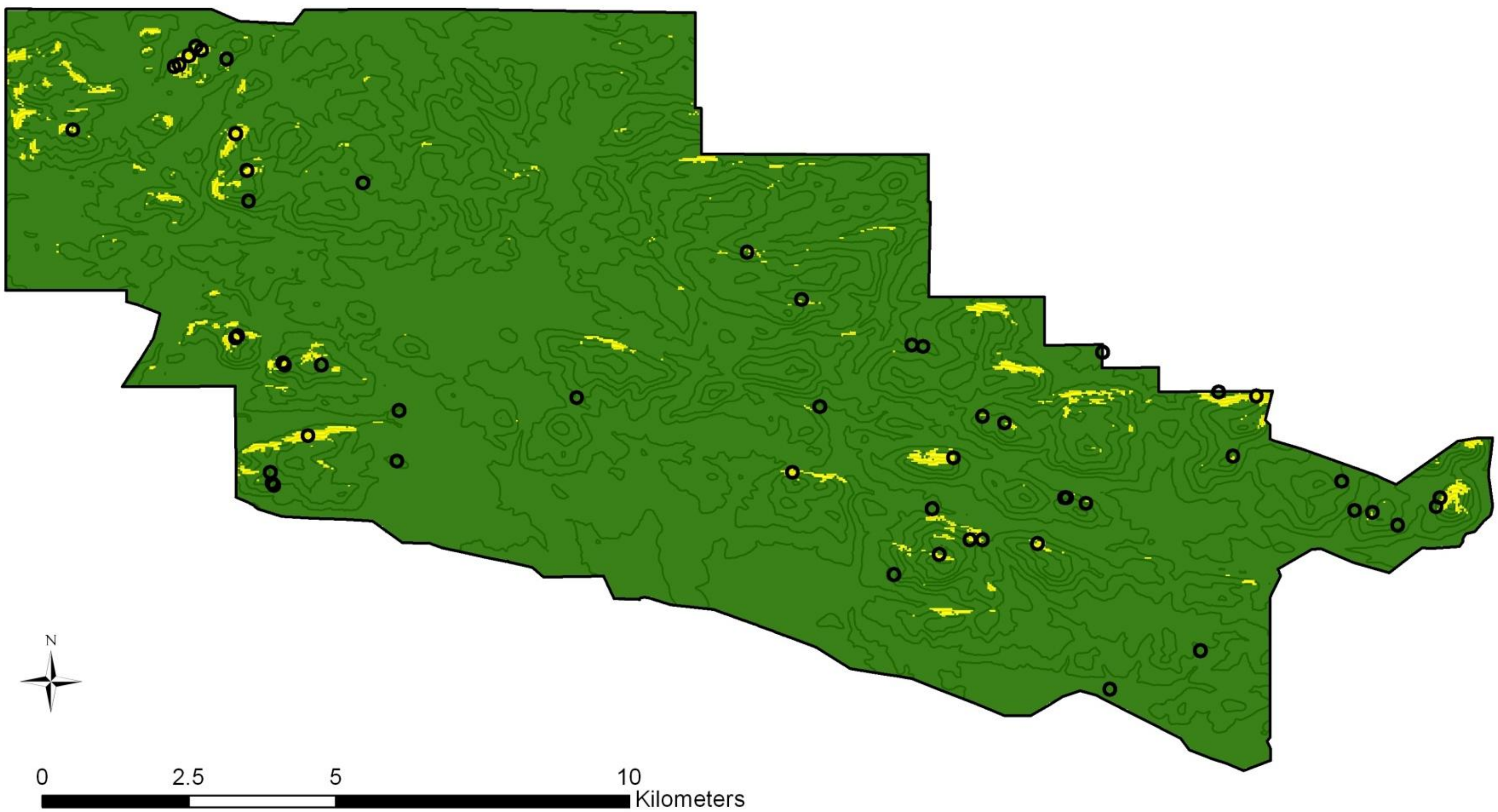

Figure 3.11. Spatial depiction of historic ERC distribution showing expected locations of ERC > 110 years of age in yellow polygons, with point locations of actual sampled ERC > 110 years old from study plots.

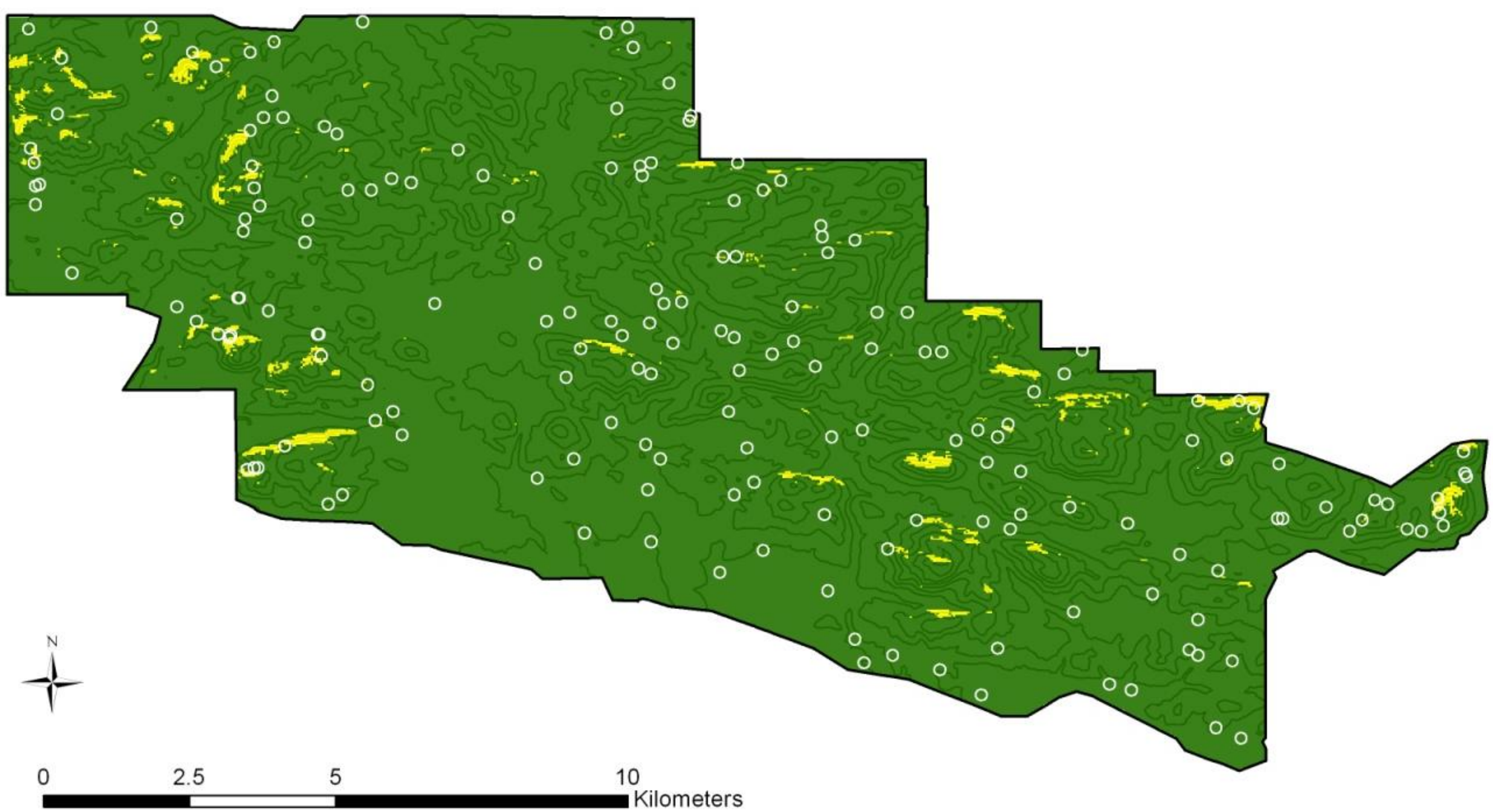

Figure 3.12. Spatial depiction of historic ERC distribution showing expected locations of ERC > 110 years of age in yellow polygons, with point locations of actual sampled ERC < 111 years old from study plots (white circles).

from the slope measurement, and the statistical difference between the two was negligible. Slope was used in the final logistic model because it was more readily extrapolated spatially on a predictive map, and it appeared to serve the same function as TRI in terms of relating plot topography to ERC presence.

The CART model (Figure 3.13) selected percent prairie ground cover as the environmental predictor most strongly related to ERC presence, followed by deciduous tree cover (aircovdecid), solar radiation, and slope. Percent prairie ground cover split at 88% with nearly all ERC present observations occurring at 88% or less prairie ground cover. At greater than 88% prairie ground cover, deciduous tree cover was the next splitting factor, and where there was zero deciduous cover, there was a zero percent probability of encountering ERC (n = 33). Where there was greater than zero percent deciduous cover, the probability of ERC occurrence was approximately 0.57 (n = 7). At less than 88% prairie cover, deciduous tree cover was also the splitting factor, and with deciduous tree cover at less than a trace amount (0.2%), slope became the final variable split. Where slope was less than seven degrees, there was approximately a 4% chance of ERC presence (n = 28), but at a slope of greater than 7 degrees, there was a 39% chance of ERC presence (n = 13). Below 88% prairie cover and with more than a trace amount of deciduous cover, solar radiation (solarrad) was the next splitting feature, with a nearly 99% chance of ERC presence with solar radiation values at or below 52,271 wh/m^2 (just under its mean value of 53,819 wh/m^2) (n = 99). Above the solarrad threshold value, deciduous tree cover split the remaining observations again, with the majority of ERC present occurrences at greater than 15% deciduous cover with a probability of 0.86 (n = 110), and a 60% chance of ERC presence at ≤ 15% (n = 51).

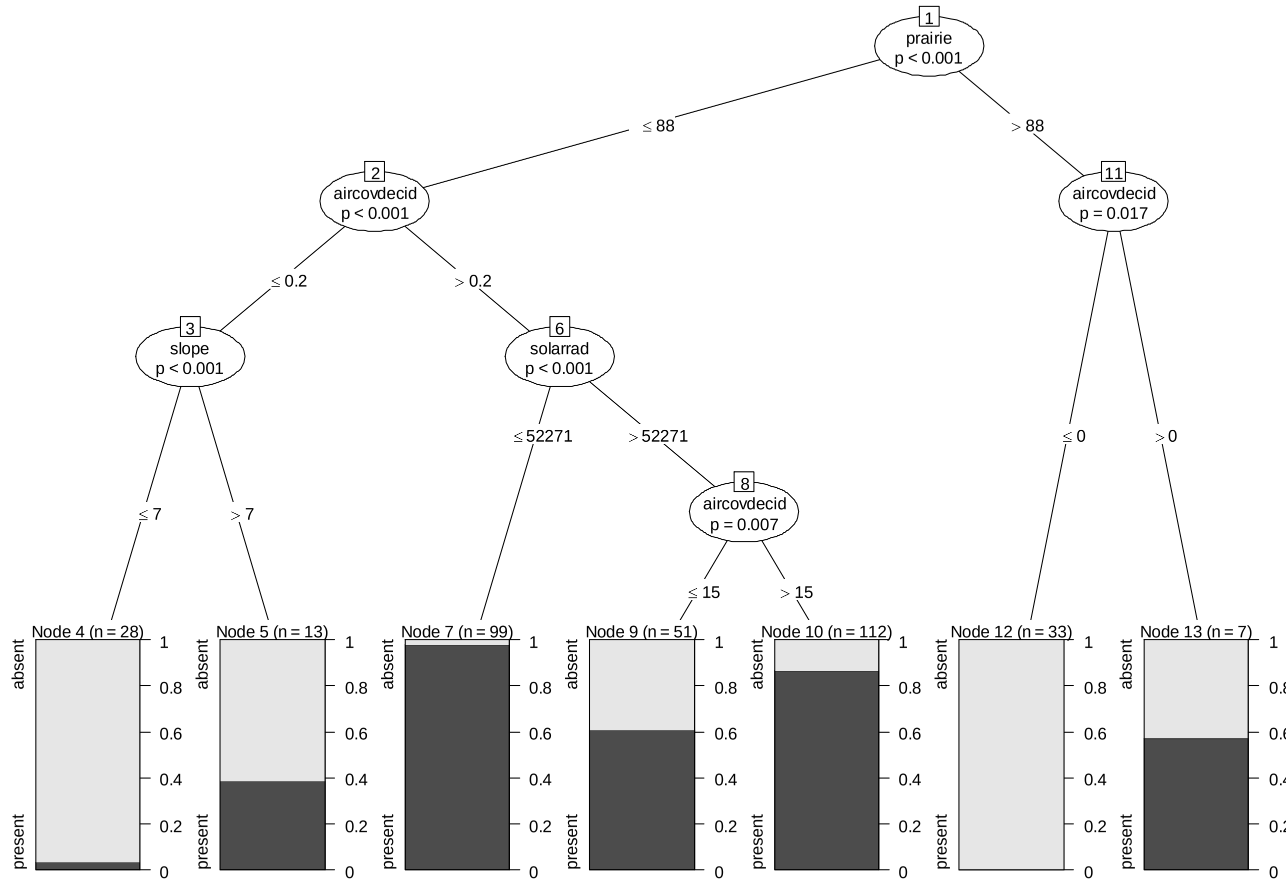

Fig. 3.13. CART analysis of environmental predictors of ERC presence/ absence. Dark shading in bar charts indicates probability of ERC presence for each final variable split. Numbers in between broken lines describe the numeric threshold which splits each variable.

In the logistic model (Table 3.13), probability of ERC presence increased with increasing percent deciduous cover and slope, and decreasing solar radiation and prairie ground cover. Top model selection for predictive mapping was based on AIC scores and significance of the intercept and all variables (Wald Chi square test, $p < 0.05$) (Table 3.13). The selected logistic model took the form of the following equation that was used for mapping ERC occurrence probability:

P (probability of ERC occurrence) = (2)

$$\frac{\exp(5.6075 - 0.00010(\text{solarrad}) + 0.0681(\text{slope}) - 0.0204(\text{prairie}) + 0.0672(\text{aircovdecid}))}{1 + \exp(5.6075 - 0.00010(\text{solarrad}) + 0.0681(\text{slope}) - 0.0204(\text{prairie}) + 0.0672(\text{aircovdecid}))}$$

CART and logistic models were attempted for all ERC tree forms (seedling, sapling, tree, and strip-bark) and little difference in selected environmental variables occurred between ERC seedlings, saplings and trees. Similar to the max age regression results, strip-bark and older tree presence was predicted by increasing rock ground cover and slope, while younger ERC presence was predicted by percent deciduous tree cover or density of non-ERC tree stems present.

Table 3.13. Logistic regression model predicting ERC presence

Parameter	Estimate	SE	Pr > ChiSq
Intercept	5.6075	1.5524	0.0003
solarrad	-0.0001	0.000023	<0.0001
slope	0.0681	0.0327	0.0375
prairie	-0.0204	0.0075	0.0065
aircovdecid	0.0672	0.0117	<0.0001
c	0.8984		

Spatial Modeling of ERC Presence/ Absence

The logistic model (Table 3.13) was applied in a GIS to produce a spatial model of ERC occurrence probability across the Special Use Area of the refuge (Fig. 3.13). Darker shading corresponds with increasing probability of ERC presence. The areas of high probability of ERC presence correspond with vegetated areas visible on an aerial photo (Fig. 3.14). Presence of existing deciduous tree cover appears to be the dominant environmental predictor of ERC presence across the landscape.

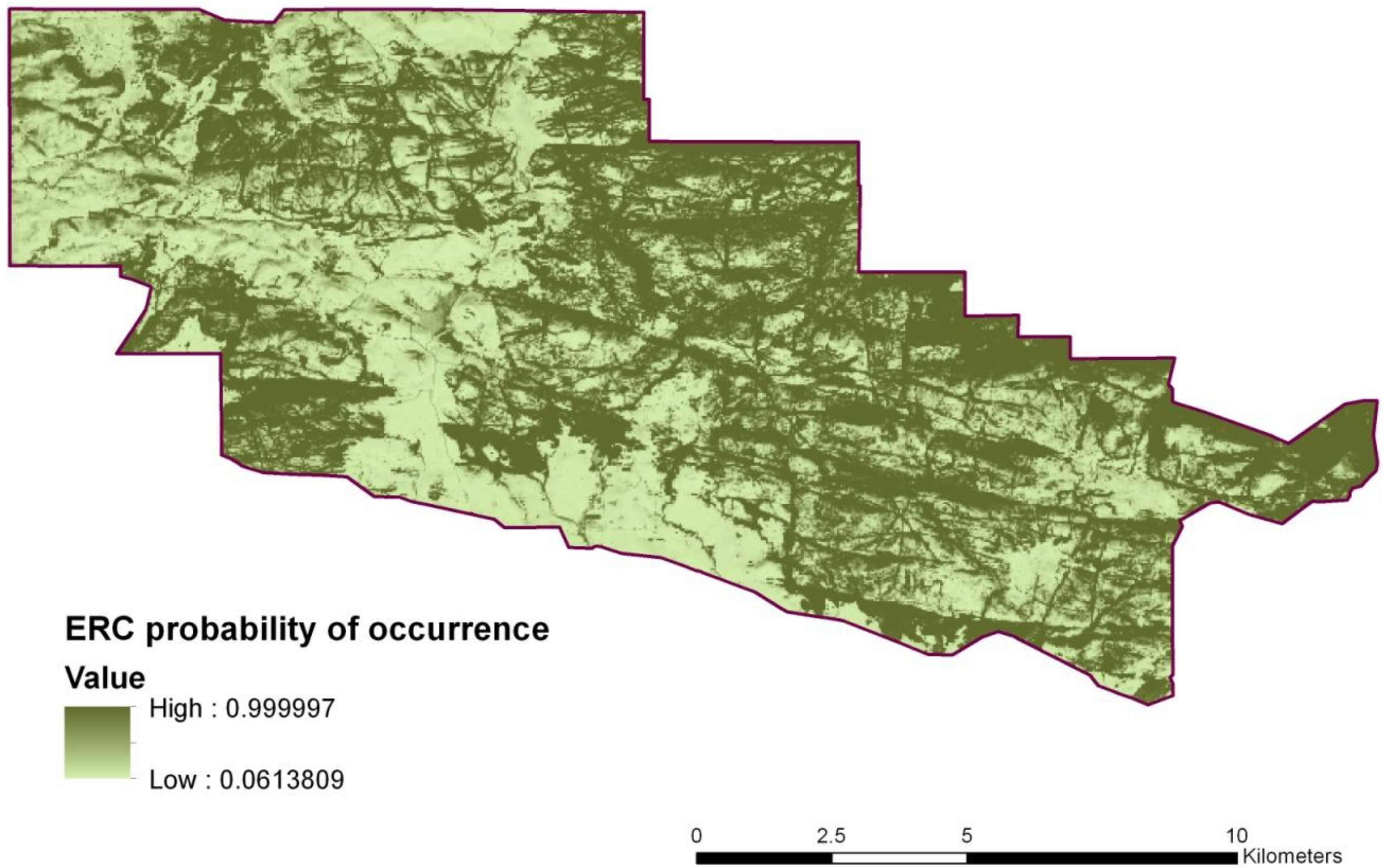

Figure 3.13. Spatial model predicting ERC presence across the study area. Darker shading indicates increased probability of ERC presence.

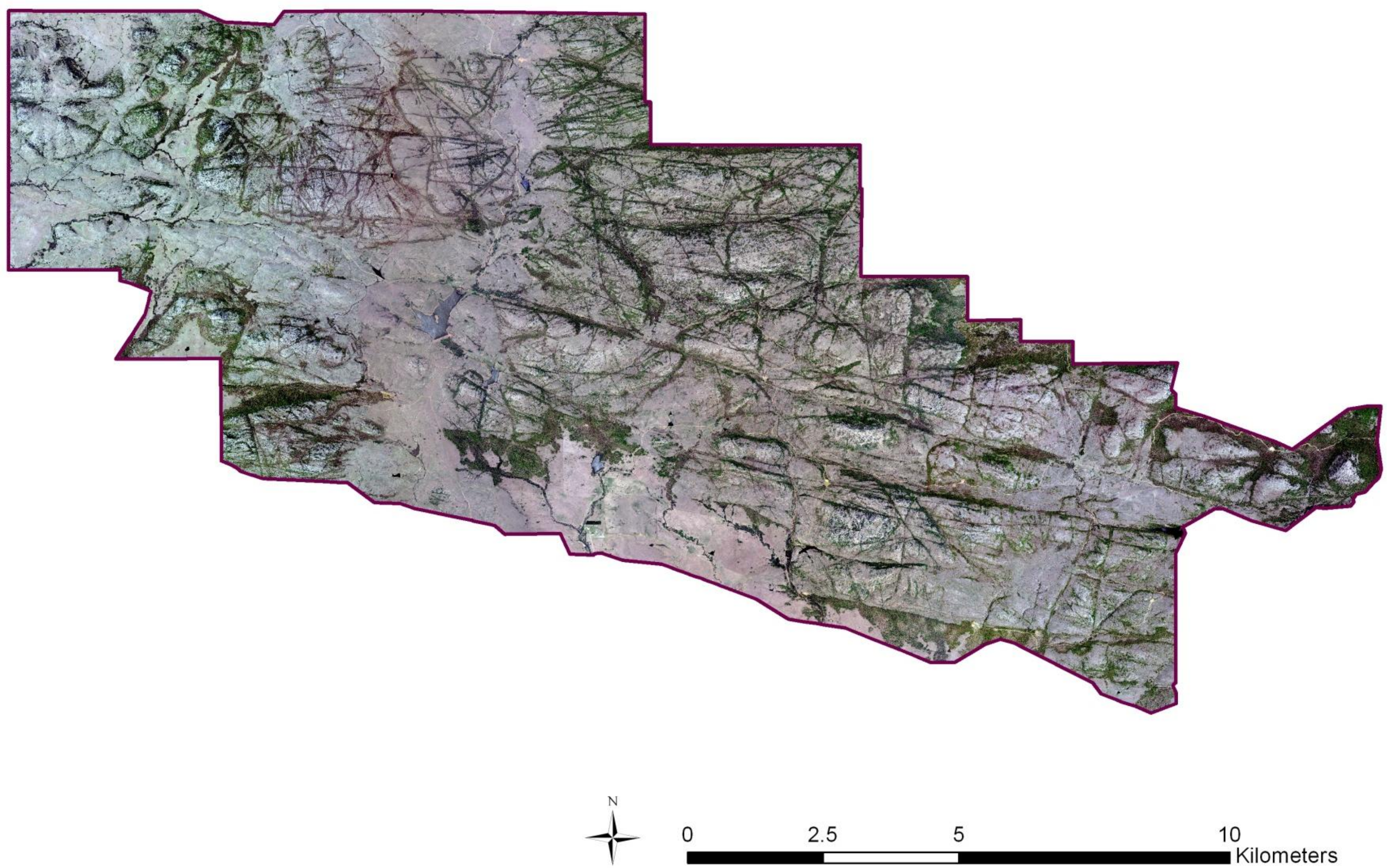

Figure 3.14. Aerial photo of the study area. Vegetated areas appear dark; lighter colored areas correspond with rock or grassland cover.

Chapter 4

DISCUSSION

Environmental Variables and Land Type Classification

Mean values of environmental variables measured by this study describe a prairie/ oak-woodland matrix with variable tree density ranging from open grassland to closed-canopy woodland. On average, across all sampled plots, mean canopy openness was high and percent tree cover was low, though mean tree cover was much higher in woodland areas. Topographic roughness was lowest within the grasslands. Highest elevation and TRI values in the rocky areas helped to validate delineation of this land type. Solar radiation was generally high for the study area, with highest predicted values occurring in grasslands and lowest predicted values in the rocky land type.

Grasslands were described as having more than 25% combined grass and forb cover and less than 25% deciduous (tree and shrub) cover, and in general, classification results match expected observations with most grassland plots occurring in low elevation prairie areas. The mean elevation for all grassland plots was slightly higher than the mean elevation for woodland plots, likely due to sparsely vegetated, grassy hilltops that were included with lowland prairie areas. Within the grassland classification, there was considerable variation in elevation, TRMI, slope, and vegetation density, with grasslands occurring on loamy bottomland soils as well as on thin, rocky soils on upper slopes. Additionally, the vegetation classification was based on data collected at the plot scale (30 meter diameter) and is inherently scale-dependent. Vegetation classification results based on data from a larger surrounding area (e.g., 1 km^2 vs. 30 m^2) would likely differ due to the highly heterogeneous and patchy vegetation structure in the study area.

The classification terms and vegetation cover thresholds used in this study represent a necessary yet imperfect attempt to broadly classify several point locations in order to describe their relationship to the broader landscape and dominant land types. The name of this heterogeneous vegetation community has changed over time, alternatively named oak savanna, woodland, pygmy forest, shrub-land, grassland-forest ecotone (Dyksterhuis, 1957). In 1957, Dyksterhuis applied the "savannah concept" to this region, describing different types of savanna that are defined by a "savanna climate" but may be structurally altered by anthropogenic or other factors resulting in increased or decreased tree density over time. Rice and Penfound (1959) favored a classification of oak savanna or "savanna-like forest" for the region, having defined savanna as a grassy landscape with widely spaced trees. Penfound (1962) concluded that much of western Oklahoma was probably historically savanna but was shifting toward forest and woodland, with the distinction between each dependent on the ratio of tree stem spacing to crown-diameter width.

Useful application of the label savanna may be scale dependent (temporally and spatially) across a forest-prairie transition region. Wetter climatic conditions favor increased woody species expansion and density, while drier conditions favor grasses and forbs and reduced woody density. Heavy grazing and fire suppression promote woody expansion, while moderate grazing and regular disturbance by fire inhibit expansion. The definitions published by Hoagland (2000) for Oklahoma vegetation communities provide a structure-based classification system, largely using canopy cover thresholds to distinguish between grasslands, woodlands and forests. In Missouri, Nelson (2005) distinguishes between woodland and forest using a combination of canopy closure ranges, tree heights and the relative density of shade-tolerant woody understory species to perennial grasses and ephemeral forbs. In this study distinctions were made between grassland, woodland and sparsely-vegetated, rocky lands using canopy cover thresholds, but the variable spatio-temporal gradient from savanna to forest within the woodland community was not specifically described.

Tree Density

Seedling density varied widely between plots. Due to their sometimes ephemeral nature, seedlings were assumed to be less important in terms of identification of long term population dynamics, and were not included in the tree density summary except in the percent occurrence metric, where seedling presence was included as presence of a species in a plot.

The overall mean tree density in all measured plots was very similar to the density and basal area reported by Rice and Penfound (1959), however, their study sites were restricted to upland forested stands. Excluding plots classified as grassland or rocky and comparing woodland plot means to the forested stands measured by Rice and Penfound between 1953 and 1957, basal area has nearly doubled, but increases in sapling and tree stems per hectare in the intervening half century have been much more modest. The tree density data from this study was not directly comparable with the study conducted by Rice and Penfound due to the different size classification used for saplings and trees. The sapling tally for this study included stems with a dbh of < 2.5 cm, while the Rice and Penfound study did not record saplings smaller than 2.5 cm dbh. To enable approximate comparisons, half of the saplings tallied by this study were assumed to be 2.5 cm dbh or smaller and excluded from the following summary statistics. In addition, Rice and Penfound summarized data for regions of Oklahoma. Their western survey region included the WMWR, but also included points farther west, which would be expected to receive less precipitation. Similarly, the central region was located immediately to the east of WMWR, and encompassed forested stands receiving increased precipitation. Because the refuge represented the easternmost survey area in Rice and Penfound's western study region, averages between the western and central regions were used for comparison. Resulting from these comparisons, the overall density of sapling and tree stems has increased by approximately 49% in the past 55 years and the basal area increased by 56% (84% compared to the western region). These increases are similar to those calculated between 1961 and the present, based on comparisons to a study within the refuge boundaries by Buck (1964). Buck reported 29% higher basal area than was measured in wooded plots by this study, though stem densities have nearly doubled 50 years later with an increase of 91%.

Dooley (1983) re-measured Buck's WMWR stands in 1981 and reported variable increases and decreases in basal area and stem density depending on the individual forested stands being measured. Overall, Dooley reported very similar stem densities and a 20% increase in basal area in approximately half the stands measured by Buck. Interestingly, both Buck and Dooley reported low numbers of saplings, but due to the overlapping sapling and tree size classifications used, it was not possible to identify change in that specific age structure component of the density measurements.

The magnitude of change between Rice and Penfound's measurements and densities reported by this study was similar to results of a resample study by DeSantis et al. (2010), which documented a total tree density increase of more than 71%, and an increase in basal area of more than 94% in forested stands over a 50 year period. These increases correspond to forested stands distributed throughout western, central and eastern Oklahoma, which encompass the oak-hickory association of the eastern Cross Timbers that receive greater precipitation than the western woodlands of this study area.

Regarding relative species abundance and dominance, post oak, blackjack oak and eastern redcedar were similarly ranked in descending order of importance by Buck, Dooley, and this study. These differ from the results of Rice and Penfound (1959) in which blackjack oak was most important species followed by post oak in the western region. This order was reversed for the central region, and eastern redcedar did not rank among the important species recorded in their study. These species rankings provide evidence for ERC expansion throughout Oklahoma, but suggest that eastern redcedar has been an important part of the tree community in the WMWR for longer than the past 50 years, likely in a patchy spatial configuration.

The oak-dominated woodland stands appear to have increased in density by approximately 49% to 91% over the past 50 years. Using the ERC maximum age frequency histogram and comparing the mean frequency of pith dates from the 1910 – 1960 and 1960 – 2010, the ERC population appears to have increased by more than 80%

refuge-wide. Similarly, comparing woodland to rocky area combined ERC sapling and tree densities, the younger, woodland community has a 98% higher density of ERC saplings and trees than does the rocky land type. These comparisons suggest that ERC density may be occurring at a slightly faster rate than increases in other woody species.

The average canopy closure in woodland stands of 35 – 55% suggests that additional tree density increase may be possible in the study area, though maximum woody cover at this location may be limited by other abiotic factors such as water, nutrient or substrate availability. Rice and Penfound (1959) noted significant death of trees (mostly blackjack oak) due to drought in 1950's (nearly 11% in Comanche County) suggesting that water availability may be a critical abiotic factor in tree density determination for this region. In general, Oklahoma experiences droughts approximately every 20 years (Hoagland, 2000).

All woodland tree species were represented by a higher density of saplings than mature trees. This understory tree regeneration indicates that woodland tree densities are increasing, and that trees are not likely limited by light, although there may be other factors which limit survival of saplings and subsequent and recruitment into the overstory. Without quantification of mortality and survival of seedlings and saplings, it is unknown what percentage will die before attaining reproductive capacity and advanced age. Sources of seedling and sapling mortality include: fire, drought, animal browse and trampling, and competitive interactions with herbaceous and other woody vegetation.

ERC Maximum Age Distribution

The overall oldest ERC age distribution across the study area appears to follow a J-shaped distribution, which describes an increasing population with ample reproduction and disturbance-caused fluctuations in recruitment and mortality (Oliver and Larson, 1990). The steep increase in tree abundance in younger age classes suggests several things: 1) a high chance of mortality with increasing age may exist for ERC; 2) ERC may have a high rate of reproduction, with apparent "pulses" in reproduction and survivorship; 3) ERC can be long lived, with live individuals extending back in time to the 15th century; 4) Long lived individuals (i.e. > 200 years in age) occur infrequently on the landscape. The relatively small population of old trees sampled may reflect historically higher mortality rates with increasing age or a historically lower rate of reproduction or seed abundance. This small population of old trees may also reflect the true number of "micro-sites" or protected landscape positions capable of sustaining long-lived cedar over time amidst periodic fires and droughts.

Departing from this exponential curve was an apparent stepwise increase in population frequency during three distinct time periods. A small, relatively stable population over time of old individuals occurred in the record from the late 15th century to the mid 19th century. Subsequently, the age structure showed a major increase in surviving cohorts establishing in the mid-19th century, at the turn of the 20th C, and in the last half of the 20th C, which could have been related to increased reproduction and/ or decreased mortality. Changes in the fire regime and eventual fire and grazing policies at the time of forest reserve establishment, in addition to favorable climatic conditions following the Civil War drought, may have favored ERC establishment and survival beginning in the late 1800's. During the "conflict and settlement period" of the late 1800's, a fire history of the refuge shows an increase in fire frequency with a mean fire return interval of 1.3 years (Stambaugh et. al., unpublished data). With near annual fires, the resulting fuel load and severity would have been low, resulting in lower tree mortality. Following forest reserve establishment in 1901, the fire policy was comprised of complete fire suppression, which lasted until 1935. This fire suppression period overlapped with a period of heavy grazing of domestic cattle on the refuge, from1880 until the termination of all domestic grazing leases in 1937. Though grazing interacts with fuels to reduce fire severity, heavy grazing can negatively impact woody plants like ERC that are browsed and trampled when young (DeSantis, 2011). Heavy grazing can also increase bare ground and reduce vigor of herbaceous vegetation, likely increasing germination potential for ERC and other woody grassland invaders (McPherson et. al., 1988). Following the end of grazing allotments in the 1940's, a large increase occurred in the 1950's ERC cohort that continued to increase through the 1960's. In 1976, the refuge initiated a prescribed fire program and coincidentally, cohort sizes declined throughout the remainder of the 20th century.

When looking at the age structure on different land types within the study area, a spatial pattern of change over time emerges. Young trees heavily dominate the grasslands and woodlands, while a more even distribution of all ages including the oldest trees on the refuge occurs in the rocky areas, supporting the concept of ERC expansion from fire-protected, rocky refugia. Because the sampling method consisted of sampling the oldest trees per plot, the abundance of younger trees on each land type and refuge wide was under-represented in the frequency histograms. However, dominance of the younger cohorts indicates the establishment by the species in a given plot and explicitly describes the lack of older trees present. Analysis of the dead ERC stem tally revealed that dead strip bark trees were not tallied in any plots not also containing a living strip-bark tree, suggesting that live strip-bark tree ages and spatial locations recorded in the study were representative of "old-tree" locations. The dominance of young ERC on the landscape supports the concept of expansion; in plots where the max age was young (<100 years), no older, living trees were present. Of all ERC stems tallied: < 1% of seedlings were dead; 6% of ERC saplings were dead; 14% of ERC trees were dead; 22% of ERC strip-bark were dead, and 8% of ERC bush-form were dead. The presence of standing dead trees, including strip-bark trees with a mean age of 145 years, indicates that stand replacing fire had not burned over much of the study area in at least the past 150 years. Additionally, the old oak community cohort was 300-350 yrs old in locations across the SPU (Stambaugh et. al, unpublished), so stand replacing fire had not affected parts of the oak community for at least the past three centuries.

The age distribution of a multi cohort stand would be expected in this location due to the known history of frequent fire events that were infrequently stand replacing (Oliver and Larson, 1990); some survival from all cohorts would be expected in a patchy spatial configuration for most fires. Generally fire of all intensities would be expected to kill ERC seedlings and saplings, though cooler fires would not be expected to kill all mature trees (Engle and Stritzke, 1995). The dominant, regular disturbance events affecting ERC recruitment and mortality in all land types are drought and fire (DeSantis et al., 2011), though the large boulders in the rocky land type act as physical barriers to fire, creating discontinuity in vegetation and fuels for fire, thus reducing fire frequency and likely severity. To this end, the rocky land type vegetation communities may be more reflective of drought disturbance than fire effects.

Data from the US Great Basin suggests the juniper expansion of the past 150 years may be a synchronous event across much of the US. The timing of the expansion of ERC at WMWR is synchronous with the expansion of western juniper and other juniper species throughout much of the Great Basin beginning in 1880's. While expansion and contraction of the range of juniper has been documented throughout much of the Holocene, particularly in the past 5-6,000 years, past juniper expansion rates occurred during cooler and wetter climate modes involving growing season precipitation (Miller and Wigand, 1994). In contrast, the 1880's expansion period was initiated in warmer and drier conditions, apparently in response to decreased anthropogenic fire and a period of very heavy grazing in which all or much of standing fine fuel was heavily reduced (Miller and Wigand, 1994). The fact that the timing of the WMWR juniper expansion is synchronous with juniper expansion throughout the Great Basin would theoretically suggest that a broad extrinsic force like climate would be the proximate cause (of the expansion), however, the same anthropogenic forces were also being exerted in both locations, namely, suspension of the historic fire regime due to dramatic population reductions and near extirpation of Native American peoples, and very heavy grazing of introduced herbivores. Coupled together, absence of fire and heavy grazing appear to have been the dominant extrinsic forces causing the expansion of juniper throughout the Great Basin, and perhaps also, in the oak savannas of the WMWR.

Modeling ERC Distribution

In the max age model, distributions of some environmental variables did not exactly fit linear or log transformed models. It is possible that non-parametric linear regression may better suit the complex ecological relationships than the model produced in a generalized linear model framework. Despite this potential limitation, the max age model constructed largely of topographic landscape features explained 31% of the variance in the age distribution of ERC on the landscape, which is substantial given the broad range of physical, biological and anthropogenic variables which likely interact to affect the ERC distribution.

Using CART analysis and logistic regression, prediction of strip bark tree presence was based on essentially the same predictors as were selected by the linear max age model, specifically percent rock and percent slope, while locations of younger tree forms was largely predicted by deciduous cover or deciduous tree stem density. Due to the limited size of the oldest ERC samples in the age dataset, the entire dataset was used to construct the model, so the spatial probability model was not validated with independent observations. Despite this limitation, the predictor variables in the model appear to effectively predict ERC presence at the WMWR in agreement with other modeling efforts and observed patterns of ERC presence on the landscape.

ERC Expansion Exercise

Based on the assumption that the rocky land areas represent the historic range of ERC in the study area, the ratio of rocky land area to woodland and grassland areas was a model for ERC expansion from historic rocky refugia to its present day spatial distribution. Using the ERC age structure and density data collected in this study, a tree (density increase) model was constructed. A modeling exercise was conducted as follows:

Rocky outcrop areas comprise 6% of the refuge land area (USFWS, 1985) and 80% of the surveyed rocky outcrops were occupied by ERC, so the historic ERC occupancy was estimated to cover 4.8% of the refuge (6 * 0.8). Grasslands and woodlands comprise 92.5% of the refuge land (USFWS, 1985), and mean ERC occurrence on surveyed woodlands and grasslands combined (in 2010) was 64%, so ERC expansion was calculated for 59.2% of the refuge land area (92.5 * 0.64). The temporal period for this ERC expansion exercise was designated as 145 years, or the mean age of ERC sampled in the rocky land type.

From 1866 to 2011 (a 145 year period), modeled ERC spatial extent increased from ERC occurrence on 4.8% of the refuge (1,146 hectares) to occurrence on 59.2% of the refuge (14,135 hectares). This was an increase in ERC occupancy on 12,989 hectares over a 145 year period, resulting in an average annual increase in ERC occupancy on 89.5 ha/ year. To arrive at an expansion rate of stems per hectare per year, the total combined density of measured ERC stems per hectare on the grassland and woodland land types in 2010 (652 stems/ ha) was divided by 145 years. This calculation resulted in an expected increase of 4.5 stems per hectare per year over the 145 year time period to arrive at the measured (2010) density levels. To account for continued density increase on land areas with ERC present in addition to those newly colonized land areas, the annual rate of increase was additive on each land area once ERC was present.

As a result, modeled tree density increased at a rate of 4.5 trees per hectare per year in 89.5 hectares per year spatial increments. This exercise results in a total modeled increase of 4,263,109 ERC stems over 12,989 hectares during the period from 1866 to 2010. Based on these modeled expansion results, the 2011 ERC density on approximately 55% of the refuge was projected to be 328 trees per hectare. The modeled results were greater than the actual density of ERC found in 2010 in the woodland land type of 260 stems per hectare of saplings and trees combined (but excluding seedlings) (Table 3.6). With the addition of seedlings, tree density between simulated and actual results could be similar. Though the rate of ERC increase would likely become exponential after ERC reach reproductive capacity in 10-30 years, the mortality rate of seedlings and saplings would also likely increase. Non-linear increases in establishment and mortality rates were left out of the model for simplicity under the assumption that inter-annual variation in establishment and mortality over time would likely result in a steady, slow population increase.

This exercise supports the hypothesis that ERC has expanded spatially from the rocky outcrops to other land types, where it has increased in density over time. This model was based in part on the well-supported assumption that fire was the dominant disturbance that historically prevented ERC from establishing long-term populations in fire-prone land types (such as grasslands and woodlands).

Conclusion

ERC age structure data and refuge tree density data support the hypothesis that ERC density has increased refuge-wide since the time of Euro-American settlement and refuge establishment. The 20th century density increase in tree species, particularly ERC in woodlands, is likely a direct result of altered fire and grazing regimes of the 19th and 20th centuries. DeSantis et al., (2010, 2011) provide evidence of transition within the oak forests of Oklahoma away from oak dominance toward closed-canopy forests dominated by shade tolerant species, as has been documented throughout 20th century oak forests of eastern North America. However, the ample reproduction among all tree species in the study area suggests that a similar conversion to shade tolerant species may not be occurring in the WMWR at the western-most extent of these eastern deciduous species' ranges. Though density of the dominant tree species in the study area has increased over the past century, it is unknown how much density increase can be supported by the climate regime, disturbance regimes, and other limiting abiotic factors at the study site. Nonetheless, the ERC expansion rate and spatial distribution modeling results from this study suggest that the ERC population will likely continue to increase into the future.

LITERATURE CITED

Abrams, M.D., Nowacki, G.J., 2008. Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. The Holocene 18 (7), 1123–1137.

Archer, S., 1989. Have Southern Texas Savannas Been Converted to Woodlands in Recent History? The American Naturalist 134 (4), 545–561.

Archer, S., Scifres, C., Bassham, C.R., Maggio, R., 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58 (2), 111–127.

Auken, O.W.V., 2000. Shrub Invasions of North American Semiarid Grasslands. Annual Review of Ecology and Systematics 31, 197–215.

Bradley, B.A., Fleishman, E., 2008. Relationships between expanding pinyon–juniper cover and topography in the central Great Basin, Nevada. Journal of Biogeography 35, 951–964.

Bragg, T.B., Hulbert, L.C., 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29 (1), 19–24.

Briggs, J.M., Hoch, G.A., Johnson, L.C., 2002. Assessing the Rate, Mechanisms, and Consequences of the Conversion of Tallgrass Prairie to Juniperus virginiana Forest. Ecosystems 5 (6), 578–586.

Buck, P., 1964. Relationships of the Woody Vegetation of the Wichita Mountains Wildlife Refuge to Geological Formations and Soil Types. Ecology 45 (2), 336–344.

Burkhardt, J.W., Tisdale, E., 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57 (3), 472–484.

Clark, S.L., Hallgren, S.W., 2003. Dynamics of oak (Quercus marilandica and Q. stellata) reproduction in an old-growth Cross Timbers forest. Southeastern Naturalist 2 (4), 559–574.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111 (982), 1119–1144.

Cottam, G., Curtis, J.T., 1956. The Use of Distance Measures in Phytosociological Sampling. Ecology 37 (3), 451–460.

DeSantis, R.D., Hallgren, S.W., Lynch, T.B., Burton, J.A., Palmer, M.W., 2010. Long-term directional changes in upland Quercus forests throughout Oklahoma, USA. Journal of Vegetation Science 21 (3), 606–618.

DeSantis, R.D., Hallgren, S.W., Stahle, D.W., 2011. Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone. Forest Ecology and Management 261, 1833-1840.

Dooley, K. 1983. Description and dynamics of some western oak forests in Oklahoma. Dissertation, University of Oklahoma, Norman, USA.

Dyksterhuis, E.J., 1948. The Vegetation of the Western Cross Timbers. Ecological Monographs 18 (3), 325–376.

Dyksterhuis, E.J., 1957. The Savannah Concept and Its Use. Ecology 38 (3), 435–442.

Edmondson, J.R., 2010. The Meteorological Significance of False Rings in Eastern Redcedar (Juniperus virginiana L.) from the Southern Great Plains, USA. Tree-Ring Research 66 (1), 19–33.

Elliott, G.P., 2012. Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. Ecology 93 (7), 1614–1625.

Engle, D.M., Stritzke, J.F., 1995. Fire behavior and fire effects on eastern redcedar in hardwood leaf-litter fires. International Journal of Wildland Fire 5 (3), 135–141.

Francaviglia, R.V., 2000. The cast iron forest: a natural and cultural history of the North American Cross Timbers. University of Texas Press, Austin, USA.

Fuhlendorf, S.D., Smeins, F.E., Grant, W.E., 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecological Modeling 90 (3), 245–255.

Gesch, D., Evans, G., Mauck, J., Hutchinson, J., Carswell Jr., W.J., 2009, *The National Map*—Elevation: U.S. Geological Survey Fact Sheet 2009-3053, 4 p. http://ned.usgs.gov

Griffin, R., Stahle, D., Therrell, M., 2005. Repeat photography in the ancient cross timbers of Oklahoma, USA. Natural Areas Journal 25 (2), 176–182.

Guyette, R., McGinnes, E., Probasco, G., Evans, K., 1980. A Climate History of Boone County, Missouri, From Tree-Ring Analysis of Eastern Redcedar. Wood and Fiber Science 12 (1), 17–28.

Hoagland, B., 2000. The vegetation of Oklahoma: A classification for landscape mapping and conservation planning. The Southwestern Naturalist 45 (4): 385–420.

Hoagland, B.W., Butler, I.H., Johnson, F.L., Glenn, S., 1999. The Cross Timbers: Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press, New York, New York, USA, pp. 231–245.

Hobbs, R.J., Harris, J.A., 2001. Restoration Ecology: Repairing the Earth's Ecosystems in the New Millennium. Restoration Ecology 9 (2), 239–246.

Holthuijzen, A.M.A., Sharik, T.L., Fraser, J.D., 1987. Dispersal of eastern red cedar (*Juniperus virginiana*) into pastures: an overview. Canadian Journal of Botany 65 (6), 1092–1095.

Hothorn, Torsten, Hornik, K., and Zeileis, A., (2006). Unbiased Recursive Partitioning: A Conditional Inference Framework. Journal of Computational and Graphical Statistics, 15(3), 651—674.

Lassoie, J.P., Dougherty, P.M., Reich, P.B., Hinckley, T.M., Metcalf, C.M., Dina, S.J., 1983. Ecophysiological investigations of understory eastern redcedar in central Missouri. Ecology 64 (6): 1355–1366.

Marcy, Randolph, B. Exploration of the Red River of Louisiana, in the year 1852; by Randolph B. Marcy, Captain Fifth Infantry U.S. Army; assisted by George B. McClellan, Brevet Captain U.S. Engineers. Washington, A.O.P. Nicholson, Public Printer, 1854.

McPherson, G.R., Wright, H.A., Wester, D.B., 1988. Patterns of Shrub Invasion in Semiarid Texas Grasslands. American Midland Naturalist 120 (2), 391–397.

Miller, R.F., Wigand, P.E., 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44 (7), 465–474.

Nelson, P.W., 2005. The Terrestrial Natural Communities of Missouri. The Natural Areas Committee, Missouri, USA.

Nowacki, G.J., Abrams, M.D., 2008. The Demise of Fire and —Mesophication" of Forests in the Eastern United States. BioScience 58 (2), 123–138.

Oliver, C.D., Larson, B.C., 1990. Forest Stand Dynamics. McGraw-Hill, Inc.

Ormsbee, P., Bazzaz, F.A., Boggess, W.R., 1976. Physiological Ecology of Juniperus virginiana in Oldfields. Oecologia 23 (1), 75–82.

Parker, A.J., 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Physical Geography 3 (2), 160–168.

Penfound, W.T., 1962. The Savanna Concept in Oklahoma. Ecology 43 (4), 774–775.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rice, E.L., Penfound, W.T., 1959. The upland forests of Oklahoma. Ecology 40 (4), 593–608.

Rykiel, E.J., Cook, T.L., 1986. Hardwood-Redcedar Clusters in the Post Oak Savanna of Texas. The Southwestern Naturalist 31 (1), 73–78.

Schmidt, T.L., Leatherberry, E.C., 1995. Expansion of Eastern Redcedar in the Lower Midwest. Northern Journal of Applied Forestry 12 (4), 180–183.

Stahle, D.W. 1990. The Tree-Ring Record of False Spring Events in the Southcentral USA. Dissertation, Arizona State University, Tempe, USA.

Stahle, D.W. 1996. Tree rings and ancient forest relics. Arnoldia 56 (2), 10.

Stambaugh, M.C., Guyette, R.P., 2008. Predicting spatio-temporal variability in fire return intervals using a topographic roughness index. Forest Ecology and Management 254 (3), 463–473.

Stambaugh, M.C., Guyette, R.P., Godfrey, R., McMurry, E.R., Marschall, J.M., 2009. Fire, Drought, and Human History Near the Western Terminus of the Cross Timbers, Wichita Mountains, Oklahoma, USA. Fire Ecology 5 (2), 51–65.

Stokes, M.A., Smiley, T.L., 1996. An Introduction to Tree-Ring Dating. University of Arizona Press.

Tausch, R.J., West, N.E., Nabi, A.A., 1981. Tree Age and Dominance Patterns in Great Basin Pinyon-Juniper Woodlands. Journal of Range Management 34 (4), 259–264.

Therrell, M.D., Stahle, D.W., 1998. A predictive model to locate ancient forests in the Cross Timbers of Osage County, Oklahoma. Journal of Biogeography 25 (5), 847–854.

Tyrl, R.T., Bidwell, T.G., Masters, R.E., Elmore, R.D., 2008. A Field Guide to Oklahoma Plants: Commonly Encountered Prairie, Shrubland, and Forest Species. Oklahoma State University, Stillwater, OK, USA.

US Fish and Wildlife Service Refuge Management Plan, Part 2, Chapter 1, Grassland Management Plan. Refuge Manager, Robert Karges, Wichita Mountains National Wildlife Refuge, Indiahoma, Oklahoma, USA. August 1, 1985.

Whitlock, C., Shafer, S.L., Marlon, J., 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. Forest Ecology and Management 178 (1-2), 5–21.