SPATIAL PATTERN AND UNCERTAINTY OF SOIL CARBON AND NITROGEN IN A SUBTROPICAL SAVANNA LANDSCAPE IN SOUTHERN TEXAS

A Dissertation

by

FENG LIU

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2007

Major Subject: Rangeland Ecology and Management

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Approved by:

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ABSTRACT

Spatial Pattern and Uncertainty of Soil Carbon and Nitrogen in a Subtropical Savanna Landscape in Southern Texas. (August 2007)

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Woody invasion into grasslands has been reported world-wide and has affected both the magnitude and spatial heterogeneity of soil carbon (C) and nitrogen (N). Since grasslands cover a large portion of the Earth's land surface, invasion of woody plants could have impacts on regional and global biogeochemistry. To understand large-scale ecological and policy implications of woody invasion, it is critical to understand the spatial pattern and uncertainty of soil C and N and their relationship with vegetation and soil attributes, as well as develop effective approaches to estimate soil C and N over large landscapes and regions.

The goal of this study was to improve our understanding of the spatial pattern of soil organic carbon (SOC) and total nitrogen (TN) and their controlling factors in savanna landscapes and develop efficient sampling strategies for evaluating the effects of woody invasion. Specific objectives of this study were to: (1) Quantify the spatial pattern and uncertainty associated with SOC and develop efficient sampling strategies to estimate SOC storage; (2) Assess the influence of soil and vegetation factors on spatial distribution of SOC and TN; and (3) Determine the influence of physical variables related to landscape position and soil on woody vegetation structure.

Conditional sequential indicator simulations indicated that woody encroachment into grassland increased both spatial heterogeneity and uncertainty of SOC, which increased errors in estimating SOC storage. Stratified random sampling with higher density in woody patches, plus structured sampling in cluster with strong spatial pattern, substantially increased estimation accuracy. Efficient sampling strategies for estimating SOC storage were developed based on these findings. Direct and spatial correlation and scaling analyses showed that SOC and TN were strongly correlated with litter and root biomass. Invaded woody vegetation has the most impact on spatial distribution of SOC and TN. Canonical correspondence analysis showed that variables related to landscape position were the primary factors determining the spatial distribution of woody species. These new insights will facilitate the estimation of soil C and N pools at landscape and regional scales, and will help evaluate the potential impacts of woody plant encroachment on the biogeochemistry of C and N.

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CHAPTER I

INTRODUCTION

Woody encroachment has been reported in many arid and semi-arid ecosystems around the world (Archer 1995, McPherson 1997). Explanations for this vegetation change include livestock grazing, suppression of fire, climate change, and atmospheric CO_2 enrichment (Archer 1995, Van Auken 2000). In the Rio Grande Plains of southern Texas, the conversion of grass to woody plant domination has occurred over the past century (Archer et al. 1988). This has been illustrated by studies using historical aerial photography, tree rings, carbon isotopes and ecosystem models (Archer et al. 1988, Scanlan and Archer 1991, Flinn et al. 1994, Boutton et al. 1998, Hibbard et al. 2001).

The invasion of woody plants in this region is often initiated by the establishment of *Prosopis glandulosa* (honey mesquite), which serves as a nurse plant by influencing soils and micro-environment and facilitating the dispersal of other woody plants beneath its canopy (Archer 1995). *Prosopis* has many unique biological properties such as the ability to nodulate and engage in symbiotic N_2-fixation (Johnson and Mayeux 1990, Zitzer et al. 1996), high emergence and survival rate (Brown and Archer 1989), and tolerance of defoliation early in its life cycle (Weltzin et al. 1998), all of which could potentially contribute to its successful establishment.

The current landscape at the La Copita Research Area (LCRA) consists of uplands with scattered woody patches embedded in a grassland matrix, and low-lying drainages with closed canopy woodlands. *Prosopis* dominates the tree layer of all woody components in the landscape. As *Prosopis* and other woody species establish and develop in uplands, clusters begin to form and coalesce (Archer 1995). The uplands consist of discrete woody clusters (comprised of a single *Prosopis* tree with up to 15

This dissertation follows the style of *Ecology*.

understory tree/shrub species) and larger groves (comprised of several woody clusters that have fused together) embedded within the grassland matrix. Evidence suggests that processes associated with woody cluster establishment and development are ongoing in the uplands, and have progressed to closed-canopied woodlands in low-lying drainages. Studies also indicated that population dynamics of native herbivores (Weltzin et al. 1997), and soil physical properties (Loomis 1989) may have effects on the rate and extent of woody encroachment in the uplands.

The shift from grass to woody domination has important impacts on microclimate, ecosystem structure, soil, hydrology and soil microbial activities (Scholes and Archer 1997). Invasion of woody plants into grasslands alters soil by forming "fertile islands" (Burke 1989, Jackson and Caldwell 1993, Schlesinger et al. 1996, McPherson 1997) and has impacts on both the magnitude and spatial heterogeneity of soil nutrient pools (Jackson and Caldwell 1993, Boutton et al. 1998). Since a large portion of the world's land surface is covered by arid and semi-arid ecosystems (Daly et al. 2000), woody invasion into these ecosystems can have important implications for regional and global biogeochemistry (Archer 1990, Schlesinger et al. 1990, Boutton et al. 1999, Martin et al. 2003, Asner et al. 2004). Although recent estimation of the C budget in USA treats shifts from grass domination to woody domination as a major C sink (Houghton et al. 1999, Schimel et al. 2001, Houghton 2003), there is still uncertainty about whether woody invasion increases, decreases, or causes no effect on soil organic carbon (SOC) storage. Many previous studies have found increased SOC storage after woody invasion in some ecosystems (Jackson and Caldwell 1993, Schlesinger et al. 1996, Archer et al. 2001, McCulley et al. 2004, Liao et al. 2006b, Boutton et al. 2007), while some other studies showed that invasion of woody plants caused net loss or no change in soil C storage (Jackson et al. 2002, Chapman et al. 2003). Furthermore, despite the fact that many woody species increasing in grass-dominated ecosystems around the world are capable of symbiotic N_2-fixation, little is known regarding the impact of woody invasion on soil total nitrogen (TN).

In order to evaluate the effects of woody invasion on SOC and TN storage at regional and global scales, it is necessary to develop appropriate methodologies to permit up-scaling from point measurements to these broader spatial scales. Since woody plant encroachment increases spatial heterogeneity of both vegetation and soil (Schlesinger et al. 1996, Bekele and Hudnall 2006), spatial variability and uncertainty of SOC and TN need to be considered in sampling designs to estimate their pool sizes (Conant and Paustian 2002, Legendre et al. 2004).

It is time consuming and expensive to collect and analyze large numbers of soil samples to estimate SOC and TN storage. Therefore, a better understanding of the spatial variability and uncertainty of soil attributes is required in order to optimize field sample designs aimed at achieving accurate estimates of SOC and TN storage with minimum sampling effort. Although several studies have been conducted to quantify spatial heterogeneity of soil properties after woody invasion (Jackson and Caldwell 1993, Schlesinger et al. 1996, Bekele and Hudnall 2006), few have explored the spatial uncertainty associated with soil C and how this spatial uncertainty could affect sampling designs to estimate SOC and TN storage.

The overall goal of this dissertation was to gain a better understanding of the spatial patterns of SOC and TN and their controlling factors in savanna landscapes, and to develop efficient sampling strategies for evaluating the effect of woody invasion on the SOC and TN pools at large scales.

Conditional stochastic simulations generate a large number of realizations based on known sample data, and the conditional probability distribution of the variable of interest at each location can be obtained from these realizations (Isaaks and Srivastava 1989, Goovaerts 1999). The probability distributions can provide information on spatial distribution of uncertainty in estimations, which can help in designing efficient point sampling strategies. In this study, conditional sequential indicator simulation (SIS) was conducted to understand the spatial patterns and uncertainties in SOC and TN distributions in relation to invasion of woody vegetation, and to facilitate the design of efficient sampling strategies. Sampling experiments were conducted based on the landscape structure and kriging maps of intensively sampled areas to evaluate different sampling strategies for their effectiveness in estimating soil C over the savanna landscapes. An efficient sampling strategy for quantifying the spatial pattern of SOC in the upland landscape of La Copita was developed and recommendations for sampling strategies for estimating SOC in similar arid and semi-arid landscapes undergoing woody encroachment were proposed.

Understanding which environmental factors influence soil C and N and their spatial scales is necessary for estimating SOC and TN storage across different scales. Many previous studies have examined correlations between SOC, TN and environmental factors such as climate (Burke et al. 1989), topography (Burke et al. 1999, Powers and Schlesinger 2002), soil moisture (Wang et al. 2002), plant species (Lovett et al. 2004), and time (Schlesinger et al. 1990). Their results suggested that not all factors have equal importance on the concentration and spatial distribution of SOC and TN, and the relative importance of environmental factors may change with scale. There has also been an increasing awareness of spatial autocorrelation of ecological variables and their effects on the validity of conventional statistical tests of significance in correlation analysis (Legendre et al. 2002). In this study, a 309 m transect was established along a topographic gradient running from an upland through a low-lying drainage woodland and into a playa in order to evaluate relationships between SOC, TN, vegetation, and soil attributes, as well as spatial scaling of those variables. Direct correlation of SOC and TN to vegetation and soil variables were examined using Pearson's correlation coefficient with modified t-test (Dutilleul et al. 1993) that corrected for spatial autocorrelation. Spatial cross-correlations between the variables were evaluated using cross-Mantel test

(Wu and Mitsch 1998). Quadrat variance methods (Hill 1973, Ludwig and Goodall 1978, Dale 1999) were used to detect the domains of scale for all variables. Results of these analyses were used together to understand the influence of vegetation and soil variables on the spatial distribution of soil C and N.

It has been hypothesized that in the presence of grazing livestock and in the absence of fire, the present savanna parkland in Rio Grande Plains of southern Texas represents an intermediate stage in the conversion of a grassland to a continuous woodland (Archer 1995). Studies suggested that soil texture and surface hydrological processes might influence the rate and extent of this proposed succession (Loomis 1989, Wu and Archer 2005). Previous studies also indicated that interactions between woody species and coexistence between woody species and herbaceous plants in savannas affect vegetation dynamics and woody species composition (Brown and Archer 1990, Francopizana et al. 1995, Barnes and Archer 1996, 1999). However, few have examined how environment factors (such as elevation, soil moisture, and soil nutrients) influence woody species assemblages and how the influence varies in different successional stages of the vegetation. In this study, we examined the spatial distribution of woody species along a topoedaphic gradient and explored the relative importance of environmental factors in affecting woody species distribution using canonical correspondence analysis (CCA) with vegetation and soil data along a transect across the topoedaphic gradient.

This dissertation is organized into five chapters. Chapter I provide a general introduction to the background and objectives of the dissertation work. Chapter II focuses on quantifying the spatial pattern and uncertainty associated with SOC through conditional stochastic simulation and sampling experiments, and developing efficient sampling strategies for quantifying SOC pattern in savanna landscapes. Chapter III deals with identifying soil and vegetation attributes and quantifying their influence on spatial distribution of SOC and TN through examining their direct and spatial correlation and scaling. Chapter IV aims at determining the influence of physical variables related to landscape position and soil C and N on woody vegetation structure and possible feedback of woody invasion process using canonical correspondence analysis (CCA). Chapter V provides an overall summary of the main findings of this dissertation.

CHAPTER II

SPATIAL PATTERN AND UNCERTAINTY OF SOIL ORGANIC CARBON IN A SUBTROPICAL SAVANNA LANDSCAPE AND IMPLICATIONS FOR SAMPLING DESIGN

Introduction

Woody encroachment has occurred in many arid and semi-arid ecosystems all over the world (Archer 1995, McPherson 1997). Causes of this change include several or all of the following: climate change, livestock grazing, suppression of fire, and atmosphere CO_2 enrichment (Boutton et al. 1994, Archer et al. 1995, Brown et al. 1997, Van Auken 2000). The shift from grass domination to woody domination has important impacts on the microclimate, ecosystem structure, soil, hydrology and soil microbial activities (Scholes and Archer 1997). Since a large portion of the world's land surface is covered by arid and semi-arid ecosystems (Daly et al. 2000), woody invasion into these ecosystems can have important implications on regional and global biogeochemistry and climate (Archer 1990, Boutton et al. 1999, Martin et al. 2003).

Studies using historical aerial photos, tree rings, carbon isotope and ecosystem models have shown that woody plant invasion has occurred in the southern Texas over the past 100 years (Archer et al. 1988, Archer 1989, Scanlan and Archer 1991, Flinn et al. 1994, Boutton et al. 1998). Previous studies indicated that the presently C_3 woody dominated savanna system was once dominated by C_4 grasses (Boutton et al. 1998). This alternation in the relative abundance of woody vs. herbaceous life forms was initiated by the establishment of honey mesquite (*Prosopis glandulosa*), an arborescent legume. Mesquite trees served as nurse plants by influencing soils and microclimate and the dispersal of seeds of other woody plants beneath their canopies (Archer 1995).

Invasion of woody plants into grasslands has impacts on both the magnitude and spatial heterogeneity of soil nutrient pools (Jackson and Caldwell 1993, Boutton et al.

1998). Previous studies have found increased soil organic carbon (SOC) storage after woody invasion in some ecosystems (Jackson and Caldwell 1993, Schlesinger et al. 1996, McCulley et al. 2004, Liao et al. 2006b), but no net change or decreased SOC storage in others (Gill and Burke 1999, Jackson et al. 2002). Due to the large extent of woody invasion into grasslands across the world, many studies have been focused on how these woody invasions could affect soil carbon dynamics and potentially atmospheric CO_2 and the climate system. Accurate measurement of SOC storage across multiple spatial scales is critical in order to evaluate the effects of woody invasion on the carbon cycle.

Understanding spatial variability and uncertainty of soil attributes is necessary for their accurate estimation. Studies indicated that spatial pattern and heterogeneity needed to be considered in sampling designs to estimate changes in soil attributes (Conant and Paustian 2002, Legendre et al. 2004). However, it is time consuming and expensive to collect and analyze large numbers of soil samples, so a better understanding of the spatial uncertainty and variability of soil attributes could be used to optimize field sample design in order to accurately estimate SOC storage with minimum sampling effort. Though several studies have been conducted to quantify spatial heterogeneity of soil properties after woody invasion (Jackson and Caldwell 1993, Schlesinger et al. 1996, Bekele and Hudnall 2006), none have explored the spatial uncertainty associated with SOC and how this spatial uncertainty could affect estimation of SOC storage.

Conditional stochastic simulations like Sequential Gaussian Simulation (SGS) and Sequential Indicator Simulation (SIS) can be used to assess the spatial uncertainty of a variable by generating a large number of realizations based on known sample data. Through simulation, the conditional probability distribution of the variable of interest at each location could be obtained from these realizations (Isaaks and Srivastava 1989, Goovaerts 1999). These probability distributions could quantify the amount of uncertainty associated with the variable at different topographic locations and under different vegetation types. By using the information on spatial uncertainty associated with soil attributes and spatial correlation between aboveground vegetation and soil attributes, we could design efficient point sampling strategies to minimize soil sampling density while achieving a desired accuracy for landscape scale SOC estimation. Sampling designs could be evaluated either by comparing results generated from reduced data sets with those based on the full data set (Atkinson et al. 1994), or by comparing their spatial properties (Chang et al. 1998).

The purpose of this study was to quantify the spatial pattern and uncertainty of SOC, and evaluate how this uncertainty affects the estimation of SOC in a subtropical savanna landscape where woody plants have increased in abundance during the past century. The specific objectives were to: (1) Quantify the spatial uncertainty of SOC; (2) Evaluate the performance of different sampling designs in estimating SOC storage; and (3) Develop effective sampling strategies based on the spatial pattern and spatial uncertainty of SOC.

Methods

Study site

This study was conducted at the Texas Agricultural Experiment Station La Copita Research Area (LCRA, 27°40’N, 98°12’W) located 65 km west of Corpus Christi, Texas. Elevation ranges from 75 to 90 m above sea level. The landscape grades with gentle slopes (< 3%) from uplands to drainage lowlands and bottom playas. The climate is subtropical with warm, moist winters and hot, dry summers. Mean annual temperature is 22.4 °C with an average growing season of 289 days. Mean annual precipitation is 680 mm with bimodal peaks in May and September. Uplands have sandy loam soils (Typic and Pachic Argiustolls) while drainages and playas have clay loam or clay soils (Pachic Argiustolls). The site has been grazed continuously from the late 1800’s.

Upland portions of the landscape are subtropical savanna parklands with discrete woody patches scattered in a continuous C_4 grassland matrix (Figure 1). Woody patches can be classified as smaller clusters (1-100 m^2) and larger groves (>100 m^2). Clusters usually have a honey mesquite in the center with other understory shrub species beneath its canopy. Occasionally, discrete clusters expand laterally and coalesce to form groves with overlapping mesquite canopies. Understory shrub species are similar in both clusters and groves and they include some or all of the following: *Zanthoxylum fagara*, *Celtis pallida*, *Condalia hookeri*, *Diospyros texana*, *Schaefferia cunefolia*, *Ziziphus obtusifolia* and *Berberis trifoliolata*. The grassland matrix between woody patches is dominated by C_4 grasses such as *Paspalum setaceum*, *Setaria geniculata*, *Bouteloua rigidiseta*, and *Chloris cucullata*, but also includes a significant C_3 forb component (Archer 1990).

Field sampling

In January of 2002, a 160 m ×100 m plot was established on an upland portion of the landscape. The plot was divided into 10 m × 10 m grid cells. PVC poles were installed in every corner of each grid cell and their coordinates were determined using a Trimble Pathfinder Pro XRS GPS unit (Trimble Navigation Limited, Sunnyvale, CA). Two random points within each grid cell were selected to collect soil samples (320 total, Figure 1) using a soil corer (length = 15 cm, diameter =2.24 cm). At each point, two cores were collected adjacent to each other; one core was used to determine SOC concentration, and the other was used to determine soil bulk density. Distances from each soil sampling point to two nearby poles were measured. Vegetation cover at each sample point was recorded as grassland, cluster or grove.

Within the upland plot, 3 groves, 5 clusters and 3 grassland plots (Figure 2) were selected for intensive sampling in addition to the random soil samples mentioned above. The 3 groves were selected to represent large, medium and small size groves, respectively. Each grove was divided into 5 m × 5 m grid cells. PVC poles were established to mark the corners of each grid cell and their coordinates were determined using the GPS unit mentioned above. Two random points were located within each grid cell for soil sampling. For each grove, 3 tree-to-tree transects of different orientations from grove center to the outside grassland were established. Soil samples were collected at each random point and along the 3 tree-to-tree transects in exactly the same manner as described above for the 160 m x 100 m grid. Coordinates of each soil sample point were determined by measuring distances to nearby PVC poles. A total of 63, 37, and 24 soil samples were collected from the large, medium, and small groves, respectively.

Five clusters were selected at different topographic locations and they also represented different size classes. For each cluster, 3 transects were established from the cluster centers to the adjacent grasslands with orientations at about 120 degrees from each other (Figure 3). Each transect consisted of 7 soil sample points, which were determined by their relative locations along the transect from cluster center to the outside grassland. The 7 locations were: (a) near the center of each cluster (near tree trunk), (b) 1/3 the distance between the cluster center to cluster canopy edge, (c) 2/3 the distance from the center to the canopy edge, (d) 15 cm inside canopy edge, (e) 15 cm outside canopy edge, (f) outside canopy with a distance equal to 1/3 the distance between the cluster center and its canopy edge, and (g) outside canopy with 2/3 of the distance between the cluster center and its canopy edge (Figure 3). In addition, 3 or 4 random points were selected within each cluster for soil sampling. A total number of about 25 soil samples (0-15 cm) were collected for each cluster. Four or five rebars were installed in each cluster as reference markers and their coordinates were determined using a GPS unit. Coordinates of soil sample points were determined by measuring their distances to 2 nearby reference markers.

Three grassland plots (6 m × 10 m) were established at different topographic locations within the upland plot. Each grassland plot was divided into 2 m × 2 m grid cells and their corners were marked using rebars. Coordinates of each rebar were determined using the same GPS unit. Two random points were selected within each grid cell for soil sampling. A total of 60 soil samples (0-15 cm) were collected in each

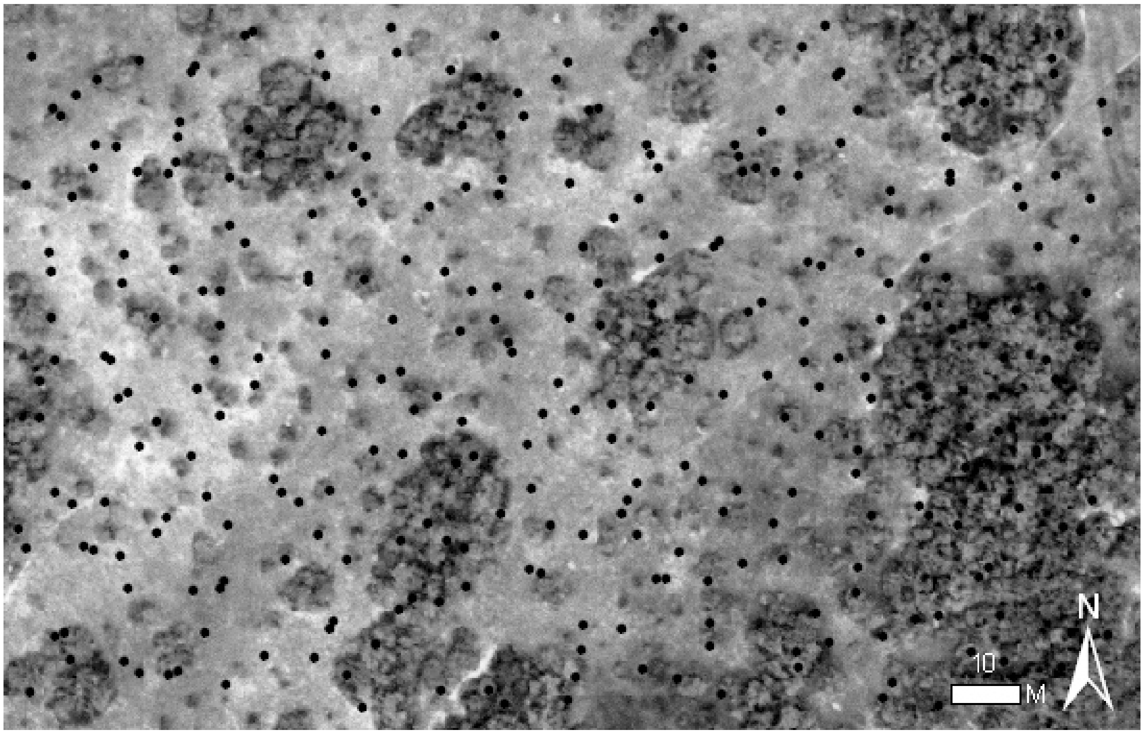

Figure 1. Aerial photograph showing the upland plot with locations of 320 random soil samples (dark points). Dark patches are clusters and groves, light grey color indicates open grassland.

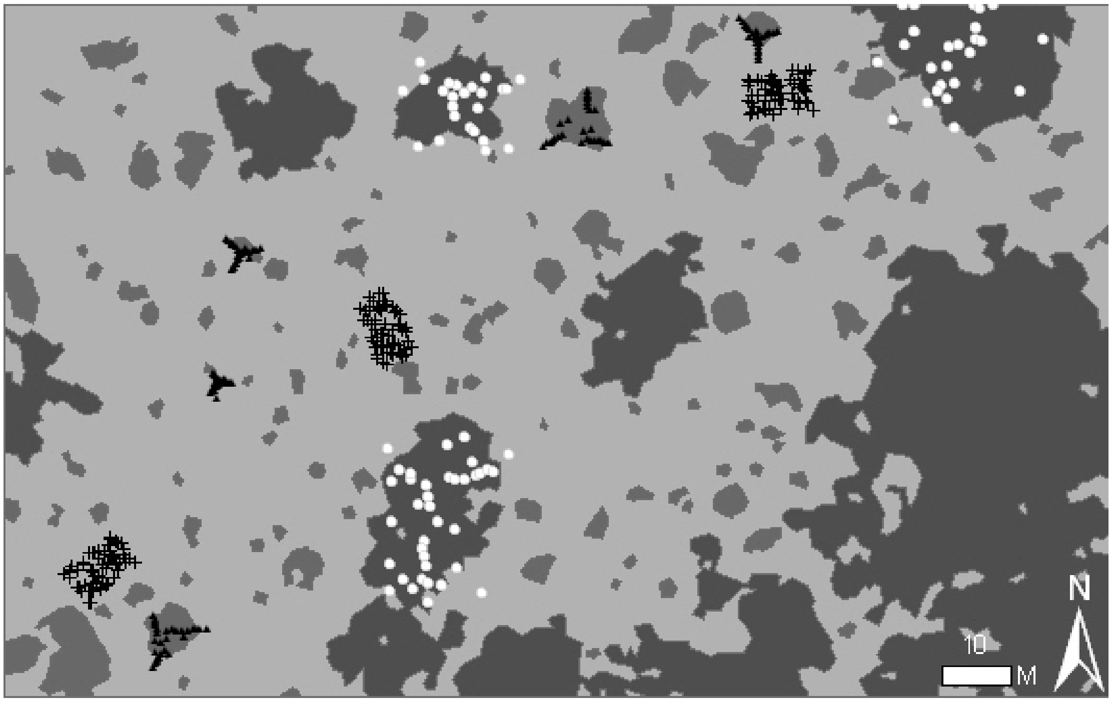

Figure 2. Classified vegetation map and intensively sampled plots in the upland plot. Dark color represents groves, grey represents clusters, and light grey represents open grassland. Intensively sampled plots are: 3 groves ("O", solid white circles), 5 clusters ("▲", black triangles) and 3 grassland plots ("+", black crosses).

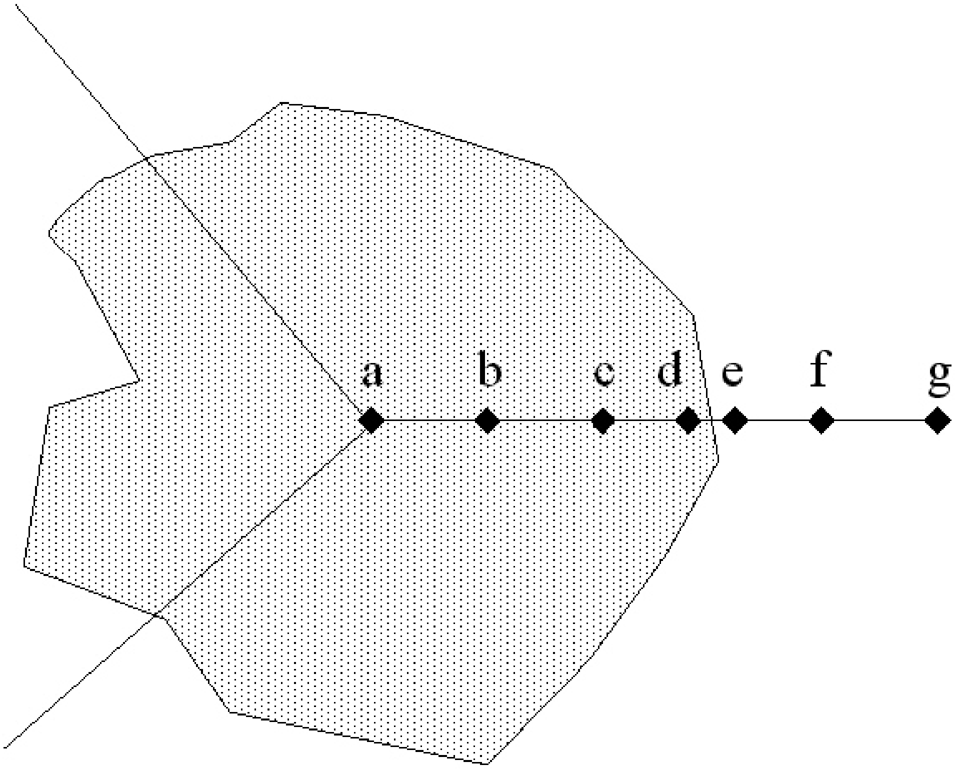

Figure 3. Diagram illustrating the relative locations of soil samples along transects in clusters. (a) Near the center of each cluster (near tree trunk), (b) 1/3 the distance between the cluster center to cluster canopy edge, (c) 2/3 the distance from the center to the canopy edge, (d) 15 cm inside canopy edge, (e) 15 cm outside canopy edge, (f) outside canopy at distance equal to 1/3 the distance between cluster center and its canopy edge, and (g) outside canopy at 2/3 of the distance between cluster center and its canopy edge.

grassland plot. Coordinates of each soil sample point were determined by measuring the distances to the 2 nearest rebars.

Two soil cores (0-15 cm) were collected at each sampling point mentioned above to determine the SOC and soil bulk density. Coordinates of these soil-sampling points were calculated and imported into ArcView GIS (ESRI, Redlands, CA). Animal disturbances (e.g., burrows, feral hog excavations, etc.) within the selected groves and clusters were also surveyed. Location and area of each animal disturbance were recorded.

Laboratory analyses

Soil cores used to determine soil organic carbon concentrations were dried at 60°C for at least 48 hours, passed through a 2 mm screen to remove gravel and coarse organic fragments, and then pulverized to a fine powder in a centrifugal mill (Angstrom, Inc., Belleville, MI, USA). Samples were weighed into silver capsules (5 x 7 mm) using a microbalance, treated with HCl vapor in a desiccator to remove carbonates (Harris et al. 2001), and then dried. SOC concentration was measured by combustion/gas chromatography using a Carlo Erba EA-1108 (CE Elantech, Lakewood, NJ) elemental analyzer. Soil bulk density was determined by core method (USDA 2004). SOC concentration was then converted into density (g m^{-2} for 15 cm) using the following equation:

$$\text{SOC (g m}^{-2}\text{)} = \text{SOC (\%)} \times \text{bulk density (g cm}^{-3}\text{)} \times 10000\ (\text{cm}^2\ \text{m}^{-2}) \times 15\ (\text{cm})$$

Color infrared aerial photography was taken in April 2003 for the upland plot. Negative photography was scanned (0.25 m nominal resolution) and geo-referenced using ERDAS Imagine (ERDAS 1997). The aerial photo imagery was then classified using unsupervised classification with Iterative Self-Organization Data Analysis (ISODATA) method (ERDAS 1997). This classification initially grouped pixels into 30 classes based on reflectance value similarities. Then these 30 classes were collapsed into either woody or non-woody classes. Woody patches smaller than 1 m^2 were treated as non-woody because data showed little difference in SOC content between grassland and clusters smaller than 1 m^2 (unpublished data). Woody patches larger than 1 m^2 were then classified as either cluster (1-100 m^2) or grove (>100 m^2) based on their sizes. The classified vegetation map is shown in Figure 2.

Geostatistical analyses

ANOVA was performed using SPSS for Windows, version 12.0 (SPSS Inc., Chicago, IL) to compare SOC under different vegetation types, i.e. grassland, cluster, or grove. Sample variogram of SOC was developed to quantify its spatial structure and a variogram model was fitted using VARIOWIN version 2.2 (Pannatier 1996). Based on the sample variogram and the fitted variogram model, GSLIB (Deutsch and Journel 1998) was used to perform kriging to predict the SOC value at unsampled locations in the upland plot.

Most ecological variables are spatially autocorrelated, which means samples closer together are more similar than those farther apart. Variogram, a plot of semivariance against separation (lag) distance, is used to quantify dissimilarity between samples at a certain distance. Semivariance is defined as half the average squared difference between sample pairs separated by a given lag distance:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{(i,j)|h_{ji}=h} i(v_i - v_j)^2$$

where $\gamma(h)$ is semivariance with a lag distance h, N (h) is the number of sample pairs separated by lag distance h, and V_i and V_j represent variable V at locations i and j. The plot of semivariance versus lag distance is often used to measure spatial structure of a variable (Isaaks and Srivastava 1989). For a typical variogram of an ecological variable with spatial autocorrelation, semivariance will increase with increased separation distance and will eventually reach a plateau value. The semivariance value where the curve levels off is called the sill. The lag distance where the curve levels off is called range, which indicates the maximum separation distance within which the variable is autocorrelated.

The semivariance value when lag distance approaches zero is called the nugget, which could be caused by factors like sampling error or variability at finer scales. The difference between sill and nugget is the structural variance. The ratio of structural variance to sill represents the proportion of the total variance explained by the spatial structure.

Kriging is a set of geostatistical approaches to predict values of a variable at unsampled locations based on sampled data and their spatial structure. The estimation at one unsampled location is calculated by using the weighted average of neighboring known samples. The weights were determined by a kriging system, which takes into account the spatial structure of the samples, with minimum estimation error variance under the constraint of unbiased estimator condition. Ordinary kriging, a best linear unbiased estimator that honors sample data, was used in this study to estimate SOC in the upland plot.

Conditional stochastic simulations

Although kriging provides an error variance, which has been often misused as a measure of the reliability of the kriging estimate (Goovaerts 1999), it is not a good measure of the uncertainty associated with the variable itself. Conditional stochastic simulations are suitable to assess spatial uncertainty by generating multiple alternative estimations while honoring the spatial structure of the sample data.

The basic idea of stochastic simulation is to generate a set of equable realizations of the spatial distribution of the variable, all reproducing reasonably the global statistic and spatial features of data samples. Each simulation is a representation of reality (Deutsch and Journel 1998). The ensemble of these realizations is thus an explicit representation of the uncertainty associated with the conceptual understanding of the single, but unknown reality (Rautman and Istok 1996). Differences among equable simulated maps could provide measures of uncertainty (for example, confidence intervals or the possibility of above or below a threshold), which accurately represents spatial variability for the variable of interest (Goovaerts 2001). Conditional stochastic simulation is more suitable in cases where uncertainty evaluation and risk assessment are important.

The idea of conditional simulation is based on the concept of random function (Isaaks and Srivastava 1989), Monte Carlo approach and conditional probabilities. A random variable can have multiple outcomes based on a probabilistic mechanism. Sampled value at a given location is a realization of the random variable. A set of such random variables in a certain space is called random function. Since sample data are treated as a representation of the random function, the sample data in such space can be viewed as one realization of the random function at sampled locations (Rossi et al. 1993). The variogram model of sample data could represent the random function's spatial structure. For this study, SOC can be treated as a random variable. At any soil sample point in the upland plot, the measured SOC value is a realization of the random variable. Based on the spatial structure of SOC samples, the probability distribution of SOC at any unsampled locations can be estimated using some form of kriging. A simulated SOC value at this location will be randomly selected from the estimated probability distribution and it will be treated as a realization of the random variable at this location. In the process of each simulation, prior simulated values are treated as known data and considered in subsequent simulations for unknown points. The simulations honor the sample data at sampling locations, and reproduce the sample histogram and the spatial structure described in the sample variogram model. Each simulation will follow a different random path over the domain and produce a distinct realization from other simulation runs.

Conditional sequential indicator simulation (SIS) is a common type of conditional simulation method. SIS uses indicator kriging to estimate the probability distribution of a random variable at any unsampled location. Sequential indicator simulation does not assume the distribution of sample data when estimating the probability distribution of the random variable. It uses an indicator variable to perform a nonparametric transformation of the data. An indicator random variable, *I* (*x*,*z*) is defined as either 0 or 1 depending on whether or not the continuous variable Z(x) exceeds some cutoff value z:

$$I(x;\, z) = \begin{cases} 1 & \text{if } Z(x) \;\leq\; z \\ 0 & \text{if } Z(x) \;>\; z. \end{cases}$$

SIS was performed 500 times to simulate SOC for the upland plot based on 320 random samples. The cutoffs chosen to transform sample SOC into indicator variable were 9 deciles plus the SOC value at 0.05 and 0.95 cumulative distribution percentages. Variowin (Pannatier 1996) was used to construct sample variograms and fit variogram models at each cutoff. SIS simulations were conducted using SISIM program of GSLIB (Deutsch and Journel 1998). Mean and standard deviations of estimated SOC at each location were calculated based on the 500 simulations. The obtained standard deviation at any location is an indication of how much uncertainty is associated with SOC at that location.

In order to examine the spatial pattern and uncertainty of SOC in each vegetation type, mean and standard deviation of SOC from the 500 SIS simulations were then overlapped with the classified vegetation map using ArcView GIS. A complete set of means and standard deviations for SOC for each vegetation type (grassland, cluster and grove) was then generated. Frequency distribution of these means and standard deviations of SOC were then developed for each vegetation type.

The SIS was accomplished 500 times through the following steps:

1. Transform the original SOC content data into indicators by using 11 cutoffs mentioned above.
2. Construct variogram model for the indicators at each cutoff using Variowin (Pannatier 1996).
3. Define a random path that the simulation will follow.

4. At each simulation node and for each cutoff, simple indicator kriging was used based on neighboring sample data and previously simulated nodes. The simple indicator kriging mean estimates the conditional probability distribution for this location.
5. Draw randomly from this conditional distribution and assign that value to the simulation node.
6. Repeat steps 4 and 5 till all simulation locations have either original value or simulated value.
7. Repeat steps 3 to 6 to generate multiple simulations; different random paths were followed for different simulations.

Design of optimum sampling regimes

Estimation error and sampling density in different vegetation types

The intensively sampled plots (3 groves, 5 clusters, and 3 grassland plots) have high sampling densities (ca. 800 per ha for groves, ca. 500 per ha for clusters and 1000 per ha for grassland plots). Therefore, kriged maps of SOC within these plots based on the intensive data can be considered as a reasonable approximation to actual distribution of SOC in these vegetation types and they can be used as reference maps to evaluate estimation errors for sampling regimes that differ in intensity. To develop these reference maps, kriging was first performed for SOC using all data in the upland plot, both the random sample data and the data from the intensively sampled plots. The intensively sampled plots from the kriged map of SOC were clipped out and used as the reference maps for the 3 correspondent vegetation types. Complete random sampling with different densities was then conducted on these reference maps to evaluate the accuracy of the estimations of SOC storage. Estimation errors were determined as the difference between estimated SOC storage from sampling of a given density and that based on the entire kriged map. The spatial uncertainty of SOC in each of the vegetation types as suggested by estimation error was also compared to the spatial uncertainty obtained through stochastic simulations.

Effectiveness of alternative sampling designs

Assuming these clipped kriged maps of intensively sampled plots are representative of the SOC content for corresponding vegetation types, SOC data for the intensively sampled plots of each vegetation type were extrapolated to represent all areas of the vegetation types in the upland plot. Based on the spatial uncertainty of SOC in different vegetation types suggested by SIS simulation results, 3 alternative sampling designs were applied to the extrapolated data set to evaluate their accuracy of estimating SOC storage. Estimation errors were measured as the difference between estimated SOC storage using each sampling design and that for the complete data set. The first design was complete random for the whole extrapolated landscape. Total SOC storage was estimated as the product of SOC concentration (based on the mean value of all random samples) and the landscape area. The second design was stratified random sampling by grassland, cluster and grove, respectively. Grassland, cluster and grove had the same sampling density. The SOC storage for each vegetation type was obtained by the average SOC concentration for the vegetation type times its area. The overall SOC storage for the landscape was calculated as the sum of SOC storage in the three vegetation types. The third design used a stratified random method with unequal densities. Due to higher spatial uncertainty of SOC in groves and clusters than in grassland as shown by SIS simulation results, the sampling density for clusters and groves was set twice as high as that for grassland. The total SOC storage was then obtained by summing the SOC storage in the 3 different vegetation types. For each of these alternative sampling designs, a series of overall sampling densities (10 - 200 samples/ha) were used to compare the accuracy of these alternative sampling designs as a function of sampling density.

Estimation errors on simulated landscapes

Assuming the pattern of spatial uncertainty of SOC in the grassland, cluster and grove areas of the upland plot is representative of similar landscapes in the area, estimation errors of the intensively sampled plots then could be used as a basis to evaluate how the estimation error vary in simulated landscapes as a function of the levels of woody invasion. Estimation errors were calculated for simulated landscapes with varying percent woody (cluster, grove) cover while keeping the cluster to grove ratio constant for simplicity.

Sampling design considering spatial pattern of SOC in clusters

Previous studies in our study site indicated that clusters had higher SOC than grassland and it has strong spatial pattern (Archer et al. 2001, Liao et al. 2006b). Both the magnitude and variability of SOC decrease exponentially from center to canopy edge of clusters (Archer et al. in preparation). Several sampling designs, both random and transect samplings, were tested in order to take into account the spatial pattern and evaluate their accuracy in estimating SOC content. These tests were conducted based on intensively sampled clusters using the kriged SOC as the reference map.

Results

Spatial pattern of SOC

SOC was significantly different between vegetation types. The average SOC content for the upper 15 cm of the soil profile decreased from groves ($\bar{x}$ = 1832 g C m^{-2}) to clusters ($\bar{x}$ = 1500 g C m^{-2}) and grasslands ($\bar{x}$ = 1282 g C m^{-2}, Figure 4). Groves had the highest variability of SOC (standard deviation [SD] = 427 g C m^{-2}) while grasslands had the lowest variability (SD = 221 g C m^{-2}, Figure 4).

Sample variogram plot of SOC indicated apparent spatial structure (Figure 5). The variogram model fitted to this sample variogram had a range of 36.8 m, which indicated the extent of spatial autocorrelation in SOC. The sill and nugget of the

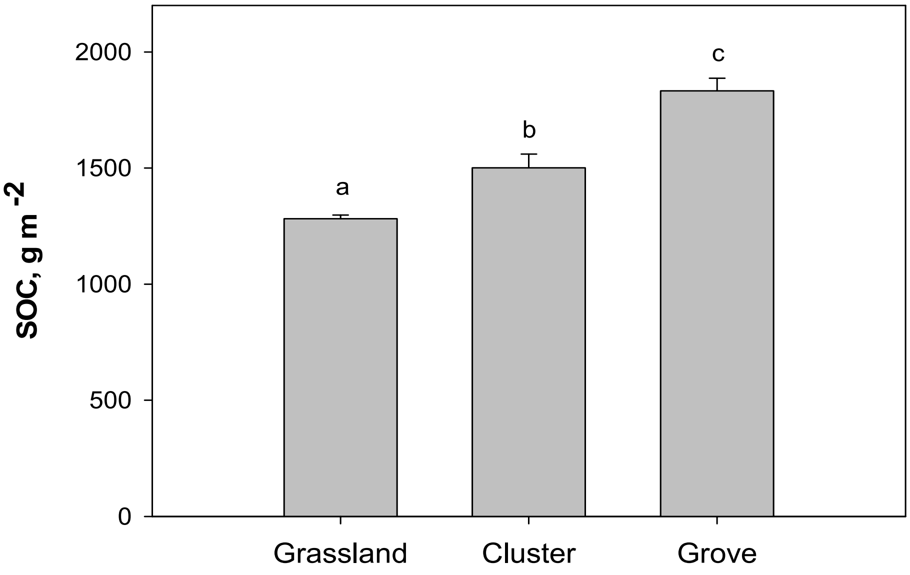

Figure 4. Average soil organic carbon (SOC) content under different vegetation types (grassland, cluster and grove). Error bars are the standard error of the mean. Different letters indicate significant difference at $P<0.05$.

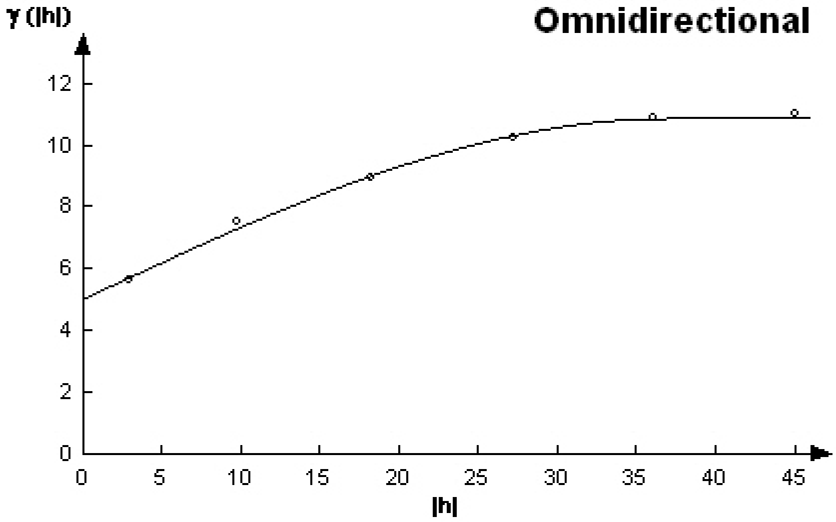

Figure 5. Sample variogram of SOC for random soil samples and fitted model with separation lag distance of 9 m. The fitted model is a spherical model with nugget = 5.07, range = 36.8 m, sill = 10.92.

variogram model were 10.92×10^4 and 5.07×10^4, respectively. The ratio of structure variance to sill was 0.54, which represents the proportion of the total variance explained by the spatial structure. The predicted map of SOC generated by ordinary kriging displayed a spatial pattern similar to that of vegetation cover, especially the distribution of woody patches (Figure 1, Figure 6). Soil under woody patches had higher SOC while soil in grassland had lower SOC. In addition, the kriged map showed that SOC was generally higher in the center compared to the edges of woody patches. Since the ordinary kriging was based on 320 random samples (2 per 10 m × 10 m grid cell), some woody patches did not show higher SOC due to the lack of random samples in these patches.

Spatial uncertainty of SOC

Two examples of the SIS simulations of SOC are shown in Figure 7. The spatial patterns of SOC in the simulation realizations were similar to those in the kriged map of SOC, but the former had greater spatial variation than the latter. Similar to the kriged map of SOC, the map of the means of the 500 simulations showed that clusters and groves had higher SOC than grasslands (Figure 8a). Higher SOC values can be found in the lower right corner of the plot and other areas occupied by woody patches. Grasslands covered most of the areas with lower SOC. Spatial distribution of SOC indicated that it was closely related to the spatial distribution of woody vegetation density (Figure 1, Figure 8).

Standard deviations of SOC at each location based on the 500 SIS simulations quantify the uncertainty associated with SOC at that location (Figure 8b). Higher standard deviations indicate higher spatial uncertainty. Higher uncertainty for SOC was associated with wooded portions of the landscape, whereas grassland areas had lower uncertainty.

The classified vegetation map (Figure 2) was overlaid with maps of mean and standard deviation of SOC obtained from the 500 simulations to get a complete set of

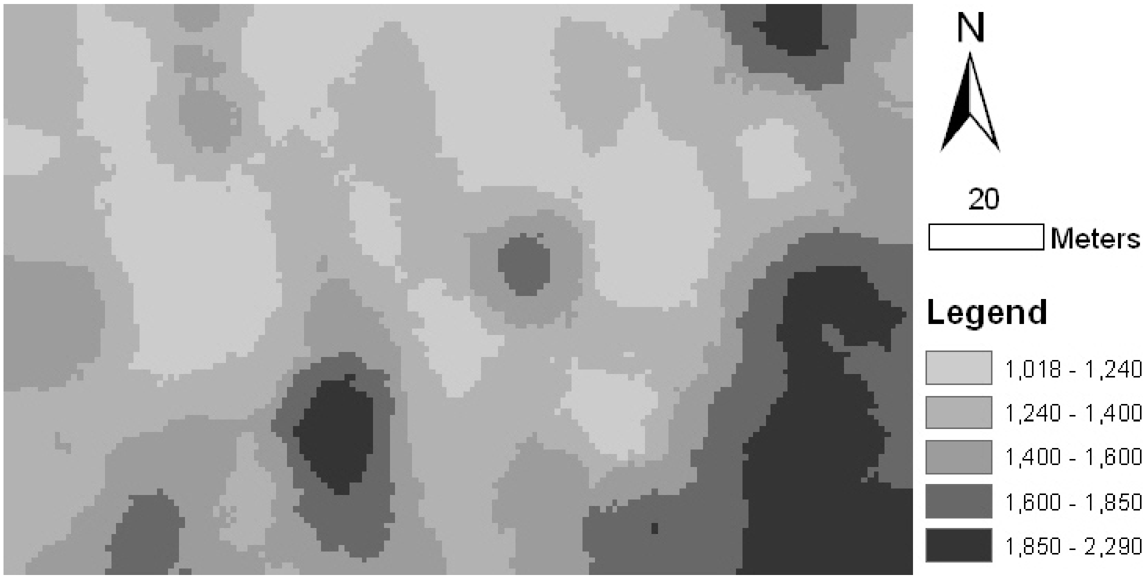

Figure 6. Kriged map of SOC (g C m^{-2}) in the upland plot based on 320 random points. SOC increases with darkness of shading.

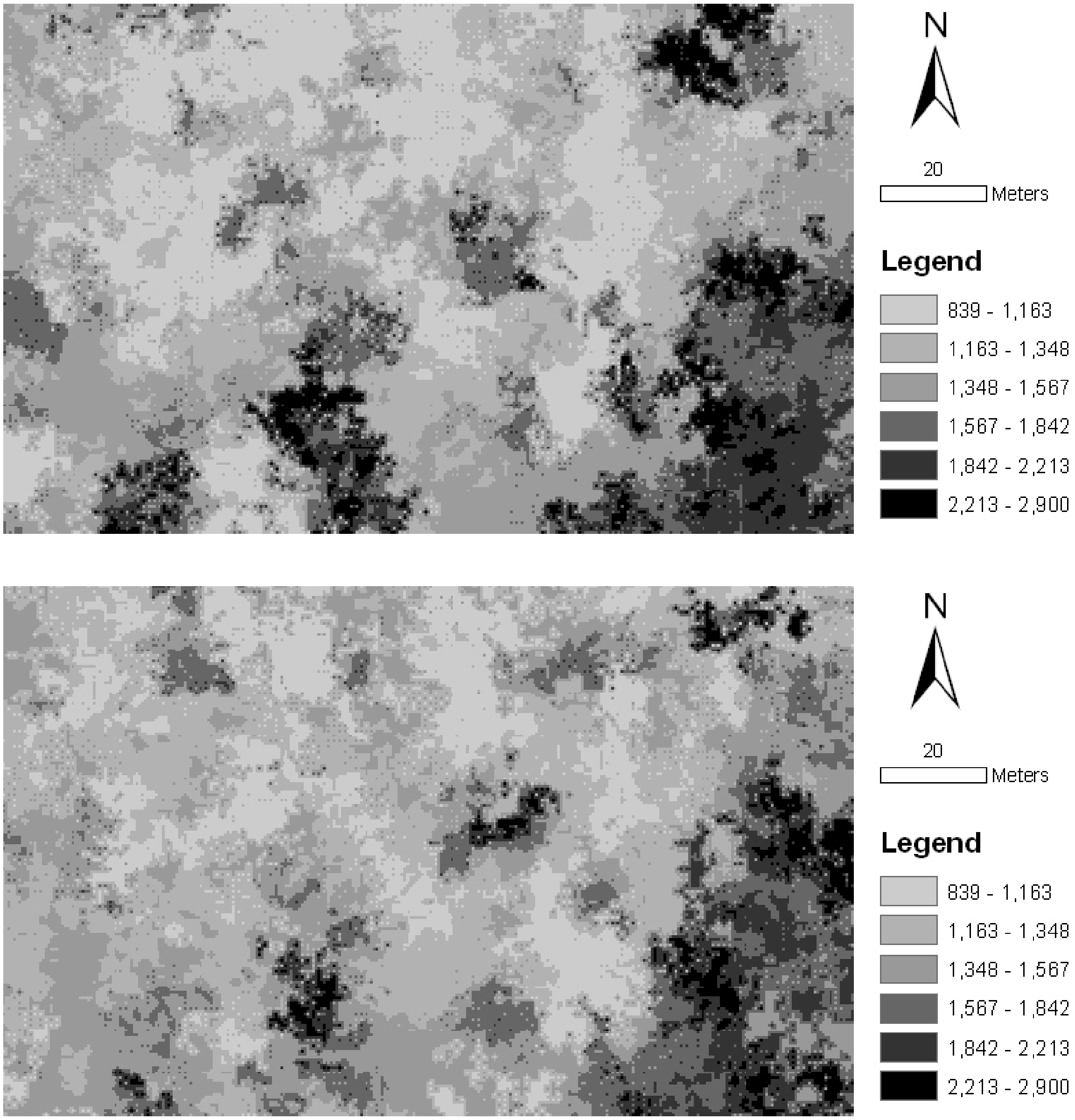

Figure 7. Two randomly selected sequential indicator simulation (SIS) realizations for mapping SOC (g C m^{-2}) in the upland plot based on 320 random samples.

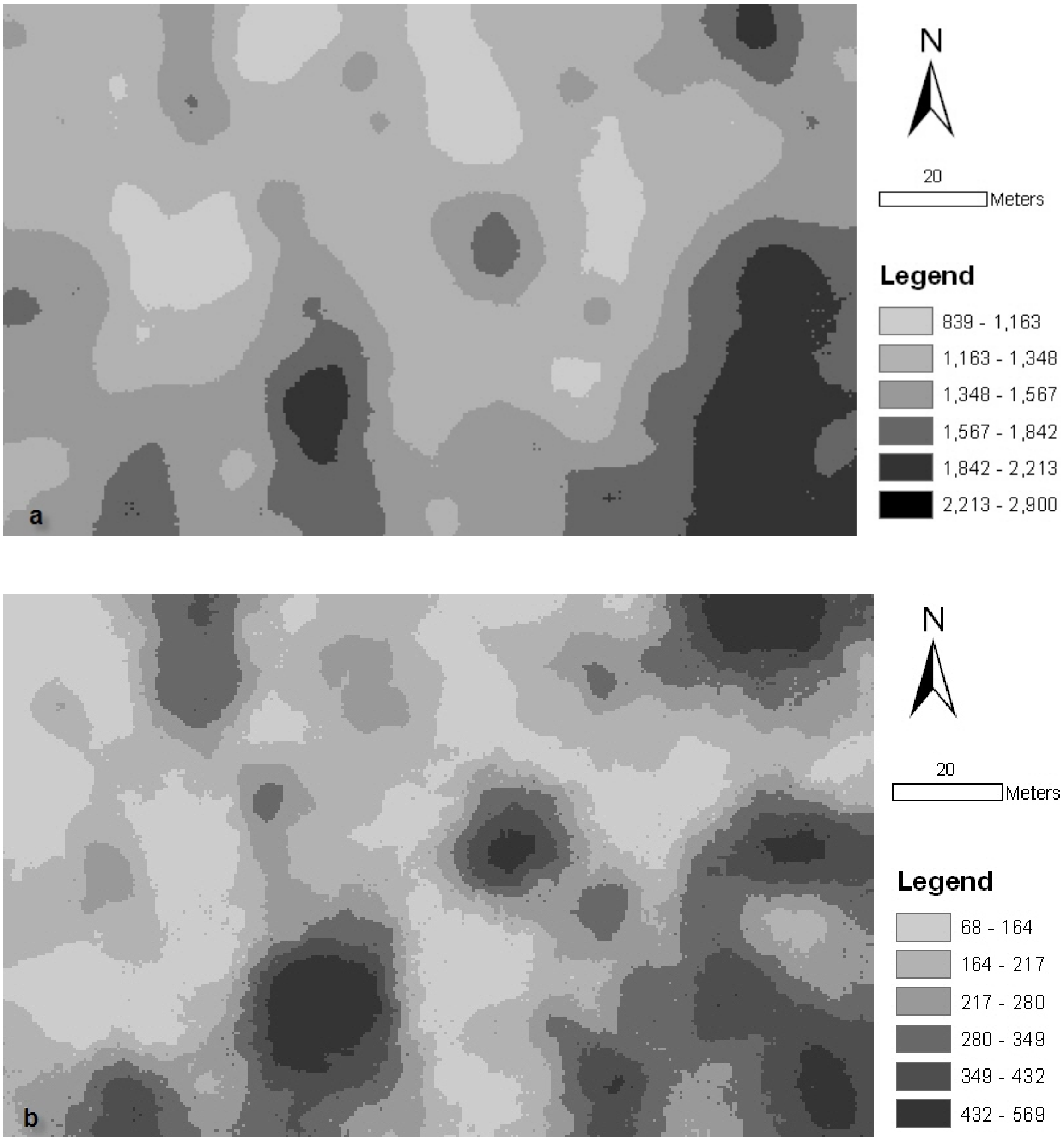

Figure 8. Mean (a) and standard deviation (b) of SOC derived from 500 sequential indicator simulations (SIS) based on 320 random sample points. SOC increases with darkness of shading.

mean and standard deviation values of SOC for each landscape element (grassland, cluster, and grove). The frequency distribution of the mean of simulated SOC content showed that most grassland areas had a low SOC with a relatively narrow spread, which indicated that grassland SOC had low spatial variability (Figure 9a). Clusters had a frequency distribution of mean SOC similar to that of grassland, but they had a higher frequency of SOC values around 1250 g m^{-2} and 1450 g m^{-2} (Figure 9a). In contrast, groves had higher percentage of higher mean SOC values. The spread of SOC distribution in groves was also wider than that in clusters and grassland, which indicated that SOC values in groves were more variable than those in clusters and grassland.

Grassland and clusters showed similar frequency distribution patterns of the standard deviation in simulated SOC except higher frequencies around 260 g m^{-2} in the clusters (Figure 9b). The standard deviations of simulated SOC in groves were much higher than those in clusters and grassland, which suggested a substantially greater uncertainty in SOC estimates in the groves than in clusters and grassland.

Optimum sampling regimes

When completely random sampling with different densities were evaluated against the kriged maps of intensively sampled plots, estimation errors decreased with increasing sampling density for all vegetation types (Figure 10). For any given density, clusters had the highest estimation error while grasslands had the lowest, which suggested that SOC in clusters was more variable than that in grassland. Estimation errors for groves were between those of grassland and clusters. For groves, estimation error decreased dramatically as sampling density increased up to approximately 50 samples/ha, suggesting this is a threshold density for estimating SOC in groves using complete random sampling. Sampling densities less than 50 samples/ha were not tested for clusters and grasslands due to the small dimensions of the intensive sampling plots in those landscape elements. There appear to be a threshold sampling density of approximately 150 samples/ha, for grasslands. In contrast, estimation errors in clusters only leveled off

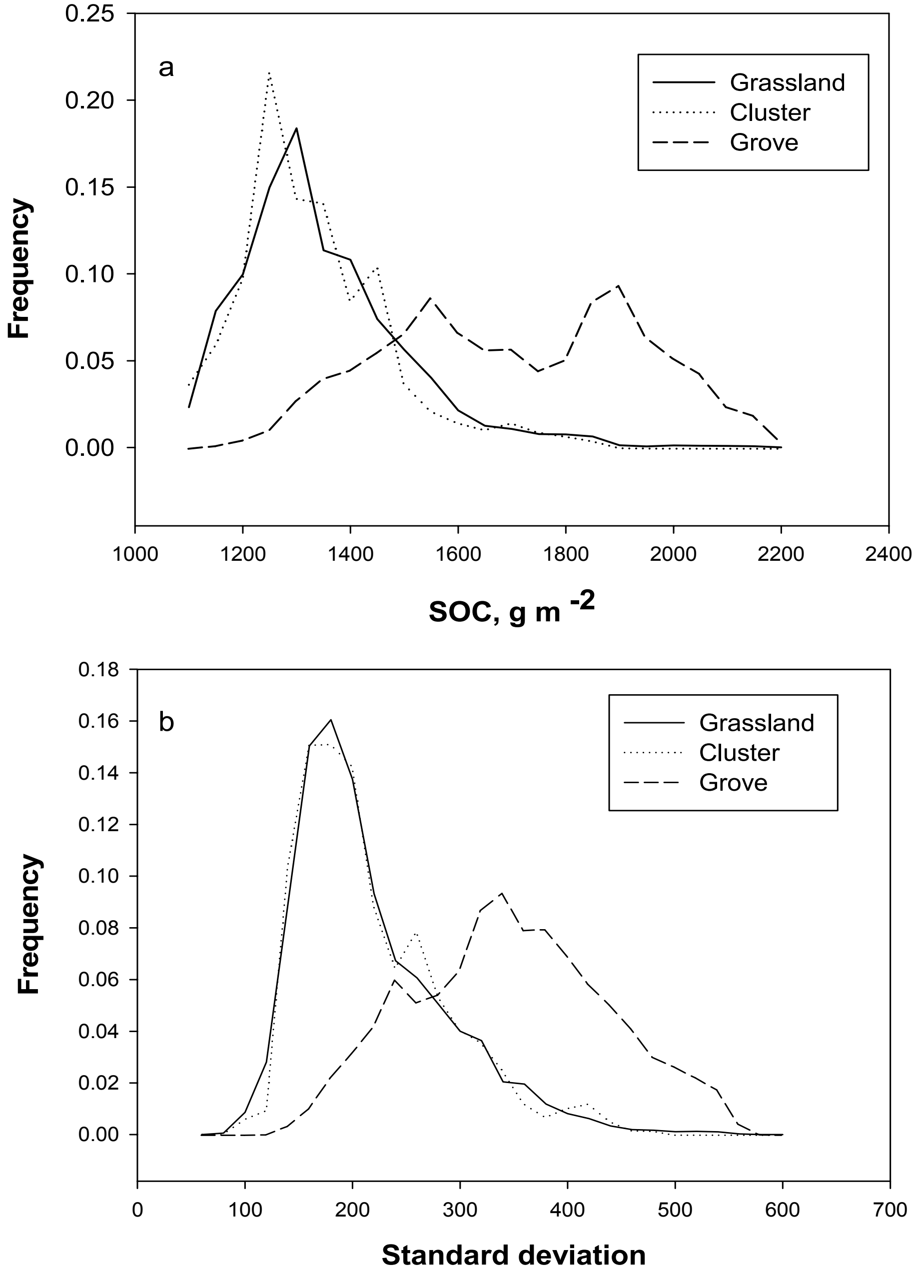

Figure 9. Histograms of SOC mean (a) and standard deviation (b) in intensively sampled grassland, cluster and grove plots based on results from 500 sequential indicator simulations (SIS).

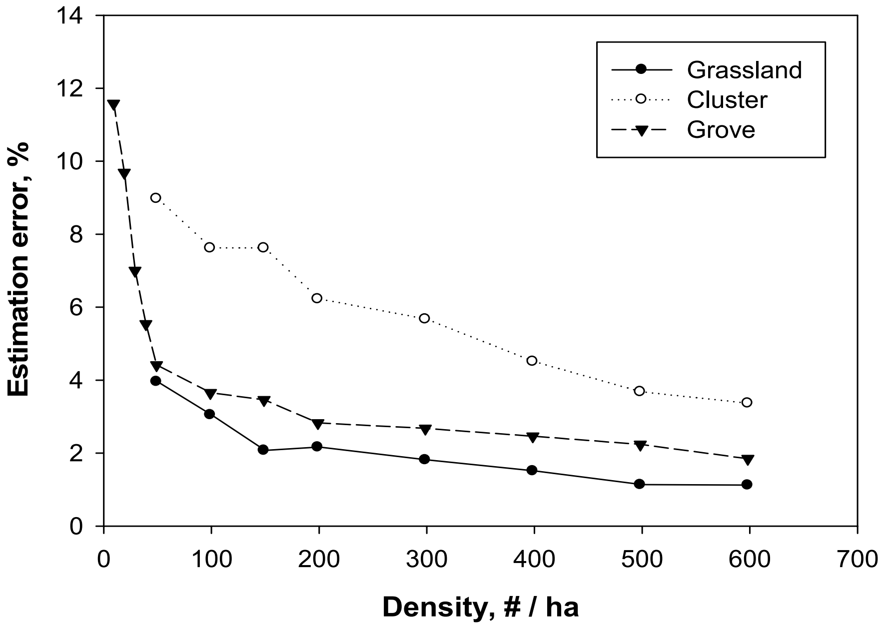

Figure 10. Estimation errors of SOC based on complete random sampling with different densities on kriged map of intensively sampled grassland, cluster and grove plots.

at a sampling density of approximately 500 samples/ha, which was much higher than that in groves and grassland.

Consistent differences in estimation error were found among the complete random sampling, stratified random sampling with even density, and stratified random sampling with uneven density (higher in clusters and groves) when tested using the extrapolated data set (Figure 11). Stratified random sampling with unequal densities in woody patches (clusters and groves) and grassland had the lowest estimation error while complete random sampling had the highest estimation error at all sampling density. At small sampling densities (< 50 per ha), estimation error of complete random sampling decreased more quickly than the other two designs as sampling density increased. When sampling densities were higher than 100 samples per hectare, estimation errors of all three designs started to level off, which suggested that an increase in sampling density after that point will not help improve estimation accuracy.

Results of the complete random sampling experiments with simulated landscapes with varying percent woody cover showed that estimation errors increased with increasing woody vegetation cover for all sampling densities (Figure 12). This suggested that estimation error of SOC storage in a given landscape is to a large degree determined by the percentage of woody cover. Relative abundance of clusters and groves in the woody cover would also influence the estimation errors.

In an attempt to reduce the large estimation errors with complete random sampling in clusters likely caused by the strong spatial pattern, different designs of sampling along the center to edge transect were tested and compared to random sampling with multiple simulations. The results showed that sampling clusters based on center-edge transects yielded better estimation of SOC storage than random sampling (Table 1). Using sample points in the middle of the center-edge transect yielded less estimation error than using samples in the center or near canopy edge. To sample 2 or 3 points on

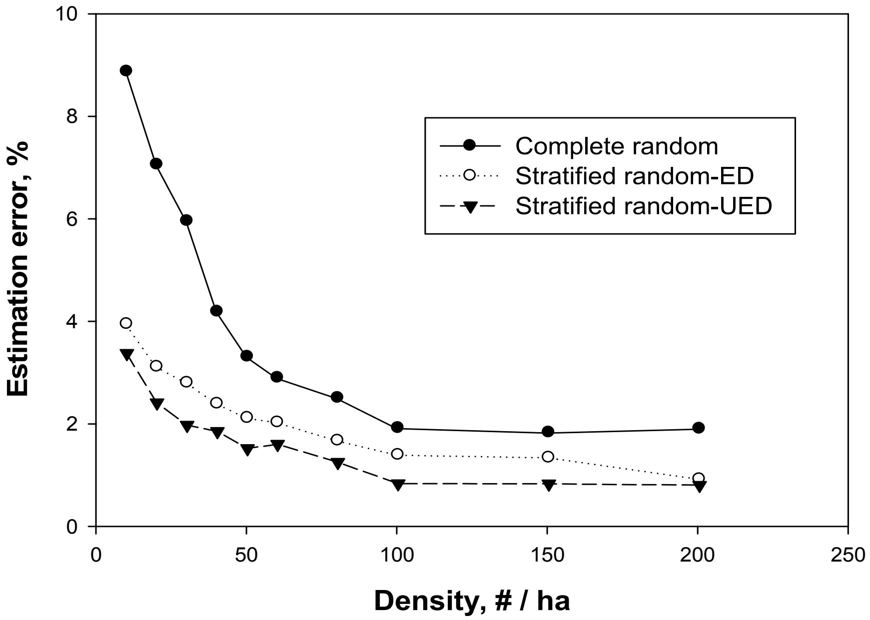

Figure 11. Estimation error of SOC content using 3 different sampling designs (complete random, stratified random with equal density between grassland and woody patches, and stratified random with unequal density between grassland and woody patches) applied to extrapolated landscape based on kriged intensively sampled grassland, cluster and grove plots.

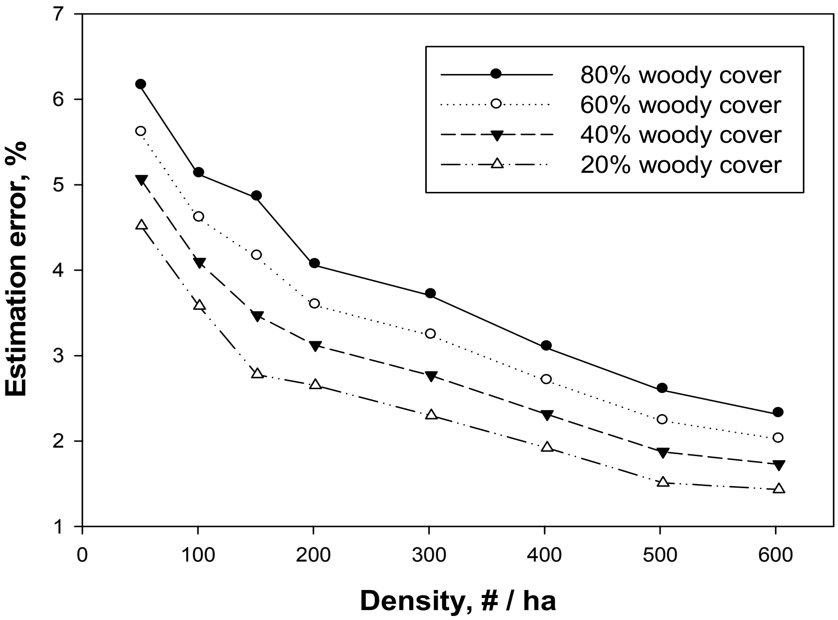

Figure 12. Estimation errors of SOC storage using complete random sampling on simulated landscapes with different ratios of woody cover, assuming clusters and groves have equal coverage for a given landscape.

Table 1. Errors of estimating SOC for different sampling designs in clusters. Letters indicate soil samples inside clusters along transects: (a) near the center of the cluster; (b) 1/3 the distance between the cluster center to canopy edge; (c) 2/3 the distance between the cluster center to the canopy edge; (d) 15 cm inside cluster canopy edge.

Number of Samples	Sampling Design	Estimation Error, %
1	random	25.54
	(b or c)	18.68
2	random	20.61
	(b or c) for 2 clusters	13.85
	b and c	11.15
3	random	17.58
	(b or c) for 3 clusters	12.66
	b, c and d	9.25
4	random	15.66
	(b or c) for 4 clusters	9.71
	(b and c) for 2 clusters	7.95
	a,b,c,d	9.31
5	random	11.21
	(b or c) for 5 clusters	10.53
	(b,c) and (b,c,d) for 2 clusters	6.98
6	random	10.84
	(b or c) for 6 clusters	9.19
	(b,c) for 3 clusters	6.62
	(b,c,d) for 2 clusters	7.5

one transect within one cluster was better than to sample 1 point in multiple clusters. To sample more than 2 or 3 points within one cluster along a transect may not be as desirable as to sample more clusters with 2 or 3 points for each cluster. It would be better to sample more clusters, each with at least 2 points, than to sample fewer clusters with more points. For example, to sample 3 clusters with 2 points each had lower estimation error (6.62 %) than to sample 2 clusters with 3 points for each cluster (7.5 %).

Discussion

Spatial uncertainty of SOC

Invasion of woody vegetation into grasslands increased both the magnitude and spatial uncertainty of SOC. Similar to results of previous studies (Archer et al. 2001, Hibbard et al. 2001, McCulley et al. 2004, Liao et al. 2006b), soils in woody patches had higher surface SOC content than those in grassland areas. SOC was more variable in groves than that in clusters and grassland (Figure 3). Both SIS simulation results and complete random sampling on intensively sampled plots indicated that the spatial uncertainty of SOC was higher under woody vegetation than that in grassland (Figure 9, Figure 10).

Spatial uncertainty of a variable was determined not only by its underlying spatial pattern, but also affected by other factors such as number of samples, sampling designs and spatial configuration of samples. Sequential indicator simulation has been very effective in quantifying spatial uncertainty of ecological variables (Rossi et al. 1993, Goovaerts 2001, Juang et al. 2004, Zhao et al. 2005). SIS simulations based on the 320 random points indicated that soil under woody vegetation had higher spatial uncertainty. However, some of the woody patches did not show higher standard deviation of simulated SOC, probably due to the lack of random samples inside these woody patches. Other studies also indicated that spatial configuration of samples can influence the detection of spatial variability of soil attributes (Buscaglia and Varco 2003, Conant et al. 2003).

SOC in clusters had a strong spatial pattern, with values decreasing from the center towards the canopy edge. SOC was also more variable near the center compared to the canopy edge (unpublished data). SIS simulation results showed that soil in clusters had a similar frequency distribution of uncertainty (standard deviation) as grassland (Figure 9). However, estimation of SOC using complete random sampling on intensively sampled plots suggested that cluster soils were more variable than both grassland and groves (Figure 10), which suggested that clusters had greater spatial uncertainty of SOC than that in groves and grassland. There were two probable reasons for this discrepancy. One is related to the random sampling density in the upland plot and cluster sizes. The intensively sampled clusters had an area of about 10-65 m^2 but there were only 2 random samples per 100 m^2 for the upland plot. Simulations based on these relatively few random samples, therefore, were unable to capture the spatial variability of SOC at smaller scales, which missed spatial variation of SOC associated with some of the smaller clusters when no sample fell within the clusters. Another reason was related to the strong spatial pattern of SOC in clusters, where SOC content was higher in the center of clusters and decreased from center to the canopy edge. Simulations with kriging using low density data would miss this pattern in most of the smaller clusters.

Groves had higher SOC and spatial uncertainty than grassland (Figure 9). Several reasons may have contributed to this higher spatial variability within groves. First, previous studies showed that surface SOC was closely related to root biomass and surface litter (Boutton et al. 1998, Hibbard et al. 2001, Rasse et al. 2005, Boutton et al. 2007). Both litter and root biomass were much higher in groves than that in grassland and their spatial variability was also higher in groves (unpublished data). Second, groves had more animal disturbance than cluster and grassland soils. Animal disturbance is an important factor that affects spatial distribution of soil nutrients (Titus et al. 2002). Field survey showed that animal-disturbed area occupied about 10% of grove areas while there was almost no animal disturbance in grassland and little in clusters. Third, groves had more complex and variable vegetation canopy cover than that in clusters and grassland, which may affect the spatial distribution of litterfall.

Sampling designs to estimate SOC

Increased spatial uncertainty of SOC under woody vegetation decreased the effectiveness of random sampling in estimating SOC storage. Estimation errors in clusters and groves were about twice as high as those in grassland (Figure 10). Complete random sampling results suggested that it requires higher sampling density in clusters and groves to attain a level of estimation accuracy to that of grassland. SOC in grassland had less spatial uncertainty and complete random sampling enabled adequate accuracy at a sampling density of approximately 100 samples/ha. SOC is closely related to litter and root biomass. Therefore, spatial pattern of SOC within groves is determined mostly by tree locations, tree and shrub canopy configuration, root distribution, and animal disturbances. Unlike clusters, groves have more overlapping canopies and higher occurrences of animal disturbances, which made the spatial pattern of SOC in groves less predictable than in clusters. Increased density of complete random sampling significantly reduced estimation error of SOC storage in groves (Figure 10).

By using stratified random sampling with higher sampling density in woody patches, the high SOC estimation errors caused by differences between vegetation types can be mitigated. Soils in woody patches had not only higher spatial variability but also uncertainty for SOC. For extrapolated intensively sampled plots, comparison of the 3 alternative sampling designs showed that stratified random sampling with unequal density in grassland and woody patches had the lowest estimation error (Figure 11). In order to obtain SOC estimates with accuracy comparable to that of grasslands, a higher density of samples is needed in woody patches.

Effectiveness of complete random sampling in woody invaded landscapes also depends on the ratio of woody vs. non-woody vegetation cover. Accuracy of SOC estimation would decrease with increasing percent woody cover over a wide range of sampling density (Figure 12).

Spatial pattern of both SOC content and its uncertainty influences the accuracy of SOC storage estimation. Both SOC content and uncertainty were higher in the center of clusters and they decreased exponentially from cluster centers to canopy edges (unpublished data). Because of this strong pattern of spatial variation, complete random sampling in clusters generated higher estimation errors compared to groves and grassland (Figure 10). Sampling designs taking the spatial pattern of SOC into account, such as sampling along a transect from cluster center to edge, generated more accurate estimations in clusters (Table 1). Sampling one cluster with an appropriate number (2 or 3) of samples along a transect from cluster center to canopy edge is more effective than taking one sample in multiple clusters. Furthermore, sampling more clusters with sufficient sample density and spatial arrangement yields better results than sampling with even higher density in fewer clusters (Table 1). More widespread smaller sampling blocks would also generate more power in testing significance when spatial autocorrelation is present (Legendre et al. 2004). These results illustrated that it is critically important to carefully consider spatial pattern of uncertainty when designing sampling regimes to estimate SOC and other soil attributes in savanna landscapes.

Suggested sampling strategies

Woody invasion into grassland ecosystems has been shown to increase spatial heterogeneity of soil properties (Archer 1995, Schlesinger et al. 1996, Bekele and Hudnall 2006). Although there is no clear consensus as to how soil carbon pools change following conversion from grass to woody plant domination (Gill and Burke 1999, Archer et al. 2001, Hibbard et al. 2001, Schimel et al. 2001, Jackson et al. 2002, McCarron et al. 2003), a tremendous amount of research interests has focused on possible implications of woody expansion on global carbon cycling (Houghton and Hackler 2000, Tilman et al. 2000, Pacala et al. 2001). Increased spatial heterogeneity in soil properties after woody invasion made it harder to quantify soil carbon content accurately (Conant et al. 2003). Extensive soil sampling and analyses are time consuming and expensive. Spatial autocorrelation in ecological variables affects classic test of statistical significance (Legendre et al. 2002) and needs to be considered in the design of experiments and field surveys (Dutilleul 1993, Cole et al. 2001, Hewitt et al. 2007). The ability to estimate SOC storage accurately and with minimum sampling effort would facilitate assessments of the impact of woody plant invasion on SOC storage at ecosystem, landscape, and regional scales. Results of this study provide a sound basis for developing efficient point sampling strategies for quantifying SOC storage in the subtropical savanna parklands of southern Texas, but should also provide general guidelines for developing efficient sampling strategies in other complex landscapes where spatial variability must be considered and quantified.

Previous studies showed that nested sampling (Bellehumeur and Legendre 1998) or systematic grid points or grid cell sampling (Buscaglia and Varco 2003) were suitable to quantify spatial structures of soil properties. Our results indicated that random sampling, stratified based on the systematic grids, worked well in capturing the overall spatial pattern of SOC. However, results of the sequential indicator simulations based on the stratified random samples revealed that spatial structure within small woody patches was not adequately captured due to limited sampling density. Therefore, it is necessary to consider small-scale sampling when fine scale spatial pattern is present. Nested sampling provides an option to capture spatial pattern of SOC at both large and small scales. The incorporation of hierarchical spatial scales into experimental and sampling designs has provided some promising results in detecting patterns (Noda 2004). Other than sampling at different scales, plot size or extent of experiment design must be adapted to the spatial pattern and scale of the variable under study (Bhatti 2004).

In order to produce estimation with acceptable accuracy, an optimized sampling design needs to account for the spatial pattern and uncertainty of the variable of interest (Hewitt et al. 2007). For the woody invaded landscape in LCRA, we can follow several guidelines to develop optimized sampling designs. Since soils in grassland have low spatial uncertainty associated with SOC, random sampling or systematic sampling could generate acceptable estimations (~ 4% error for complete random sampling) at a sampling density of 50 samples/ha. However, for woody patches, higher sampling density is necessary to obtain an estimation error comparable to that for grassland. Grove soils have higher spatial uncertainty of SOC without strong spatial structure. A sampling density of about 100 samples/ha in groves will generate an estimation error of about 4 %. Cluster soils have a strong spatial pattern of SOC variability. Our results indicated that transect sampling yielded better estimations than random sampling. Sampling multiple clusters with 2 or 3 soil samples usually generated better estimations than sampling fewer clusters with more points, or sampling many clusters with fewer points.

Therefore, a desirable sampling design for quantifying the spatial pattern of SOC in the upland landscape at La Copita should include stratified random sampling with uneven density (higher density for woody areas with high uncertainty) plus embedded transect-based sampling within clusters with strong spatial patterns. Specifically, it should include random samples in grassland (~50/ha density), random samples in multiple groves (~100/ha density), and structured samples in multiple clusters (2-3 samples in the middle section of a center-edge transect in each cluster; ~100/ha overall density).

Several general recommendations for efficient sampling strategies to quantify the pattern of SOC storage in arid and semi-arid landscapes with woody invasion can be offered: (1) consider stratified random sampling with uneven densities in different landscape elements according to their variability or uncertainty in SOC, (2) consider structured sampling, such as transect-based sampling, if a landscape element (e.g., woody cluster) has a strong spatial pattern in SOC, and (3) consider preliminary sampling to explore spatial structures in SOC within specific landscape elements and estimate appropriate sampling density for each.

Woody plant invasions of grassland ecosystems is a geographically extensive phenomenon that has the potential to alter global nutrient cycles dramatically (Houghton et al. 1999). In order to evaluate the effects of woody invasion on regional or global carbon cycles, there is a need to extrapolate SOC estimation results from smaller scales to broader scales. Sampling designs suggested above are aimed at understanding the spatial pattern and uncertainty of SOC and its relationship with vegetation structure and pattern. Remote sensed images can be used in conjunction with field samples and geostatistical techniques (e.g., cokriging) to predict soil properties such as SOC with sufficient precisions at landscape and smaller scales (Atkinson et al. 1994, Kerr and Ostrovsky 2003, Wang et al. 2004); however, it is not feasible to collect soil samples and use kriging or cokriging approaches to estimate SOC storage within larger landscapes or regions. However, understanding of the spatial structure of SOC and its relationship with vegetation structure and topoedaphic features can provide approaches to estimation of SOC at the scale of the large landscape or region.

In summary, conditional sequential indicator simulation results indicated that woody encroachment into grassland increased both spatial heterogeneity and uncertainty of SOC, which in turn increased errors in estimating SOC storage. Sampling experiments showed that increased spatial uncertainty of SOC in woody patches reduced the effectiveness of complete random sampling in estimation of SOC storage. Stratified random sampling with higher density in woody patches substantially increased estimation accuracy. Other than spatial variability and uncertainty, strong pattern of SOC could also influence estimation accuracy. Incorporation of spatial pattern and variability of SOC into sampling designs would increase the accuracy of the estimation of SOC storage. An efficient sampling strategy for quantifying the spatial pattern of SOC in the upland landscape of La Copita was developed, including stratified random sampling in grassland (~50/ha density) and multiple groves (~100/ha density) plus structured samples along center-edge transects in multiple clusters (2-3/cluster and ~100/ha overall). For similar arid and semi-arid landscapes undergoing woody encroachment, sampling strategies recommended include considerations of (a) stratified random sampling with uneven densities based on SOC variability associated with landscape elements, (b) structured sampling in landscape elements with strong spatial patterns in SOC, and (c) preliminary assessment of spatial structures and appropriate sampling density. Quantitative understanding of the spatial structure of SOC and its relationship with vegetation structures and topoedaphic features developed based on these field assessment can be combined with remote sensing to enable effective estimation of SOC over large landscapes and regions to understand the implications of woody invasion and to manage woody invaded landscapes.

CHAPTER III

CORRELATION AND SPATIAL SCALING OF VEGETATION AND SOIL C AND N IN A SUBTROPICAL SAVANNA LANDSCAPE

Introduction

Increased woody plant abundance in arid and semi-arid ecosystems has been reported worldwide (Archer 1995, McPherson 1997). Many studies showed that the invasion of woody plants into grassland alters soil by forming "fertile islands" (Burke 1989, Jackson and Caldwell 1993, Schlesinger et al. 1996, McPherson 1997, Scholes and Archer 1997). Though recent estimation of the C budget in USA treats shift of grass domination to woody domination as major C sink (Houghton et al. 1999, Schimel et al. 2001, Houghton 2003), there is still uncertainty about whether woody invasion increases, decreases, or causes no effect on soil C storage. Some studies showed that invasion of woody plants caused net loss or no change in soil organic carbon (SOC) storage (Jackson et al. 2002, Chapman et al. 2003). Woody plant encroachment also increases the spatial heterogeneity of both vegetation and soil (Schlesinger et al. 1996, Bekele and Hudnall 2006). To evaluate the impact of woody invasion on regional and global C and N cycles, it will be necessary to develop (a) methodologies for quantifying spatial patterns of SOC and soil total nitrogen (TN) at the ecosystem and landscape level, and (b) rules for scaling ecosystem and landscape level assessments of SOC and TN storage to larger spatial scales.

Previous studies have examined the role of environmental factors such as climate (Burke et al. 1989, Amundson 2001), topography (Burke et al. 1999, Powers and Schlesinger 2002), soil moisture (Wang et al. 2002), plant species (Lovett et al. 2004), and time (Schlesinger et al. 1990) in controlling SOC and TN storage. However, not all factors have equal importance in determining the concentration and spatial distribution of SOC and TN, and the relative importance of these factors is likely to change at different spatial scales.

Ecological patterns and processes differ across spatial and temporal scales (Allen and Starr 1982, O'Neill et al. 1986, Wiens 1989). Spatial heterogeneity of ecological phenomena usually has multiple-scale structure because the processes that affect these patterns usually are not the same at different scales (Levin 1992). One of the major issues in the science of ecology is the development of methodologies that will allow us to extrapolate and extend the results we obtained at one scale to other spatial and/or temporal scales (Ehleringer and Field 1993, Miller et al. 2004).

Scaling is the extrapolation of known results or transformation of information from one scale to other scales. Since different ecological processes operate at different domains of scale, the relationships between ecological patterns and functions can be different at different domains of scale. The most fundamental step in scaling is to determine domains of scale and to elucidate the driving ecological processes in each of the domains (Ludwig et al. 2000, Schneider 2001). Many statistical methods (such as geostatistics, quadrat variance methods, fractals, lacunarity, wavelets, etc.) have been used to study multi-scale questions (Sugihara and May 1990, Rossi et al. 1992, Li and Reynolds 1993, Plotnick et al. 1996, Dale and Mah 1998, Gustafson 1998, Dale 2000, Wu et al. 2000, Turner et al. 2001, Dale et al. 2002, Chave and Levin 2003). However, few studies have been conducted to simultaneously detect domains of scale and their interactions for both vegetation and soil.

The goal of this study was to quantify spatial patterns and scaling of SOC and TN, and evaluate vegetation and soil properties that may be controlling these parameters in a savanna landscape. The specific objectives were to: (1) Determine the correlations between SOC, TN and litter, root biomass, soil texture, soil bulk density, shrub basal area, tree basal area, and (2) Examine how the spatial scales of these variables relate to those of SOC and TN.

Methods

Study site

This study was conducted at the Texas Agricultural Experiment Station’s La Copita Research Area (LCRA, 27°40’N, 98°12’W) approximately 65 km west of Corpus Christi, TX, USA. The site has been grazed continuously from the late 1800’s. Elevation ranges from 75 to 90 m. The landscape grades with gentle slopes (≤ 3%) from uplands to drainage lowlands and lower-lying drainages and playas. The climate is subtropical with warm, moist winters and hot, dry summers. Mean annual temperature is 22.4 °C and the growing season is 289 days. Average annual precipitation is 680 mm with bimodal peaks in May and September. Upland soils are Typic and Pachic Argiustolls with a laterally extensive but discontinuous clay-rich, argillic horizon at 40-60 cm. The lower-lying drainages are clay loams (Pachic Argiustolls).

Woody plant encroachment in southern Texas over the past century has been well documented (Archer 1995). Historical aerial photos, tree rings, C isotopes and ecosystem models have all shown that woody plant invasion occurred in this area over the past 100 years (Archer et al. 1988, Archer 1989, Scanlan and Archer 1991, Flinn et al. 1994, Boutton et al. 1998). Honey mesquite (*Prosopis glandulosa*), a N_2-fixing tree legume, is always the first woody plant established in the grassland, where it appears to serve as a nurse plant to facilitate the establishment and development of other woody species beneath its canopy (Archer 1995).

The potential natural vegetation of the study area was classified as *Prosopis-Acacia- Andropogon-Setaria* savanna (Küchler 1964). The current vegetation differs from the potential in uplands, drainages and playas. Uplands are covered with subtropical savanna parkland vegetation, which is dominated by discrete woody patches distributed within a continuous C_4 grassland matrix (Whittaker et al. 1979). Woody patches are comprised of smaller clusters (usually one mesquite in the center with other shrub species beneath its canopy) or larger groves which appear to be clusters that have expanded laterally and fused together to form larger woody patches. Understory shrub species in both clusters and groves include *Zanthoxylum fagara*, *Celtis pallida*, *Condalia hookeri*, *Diospyros texana*, *Schaefferia cunefolia*, *Ziziphus obtusifolia* and *Berberis trifoliolata*. The herbaceous grassland matrix is dominated by C_4 grasses such as *Paspalum setaceum*, *Setaria geniculata*, *Bouteloua rigidiseta*, and *Chloris cucullata*, but also has a significant forb component (Archer 1990).

Continuous thorn woodlands are distributed in the lower-lying drainages, which are generally 1-5 m lower in elevation than the uplands. Species composition of woodlands is similar to that of upland woody patches, and mesquite still dominates the overstory canopy. Playas are oval shaped basins occupying the lowest portion of the landscape, and may have standing water following high rainfall periods. The vegetation composition of playas ranges from relatively open grassland with widely scattered mesquite trees to dense woodland with little grass cover (Farley 2000). Additional details on climate, vegetation and soil can be found elsewhere (Scifres and Koerth 1987, Archer et al. 1988, Boutton et al. 1998).

Field sampling

A 309 m transect line, which included all 5 vegetation types (grassland, cluster, grove, drainage woodland and playa) was established in 2004. This transect ran from the highest portion of an upland down through a drainage woodland and into a playa along the topographical gradient (Figure 13). Transect coordinates were determined using a Trimble Pathfinder Pro XRS system (Trimble Navigation Limited, Sunnyvale, CA) at 5 m intervals. Surface soil samples (0-15cm) were collected at 1 m intervals along the transect in Spring 2004. Three soil cores (15 cm deep 2.24 cm in diameter) were collected at each sample point; one for bulk density and texture (particle size distribution), one for SOC and TN, and one for root biomass. All soil cores were stored in a cold room at 4^{o}C before processing. At each sampling location, vegetation type (grass, cluster, grove, woodland or playa) was recorded. Elevations along the transect were determined based on a field survey conducted in April 2004 and USGS DEM data (Figure 14).

Trees with basal diameter greater than 5 cm were measured within a 12 m wide strip centered on the transect line. Species name, basal diameter and their locations were recorded. All shrubs in a 2 m wide belt centered on the transect were sampled for species and basal diameter. Litter was collected from 0.5 × 0.5 m quadrats centered on each soil sample point; herbaceous vegetation was clipped and collected from these sample quadrats. Grass, forbs, and litter were oven-dried for at least 72 hours at 60^{o}C to determine dry weight.

Lab analyses

Soil bulk density was determined by the core method (USDA 2004). The soil core for C and N determination was dried at 60°C for at least 48 hours. Coarse roots and gravel were removed by passing the soil through a 2 mm screen. Then, soil samples were pulverized to a fine powder in a centrifugal mill (Angstrom, Inc., Belleville, MI, USA). Samples were weighed into silver capsules (5 x 7 mm), treated with HCl vapor in desiccator to remove carbonates (Harris et al. 2001), dried, and sealed in the capsules. SOC and TN were measured by combustion/gas chromatography using a Carlo Erba

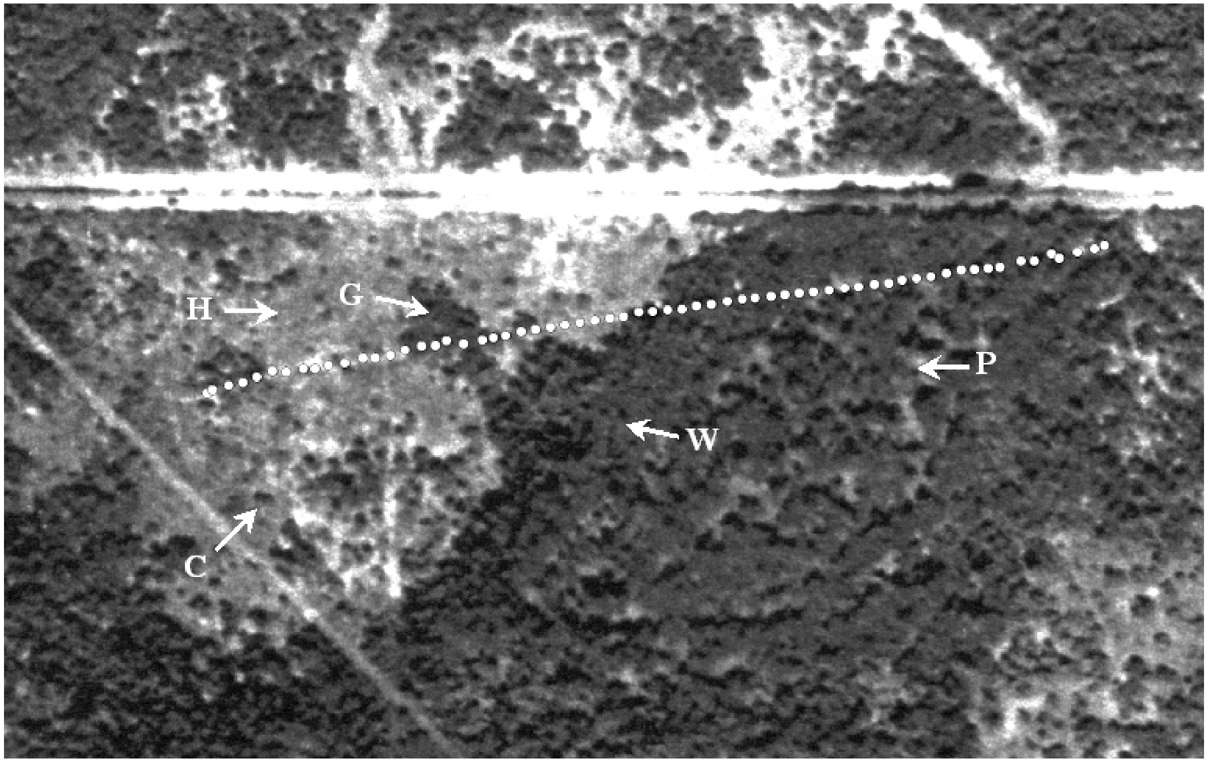

Figure 13. Aerial view of the 309 m transect showing herbaceous grassland (H), clusters (C), groves (G), woodland (W) and playa (P). Dark zones represent woody plant cover while light gray zones indicate herbaceous cover. White dots at 5 m intervals indicate the location of the transect.

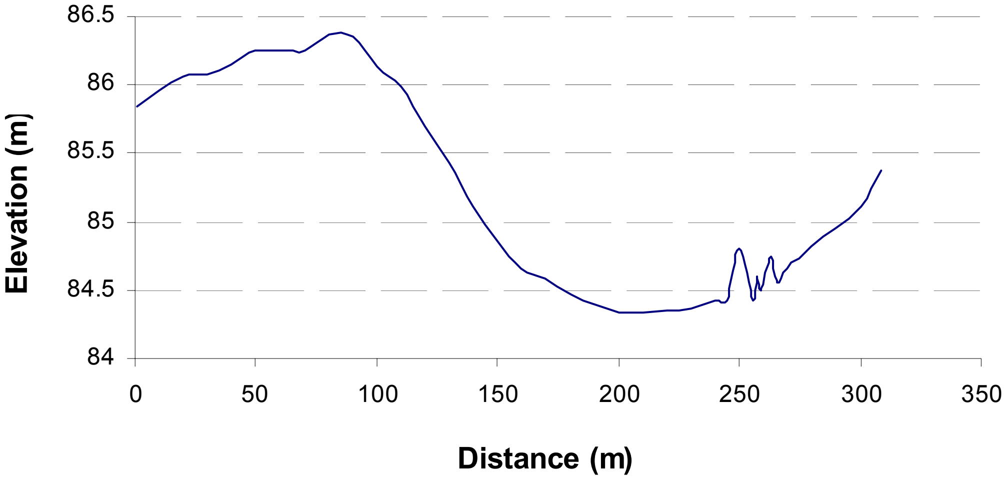

Figure 14. Elevation along the 309 m transect.

EA-1108 element analyzer (CE Elantech, Lakewood, NJ, USA). Root biomass was determined by washing soil cores through a hydropneumatic elutriation system (Gillison's Variety Fabrication Inc., Benzonia, MI, USA) (Smucker et al. 1982) equipped with 410 μm filters. The collected roots were dried for at least 72 hours at 60 ^{o}C to determine dry weight, and then ashed at 400 ^{o}C in a muffle furnace to obtain ash-free root biomass. Soil particle size distribution was measured by the pipet method (USDA 2004).

Statistical analyses

One-way ANOVA was performed to compare all measured variables in different vegetation types using SPSS version 12.0 (SPSS Inc. Chicago, IL). Post hoc comparisons of these variables in different vegetation types were conducted following the Tamhane's T2 procedure. Mantel and cross-Mantel tests (Fortin and Gurevitch 1993) were used to test spatial autocorrelation and spatial cross-correlations between variables using PASSaGE, a software package for spatial pattern analyses (Rosenberg 2001).

Pearson correlation coefficients between SOC, TN and environment and vegetation variables were calculated using SPSS. Their significance was tested following the procedure of modified t-test for correlation (Clifford et al. 1989) using PASSaGE. When calculating the correlation coefficients between two variables, the standard test is not valid for spatially autocorrelated variables. Mantel tests results showed that both SOC and TN are spatially autocorrelated. Modified t-test for correlation (Clifford et al. 1989, Dutilleul et al. 1993) tests the significance by correcting the degrees of freedom based on the amount of autocorrelation in the data.

Quadrat variance methods (Hill 1973, Ludwig and Goodall 1978, Dale 1999) were used to detect the domains of scale for all variables. Quadrat variance methods are a group of methods that calculate the variance of differences among blocks of different sizes. The pattern of variances then can be used to determine the scale of pattern. Two Term Local Quadrat Variance (TTLQV) and Three Term Local Quadrat Variance (3TLQV) (Dale 1999) were performed using PASSaGE to detect the domains of scale for all variables.

Table 2. Average measured variables in different vegetation types. Upland included grassland, clusters and groves; Drainage included woodland and playa. Non-woody included grassland; woody included clusters, groves, woodlands and playas. SE = standard error.

	Upland		**Drainage**		**Non-Woody**		**Woody**	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Forb biomass (g m^{-2})	65.44	6.24	16.52	2.62	76.01	8.90	29.15	3.47
Grass biomass (g m^{-2})	53.47	5.53	69.90	11.82	96.54	9.02	52.99	8.27
Litter biomass (g m^{-2})	265.60	31.89	725.12	45.88	30.37	3.36	643.40	35.71
Root biomass (g m^{2})	432.62	35.92	1023.57	69.58	194.19	17.25	901.07	51.90
Shrub basal area (cm^2 m^{-2})	16.70	3.37	50.72	11.25	0.48	0.22	44.35	7.92
Tree basal area (cm^2 m^{-2})	21.35	2.49	62.79	5.08	0.54	0.17	55.31	3.71
Soil bulk density (g cm^{-3})	1.30	0.01	1.18	0.01	1.40	0.01	1.19	0.01
Soil organic carbon (g m^{-2})	1549.90	46.84	3061.18	83.78	1233.11	22.05	2668.34	71.81
Soil total nitrogen (g m^{-2})	150.17	4.10	279.57	8.29	123.46	2.38	245.82	6.79
Sand (%)	78.21	0.18	64.67	0.92	78.48	0.12	68.89	0.75
Silt (%)	9.30	0.13	14.70	0.29	9.33	0.16	12.98	0.26
Clay (%)	12.49	0.12	20.63	0.65	12.19	0.13	18.13	0.51

Results

Patterns of SOC and TN along the catena

Comparisons of all the measured variables between landscape locations and vegetation cover are shown in Table 2. Drainage soils had a higher percentage of clay and silt than upland soil, while the sand percentage was lower. Soil bulk density was1.30 g cm^{-3} in drainage woodlands and 1.18 g cm^{-3} in uplands. SOC and TN content were significantly different between uplands and drainage woodland. The upland portion of the transect had a SOC and TN content of 1549.90 g C m^{-2} and 150.17 g N m^{-2}, respectively, while soils at drainage area had a higher SOC and TN content, 3061.18 g C m^{-2} and 279.57 g N m^{-2}, respectively (Table 2).

Litter, root biomass, and tree and shrub basal area were all significantly higher in drainages than uplands. But uplands had more forb biomass than the drainage portion of the transect. Soils under woody vegetation had higher SOC and TN than that in the grassland (Table1). Litter and root biomass were also much higher under woody vegetation. However, forb and grass biomass were both higher in the non-woody areas compare to the woody areas. Soils under woody vegetation had higher silt and clay percentage, but with a lower bulk density.

SOC and TN were significantly different between vegetation types. Soils in the drainage woodland and the playa had significantly higher SOC and TN than other vegetation types, while grassland had the lowest SOC and TN content (Figure 15). The groves had significantly higher SOC and TN content than the clusters, which were significantly higher than the grassland. The drainage woodland had a higher TN content (288.44 g N cm^{-2}) than the playa (252.52 g N cm^{-2}), although they were not significantly different. The playa had the highest soil C: N ratio among all vegetation types while grassland, cluster, grove and drainage woodland had comparable C: N. The drainage woodland had the highest litter and root biomass while the grassland had the lowest. The groves and clusters had comparable root biomass, while the groves had higher litter than that in the clusters. The playa had comparable litter and root biomass with the clusters. But grass cover and aboveground grass biomass were highest in the playa (255.13 g m^{-2}) while drainage woodland had the lowest grass biomass (9.15 g m^{-2}).

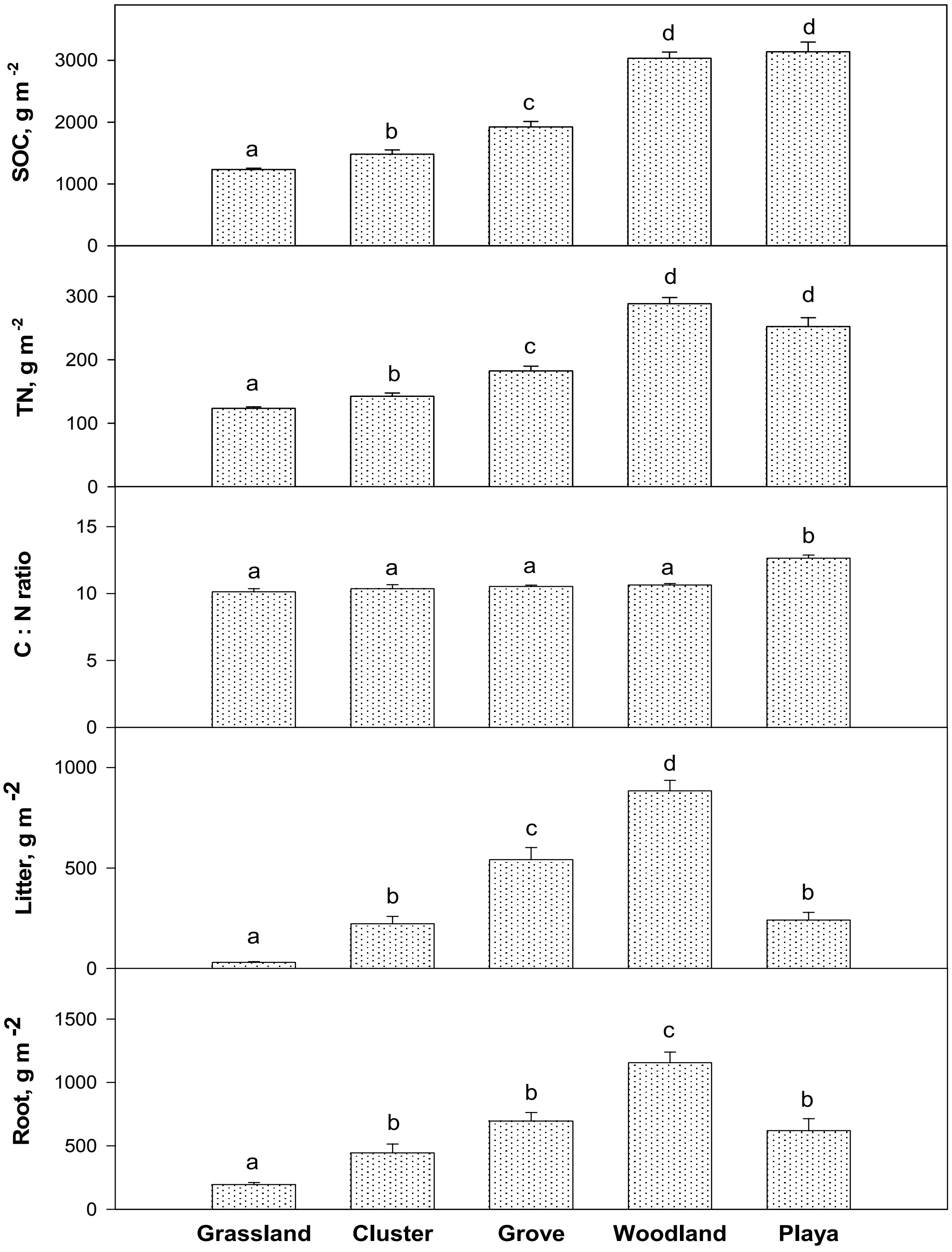

Figure 15. Soil organic carbon (SOC), total nitrogen (TN), C: N ratio, litter, and root biomass in different vegetation types (grassland, cluster, grove, woodland and playa). Different letters above bars indicate significant difference between means tested by post hoc comparisons following Tamhane's T2 procedure. Error bars are standard errors of the means.

Variability of SOC and TN were higher under woody vegetation than under herbaceous vegetation. The standard error of mean SOC in the wooded landscape elements ranged from 70-155, while that of grassland SOC was 22. The pattern of spatial variability of soil TN was similar, with higher variability in wooded areas than in herbaceous grassland (Figure 15).

Correlation between variables

Results of Mantel and cross-Mantel tests indicated that both SOC and TN were spatially autocorrelated (Table 3). Cross-Mantel test indicated that SOC and TN were significantly ($p < 0.05$) spatially correlated with litter, root biomass, shrub basal area, tree basal area, soil bulk density, and soil texture (sand, silt and clay percentages). Neither forb nor grass biomass was spatially correlated with either SOC or TN at this scale.

Using the modified t-test for correlation, SOC was strongly correlated with TN with a correlation coefficient of 0.96 (Table 4). Among the variables examined, litter had the highest correlation with both SOC ($r = 0.54$) and TN ($r = 0.61$). Root biomass had the second highest correlation with both SOC ($r = 0.51$) and TN ($r = 0.52$). Soil bulk density was negatively correlated with both SOC and TN, with correlation coefficients of -0.48 and -0.46, respectively. Tree basal area and shrub basal area were both significantly correlated with SOC and TN, but their correlation coefficients were weaker than those for the variables mentioned above (Table 4). Forb and grass biomass had no significant correlation with either SOC or TN at this scale. Soil particle size distributions were not correlated with either SOC or TN.

Domains of scale

Two quadrat variance methods were used to quantify the domains of scale for all the measured variables. Two Term Local Quadrat Variance (TTLQV) results showed a scale of 40 to 45 m for forb biomass, litter, root biomass, shrub basal area, tree basal area, SOC, TN, and soil clay content. Three Term Local Quadrat Variance (3TLQV) results also revealed scales of 40-45 m for litter, root biomass, shrub basal area, tree basal area, grass biomass, soil silt, SOC and TN (Table 5, Figure 16). These two methods yielded similar results and suggested a domain of scale of 40 to 45 m for these variables. Results of 3TLQV also indicated a smaller scale for some of the variables. For example, root biomass, SOC, TN, soil sand and clay content all had a smaller scale of about 10 m

Table 3. Mantel and cross-Mantel results for the spatial correlation between variables. The first row indicated spatial autocorrelation of SOC and TN. p is significance level.

	SOC		**TN**	
	Mantel's r	p	Mantel's r	p
	0.239	0.001	0.168	0.001
Forb biomass (g m^{-2})	0.005	ns	-0.035	ns
Grass biomass (g m^{-2})	-0.047	ns	-0.070	ns
Litter (g m^{-2})	0.306	0.001	0.396	0.001
Root biomass (g m^{2})	0.331	0.001	0.345	0.001
Shrub basal area (cm^2 m^{-2})	0.188	0.004	0.223	0.001
Tree basal area (cm^2 m^{-2})	0.229	0.001	0.200	0.001
Soil bulk density (g cm^{-3})	0.225	0.001	0.206	0.001
Sand (%)	0.217	0.001	0.104	0.006
Silt (%)	0.231	0.001	0.122	0.001
Clay (%)	0.182	0.001	0.071	0.041

Table 4. Pearson correlation coefficients between SOC, TN and other variables. r is the Pearson correlation coefficient. p is the significance level calculated using modified t-test for correlation. ns means none significant ($p<0.05$).

	SOC		**TN**	
	r	**p**	**r**	**p**
Forb biomass (g m^{-2})	-0.36	ns	-0.31	ns
Grass biomass (g m^{-2})	-0.08	ns	-0.17	ns
Litter (g m^{-2})	0.54*	0.01	0.61*	0.01
Root biomass (g m^{2})	0.51*	0.01	0.52*	0.01
Shrub basal area (cm^{2} m^{-2})	0.29*	0.01	0.32*	0.01
Tree basal area (cm^{2} m^{-2})	0.47*	0.02	0.42*	0.02
Soil bulk density (g cm^{-3})	-0.48*	0.01	-0.46*	0.01
Soil total nitrogen (g m^{-2})	0.96*	0.01		
Sand (%)	-0.49	ns	-0.35	ns
Silt (%)	0.53	ns	0.41	ns
Clay (%)	0.45	ns	0.3	ns

Table 5. Spatial scales (m) of the variables derived from quadrat variance methods. Some variables may have two scales that are separated by a comma. (TTLQV is two term local quadrat variance; 3TLQV is three term local quadrat variance).

	TTLQV	**3TLQV**
Forb biomass	45	19,47
Grass biomass	38	40
Litter biomass	43	44
Root biomass	44	9,44
Shrub basal area	5,43	5,44
Tree basal area	41	43
Bulk density	39	37
SOC	44	9,44
TN	45	9,45
Sand		10,39
Silt		9,40
Clay	43	49

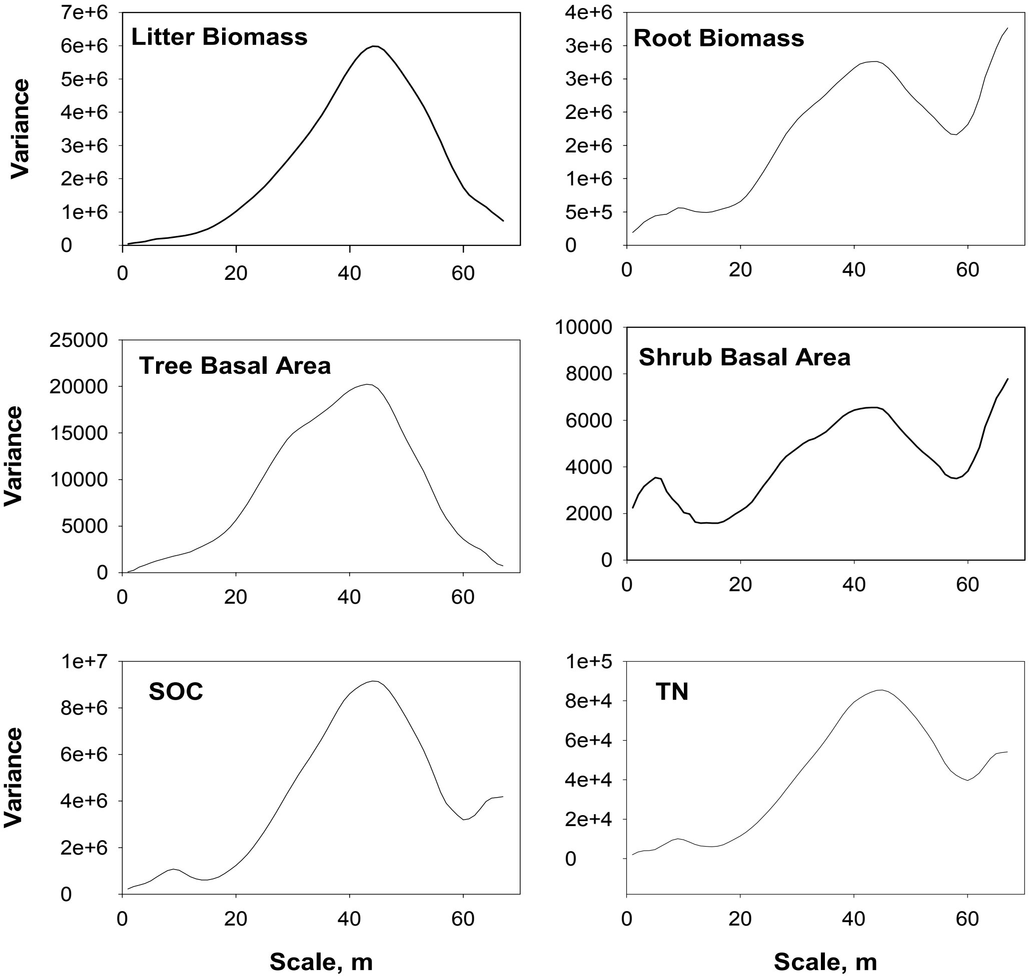

Figure 16. Three term local quadrat variance (3TLQV) results of litter, root biomass, tree basal area, shrub basal area, soil organic carbon (SOC) and total nitrogen (TN). Peaks of variance indicate spatial scales (m).

(Figure 16). The domains of scale for forb and grass biomass, soil bulk density, and soil clay content were considerably different from those of SOC and TN. Results of TTLQV and 3TLQV were consistent for most of the variables except sand and silt percentages. TTLQV results of sand and silt did not show obvious domains of scale while 3TLQV results indicated two scales.

Discussion

Pattern of SOC and TN in savanna landscape

The invasion of woody plants into grasslands alters many aspects of the ecosystem such as species composition, primary production, and microclimate. It also affects nutrient cycling and SOC storage by altering rooting depth, root turnover rate, litter quantity and quality, and soil biological communities. The process of woody invasion in the savanna landscapes in the Rio Grande Plains of southern Texas has been well studied (Archer 1995, Boutton et al. 1998, McCulley et al. 2004, Liao et al. 2006a). The invasion started with the establishment of honey mesquite, a N_2-fixing arborescent tree. Their establishment facilitated the recruitment and establishment of other woody species by modifying soils and microclimate, which led to the development and expansion of woody clusters. Groves formed when neighboring clusters enlarged and coalescenced. The resulting landscape is now comprised of woody patches of varying sizes that generally correspond to ages of the patches or time since establishment (Archer 1990).

In this study, SOC and TN had a clear pattern across the landscape with significant increases from grassland to clusters, groves, and the woodlands (Figure 15). This is consistent with previous studies that showing soils under woody vegetation had higher SOC and TN than grassland soils (Boutton et al. 1998, Hibbard et al. 2001, McCulley et al. 2004, Liao et al. 2006b). Significantly higher SOC and TN in larger woody patches suggested a positive relationship between time of woody invasion (stand age) and SOC and TN content in the soil. Similar to SOC and TN, litter and root biomass had significant increases from grassland to clusters, groves and woodland.

The playa was covered mostly by C_4 grasses (ca.50% coverage, unpublished data) with scatted trees (*Prosopis glandulosa*, *Acacia farnesiana*, *Parkinsonia aculeata* etc.), but SOC and TN in the playa were comparable with that in the drainage woodland and significantly higher than that in upland landscape elements (grasslands, clusters and groves).

Stable carbon isotopes have been used to record vegetation change from C_4 dominated grasslands to C_3 dominated woodlands (Boutton et al. 1998). Plants with C_3 photosynthesis have $\delta^{13}C$ values ranging from approximately –32 to –22‰ (mean ca. –27‰) while C_4 plants have values ranging from –17 to –9‰ (mean ca. -13‰). The natural differences of $\delta^{13}C$ derived for these two photosynthetic pathways can be traced into soil organic matter when there is a shift of domination from C_4 grasses to C_3 plants. Previous studies based on $\delta^{13}C$ showed that drainage woodlands, groves and clusters, which are dominated by C_3 woody plants now, occupied sites once dominated by C_4 grasses (Boutton et al. 1998). SOC in the playa and grassland had a comparable $\delta^{13}C$ value of -18.3‰ and -18.9‰ respectively, which indicates that most of playa SOC was from C_4 grasses. Although the grassland had similar herbaceous cover as the playa (ca. 50%), its SOC and TN were significantly lower than that in the playa.

There are several potential reasons for the higher SOC content in the playa. First is that grass biomass and litter were both substantially higher in the playa than in the upland grassland, which suggests that organic matter inputs to the soil are likely greater in the playa. The playa had an average aboveground grass biomass of 255 g m^{-2}, while grassland had an average grass biomass of 96.5 g m^{-2} (Figure 15). Similarly, litter in the playa (240 g m^{-2}) was also much higher than that in grassland (30 g m^{-2}). Though the grassland had some forbs present while the playa almost had none, the total amount of forb and grass biomass in the grassland (173 g m^{-2}) was still lower than that of grass biomass alone in the playa (255 g m^{-2}). The second possible reason is the higher clay content in the playa soil. Fine textured soils with high clay content usually accumulate and retain more SOC and TN than coarse textured soil (Schimel et al. 1985, Hassink 1997, Hook and Burke 2000, Liao et al. 2006b). Soil in the playa had significantly higher clay content (33%) than grasslands, clusters, groves, and drainage woodlands (12%, 12%, 13%, and 17% respectively). The third potential reason is the impeded decomposition in flooded and saturated soils (Schlesinger 1997). As the lowest portion of the landscape, playas will periodically be flooded with surface water drained from adjacent upland areas after rainfall events (Farley 2000). The anaerobic conditions created by the intermittent flooding of the playa could periodically reduce decomposition rates in playa soils relative to those in upland grassland soils.

Soil C: N ratio was slightly higher in the playa (~12) than in all other landscape elements (~10). Although soils in the playa and the drainage woodland had comparable SOC and TN content, the C: N ratio of soil organic matter was significantly higher in the playa (Figure 15). This suggested the potential for differences in N cycling between the playa and the woodland. Anaerobic conditions generated in inundated soils could promote the process of denitrification (Mitsch and Gosselink 2000), which results in the volatilization of soil N.

Relationship of SOC and TN to soil and vegetation attributes

Previous studies showed that many biotic and abiotic factors, such as climate, soil texture, management, and topography influence SOC and TN content at different spatial scales (Burke et al. 1989, Tilman et al. 2000, Amundson 2001, Conant et al. 2001, Hudak et al. 2003). Hook and Burke (2000) evaluated the relative importance and interaction of environmental factors with SOC in a shortgrass steppe landscape. They found that texture and topographic position played important roles in shaping soil spatial patterns. In another study on the relationship between soil C distribution and biophysical factors in a rain forest, Powers and Schlesinger (2002) found that elevation was the determining factor in SOC distribution.

The strong correlations between SOC, TN and litter and root biomass revealed in this study suggested that ecological processes related to litter and root biomass have strong influences on SOC and TN. The inputs to SOC and TN pools include aboveground sources like foliar and woody litterfall, leaching, atmospheric deposition, stemflow, throughfall, and belowground sources like root turnover, root exudation, and turnover of soil microbes and fauna. Both litter and root biomass were higher in wooded areas (clusters, groves, drainage woodlands) than in grassland (Table 2), and increased from clusters to groves to drainage woodlands, showing increased inputs of organic matter after woody invasion. The majority of the microbial activity (Schimel et al. 1985) and root biomass (Jackson et al. 1996, Mordelet et al. 1997, Boutton et al. 1999, Gill et al. 1999) occur in the upper part of the soil profile. Previous studies at La Copita also showed that effects on soil C and N by woody invasion were most pronounced in the uppermost part (~15 cm) of the soil profile (Archer 1995, Boutton et al. 1998) where soil samples were collected in this study. Studies also suggested that roots might play a greater role than litterfall in affecting SOC content (Hibbard et al. 2003, Rasse et al. 2005).

Playa and grassland are both C_4 grass dominated systems. However, playa soil had a much higher SOC and TN content than that in grassland (Figure 15). The amount of litter and root biomass were significantly higher in playa (240 g m^{-2} and 620 g m^{-2} respectively) than those in grassland (30 g m^{-2} and 194 g m^{-2} respectively). This also suggested a strong role for litter and root biomass in determining SOC and TN.

Previous studies at La Copita also found that soils in woody patches had increased C and N fluxes but increased mean residence times accompanying increase SOC and TN content (McCulley et al. 2004). Since soil in the wooded community had both increased input and output of C and N, increased soil SOC and TN content under woody vegetation suggested that increases of inputs were greater than that of the outputs of soil C after woody invasion. Lower $\delta^{13}C$ value and increased mean residence time of SOC under wooded communities suggested that some or all of the increased C was from woody resources, and that inputs derived from woody plants had a longer mean residence time than organic C derived from grasses (Boutton et al. 1998, Liao et al. 2006b).

Soil bulk density and basal areas of shrubs and trees were also significantly correlated with SOC and TN based on modified t-tests for correlation at the landscape scale (Table 4). Soil bulk density was negatively correlated with SOC and TN content. Since soils associated with woody patches had lower bulk density and higher root biomass (Table 2), the correlation between soil bulk density and SOC and TN reflects the important role that soil organic matter plays in determining bulk density. Fine textured soils usually retain more SOC and TN than coarse textured soils (Schimel et al. 1985, Amundson 2001), but the results of this study showed that soil particle size distributions were not significantly correlated with SOC and TN content. This suggests that soil physical characteristics are not as important as other factors such as litter and root biomass in determining SOC and TN in this subtropical savanna parkland landscape.

Spatial distributions of SOC and TN were strongly influenced by patterns of woody invasion. This is supported by the fact that SOC and TN had the strongest correlations with litter and root biomass as well as significant correlations with shrub and tree basal area (Table 4). Cross-Mantel test also showed that SOC and TN were spatially correlated with litter, root biomass, and basal areas of shrubs and trees. Previous studies showed that changes of soil C content are related to ages of woody patches, which have a positive linear relationship with the size of mesquite (Archer 1989, Boutton et al. 1999, Archer et al. 2004, Liao et al. 2006b, Boutton et al. 2007). Studies of other ecosystems found that the impact of woody plants on soil properties extended over a distance approximately equal to the size of their canopies (Jackson 1993, Schlesinger 1996). Since basal areas of woody plants are highly correlated with their aboveground biomass and canopy dimensions (Northup et al. 2005), the strong relationships between SOC and TN is not surprising and reflects the influence of woody plant age and canopy size on spatial distribution of soil C and N.

Spatial scales of SOC and TN patterns

Quadrat variance analysis results showed that SOC, TN, litter, root biomass, tree basal area and shrub basal area had similar scales of about 40-45 m, which was about the average distance from center of woody patches to the center of their neighboring grassland area (Figure 16, Table 5). The fact that SOC and TN had similar spatial scales with litter, root biomass, and basal areas of trees and shrubs reinforced the concept that spatial distribution of SOC and TN was influenced by those variables.

Although forb and grass biomass also showed scales at 38-47 m, they were not significantly correlated with SOC and TN at the landscape scale (Table 4). Scales detected for soil texture were not similar to those of SOC and TN suggested that soil texture was not a major factor in influencing the spatial distribution of SOC and TN. This is consistent with the lack of significant correlations between soil texture and SOC and TN.

Quantifying domains of scale and exploring the underlying processes at each scale is essential for extrapolating results across spatial scales (Wiens 1989). With the widespread occurrence of woody invasion into grasslands around the world, it is clear that this phenomenon has the potential to influence C and N cycles at regional and perhaps even global scales. The domains of scale of SOC and TN detected by the quadrat variance method in this study could represent a major step towards estimating SOC and TN storage at watershed or regional scales in southern Texas.

SOC and TN were strongly correlated with litter and root biomass. Spatial pattern of SOC and TN was influenced by aboveground woody canopies (Jackson and Caldwell 1993, Schlesinger and Pilmanis 1998) through litterfall and root turnover. Invasion of woody plants into grasslands had changed the spatial pattern of litterfall and rooting pattern, which in turn influenced the spatial pattern of soil C and N storage. The estimation of SOC and TN storage at large scales by collecting and analyzing extensive soil samples is an expensive and time consuming proposition. Based on the correlation and spatial relationships between SOC, TN, and woody canopies, we could potentially use woody cover data obtained from readily available and relatively inexpensive remote sensing imagery as a secondary dataset associated with soil samples to facilitate the estimation of SOC and TN storage in woody invaded landscapes.

Summary

This study confirmed that woody encroachment increased both SOC and TN storage in surface soil. SOC and TN were strongly correlated with litter and root biomass both in amount and in spatial pattern; they also have similar spatial scaling properties. This suggested that ecological processes related to litter and root production are the dominant processes that affect both the magnitude and spatial distribution of SOC and TN. Spatial scales of SOC and TN calculated using quadrat variance methods suggested their domains of scale, which were closely related to the spatial pattern of invaded woody vegetation.

Woody plant encroachment occurs widely in arid and semiarid regions, which cover about 40% of the world’s land surface. Therefore, the effects of woody invasion on the storage and turnover of SOC and TN could have significant implications for global biogeochemistry and perhaps the climate system. This study of correlation and spatial scaling of SOC and TN will help us better understand how woody invasion affects soil C and N content and their spatial distribution. This knowledge will enhance our ability to quantify SOC and TN pools at larger scales, and will help us evaluate the role of woody invaded grasslands as a source or sink for atmospheric CO_2.

CHAPTER IV

SPATIAL PATTERN AND CONTROL OF WOODY VEGETATION ALONG A TOPOEDAPHIC GRADIENT IN A SAVANNA LANDSCAPE IN SOUTHERN TEXAS

Introduction

Woody encroachment has occurred in many temperate and tropical grasslands and savannas all over the world (Archer 1995, McPherson 1997). This change of physiognomy has important impacts on ecosystem structure and function. It may also have significant implications for global change and biogeochemistry because these woody invaded systems occupy a large portion of the Earth's land surface.

The Rio Grande Plains of Southern Texas is one region where conversion of grass to woody plant domination has been documented in recent history. This has been confirmed by studies of historical aerial photographs, tree rings, carbon isotopes, analysis of current plant communities, and ecosystem models (Archer et al. 1988, Archer 1989, Scanlan and Archer 1991, Flinn et al. 1994, Boutton et al. 1998). Potential causes of woody invasion in grasslands and savannas include livestock grazing, altered fire regimes, climate change, and atmospheric CO_2 enrichment (Archer 1995, Van Auken 2000). Other factors like population dynamics of native herbivores (Weltzin et al. 1997), and soil physical properties (Loomis 1989) may also affect the process of woody invasion.

The process of woody invasion is often initiated by the establishment of *Prosopis glandulosa* (mesquite) in grassland, which then serves as recruitment foci for other woody species (Archer et al. 1988). *Prosopis* has properties such as N-fixation (Zitzer et al. 1996), high emergence and survival rate (Brown and Archer 1989) and tolerance of defoliation early in its life cycle (Weltzin et al. 1998), which could potentially contribute to its successful establishment. As *Prosopis* and other woody species establish and develop, discrete woody clusters begin to form and ultimately coalesce.

The establishment of pioneering *Prosopis* trees facilitates the colonization of other woody species by providing shade, modifying microenvironment, and improving soil conditions (Archer 1995). Facilitation during the early stages of cluster development may ultimately give way to competition once the woody community evolves into a steady state. Competition between understory shrubs and over-story pioneer trees appears to be asymmetrical and results in the demise of pioneer *Prosopis* plants (Archer 1995, Barnes and Archer 1999). In addition to biotic interactions, environmental factors (such as soil physical and chemical properties) and surface hydrology may also affect the location of woody plant establishment and their subsequent dynamics (Loomis 1989, Wu and Archer 2005). The coexistence of woody species and grasses depends on the mechanisms of their interactions, which are known to differ between ecosystems (Scholes and Archer 1997, Sankaran et al. 2004, Wiegand et al. 2006).

Many studies have focused on interactions among woody species (Barnes and Archer 1996, 1999) and coexistence between woody species and herbaceous plants in savannas (Brown and Archer 1990, Boutton et al. 1999). However, few have examined how environmental factors affect woody species assemblages and how they vary as succession proceeds (Midwood et al. 1998, Barnes and Archer 1999, Boutton et al. 1999, Nelson et al. 2002). The objective of this study was to identify factors that influence the composition and spatial distribution of woody assemblages along a topoedaphic gradient. More specifically, we asked the following questions: (1) What environmental variables influence spatial distribution of woody species; and (2) What are the relative strengths of these variables in determining the spatial distribution of woody species.

Methods

Study site

Field studies were conducted at the Texas Agricultural Experiment Station La Copita Research Area (LCRA), approximately 24 km southwest of Alice, Texas. The climate is subtropical with hot, dry summers and warm, moist winters and a mean annual temperature of 22.4°C. Annual precipitation is bimodally distributed with maxima in late spring and early autumn. Elevation ranges from 75 to 90 m with nearly level slopes (1-3%). The research area was heavily grazed before its designation as a research site in early 1980's, but has been lightly to moderately grazed since that time. The shift from grass domination to woody domination has occurred largely over the past 100 years (Boutton et al. 1998).

The present landscape at LCRA consists of sandy loam uplands (Typic and Pachic Argiustolls) and clay loams in the lower-lying drainages (Pachic Argiustolls). Uplands are covered by discrete woody clusters and groves embedded in a C_4 grass dominated herbaceous matrix. Discrete clusters and herbaceous zones generally occur on sandy loam soils with an argillic horizon ~40 cm below the surface, while groves generally occur on cambic soil where the argillic horizon is absent (Archer 1995). Uplands grade gently into lower-lying drainages characterized by closed canopied woodlands.

Discrete woody patches contain numerous species of understory shrubs organized around a central *Prosopis* tree. Drainage woodlands are dominated by a continuous *Prosopis* overstory with dense understory shrubs. Common shrub species in both uplands and drainage woodlands include: *Zanthoxylum fagara, Condalia hookeri, Diospyros texana, Celtis pallida, and Berberis trifoliolata* (Archer 1990). Upland grasslands consists primarily of forbs (Asteraceae) and C_4 grasses such as *Aristida*, *Bouteloua*, *Cenchrus*, *Chloris* and *Setaria* species. Oval-shaped playas occur in the basin of some drainage. The physiognomy of playas ranges from grassland to savanna depending on their location (Farley 2000). When trees are present, *Prosopis glandulosa* is typically the dominant woody species.

Field sampling and lab analyses

A 309-m long transect was established from upland to playa along a topoedaphic gradient running through all 5 major plant communities: grassland, cluster, grove, drainage woodland, and playa (Figure 17). Elevations along the transect were determined by a field survey conducted in April 2004 and a USGS topographic map.

Soil samples (15 cm deep 2.24 cm in diameter) were collected at 1 m intervals (3 soil cores per point) along the transect to measure soil bulk density, soil organic carbon (SOC), total nitrogen (TN), pH, volumetric water content (VWC), and soil texture. The coordinates of soil sampling points were measured at 5 m intervals using a GPS unit (Trimble Navigation Limited, Sunnyvale, CA). Shrubs were sampled within a 2 m wide belt centered on the transect line. The belt was divided into 2 m × 1 m quadrats centered on each of the soil sampling point. All shrubs within each quadrat were measured for their basal diameter and their species names were recorded. Trees with a basal diameter greater than 8 cm were measured within a 12 m wide belt centered on the transect line.

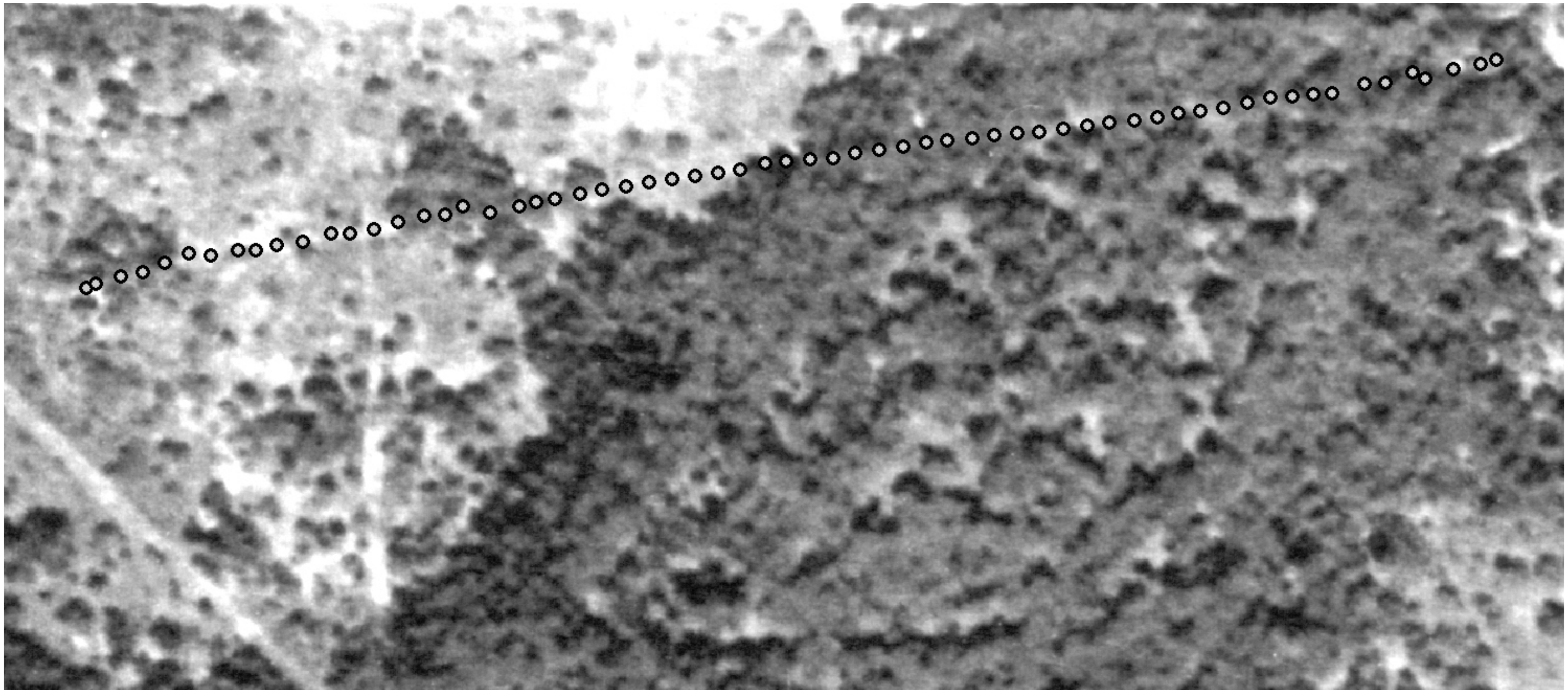

Figure 17: Aerial photograph showing transect locations. White dots are GPS locations of soil samples at 5 m intervals. Dark color indicates woody vegetation and light gray indicates herbaceous vegetation.

The distances from each tree to the nearest 2 sample points with coordinates were measured. Coordinates of trees were calculated based on the measured distances.

For each soil sampling location, one soil core was weighed before and after oven drying at 105° C to determine soil VWC and soil bulk density by the core method (USDA 2004). This same soil was then used to determine soil texture (particle size distribution) using the pipet method (USDA 2004).

A second soil sample was dried at 60°C for at least 48 hours, passed through a 2 mm screen to remove coarse organic fragments and gravel, and then pulverized to a fine powder in a centrifugal mill (Angstrom, Inc., Belleville, MI, USA). Samples were weighed into silver capsules (5 x 7 mm) using a microbalance, treated with HCl vapor in desiccator to volatilize carbonate-carbon (Harris et al. 2001), dried thoroughly, and sealed into the capsules. SOC and TN concentrations were determined through dry combustion by using a Carlo Erba EA-1108 elemental analyzer (CE Elantech, Lakewood, NJ).

Soil pH values were determined by adding 12 g soil to $CaCl_2$ solution (0.01 M $CaCl_2$). The pH of the liquid was determined with an Accumet Basic pH meter (Fisher Scientific).

Statistical analyses

In order to understand how shrubs and trees distribute along the environmental gradient, canonical correspondence analysis (CCA) (terBraak 1986) was performed using CANOCO version 4.0 (terBraak and Smiluer 1998) on two matrices: the quadrat by species matrix and quadrat by environmental variables matrix. Environmental variables include soil VWC, soil texture, SOC, TN, soil pH, and soil bulk density. Although all trees within a 12 m wide belt along the transect were measured, only those within the central 6 m wide belt were used for ordination. The 6 m wide belt was divided into 6 m × 6 m quadrats. For each quadrat, environmental variables were averaged over the 6 measurements. All shrubs measured in each 2 m × 2 m grid cell were used for ordination and the environmental variables were obtained by averaging 2 measurements in each grid cell.

In order to divide explained variation of woody species composition among explanatory environmental variables, partial CCA was conducted by using CANONCO. Inertia of ordination, which quantifies variation of species composition, is additive and can be distributed to groups of environmental variables. Since total inertia, the sum of all eignevalues of unconstrained ordination axes, is not a reliable measurement of the total variation in the data set, relative amounts of total variation explained (TVE) by different groups of environmental variables were used instead (Okland 1999, Qian et al. 2003). Environmental variables were divided into two groups: landscape location related variables (soil texture, soil VWC, bulk density and soil pH), and soil nutrient level related variables (SOC and TN). Before partitioning variance, variables in each group were first tested for independent and significant contribution to variation in species composition. The procedure of forward selection in CANOCO, which uses a Monte Carlo simulation test to assess the significance of each variable in the regression model, was used to assess the significance of each variable. Only variables that had a significant contribution ($p<0.05$) were included in the analysis of variance partitioning. Variance partitioning was conducted by using the same approach as Borcard et al. (Borcard et al. 1992) and Okland (Okland 2003).

Indicator species analysis (Dufrene and Legendre 1997) was performed by using PC-ORD version 4 (McCune and Mefford 1999) on quadrat by species matrix to calculate indicator value of tree and shrub species for each vegetation type.

Results

Species composition and environmental variables along the transect

Figure 18 illustrates variation in elevation and environmental variables (soil bulk density, pH, soil VWC, SOC, and soil texture) along the transect. Soil water content is higher in the drainage woodlands and playa than that in the upland. The highest value of soil volumetric water content is in the playa. Soil texture also changes along the topographic gradient, with higher sand percentages in the uplands and higher clay and silt percentages in the low-lying drainage woodlands and playas. SOC was higher under woody vegetation than in grassland, with highest average found in the drainage woodland. The distribution pattern of TN (data not shown) along the transect was similar to that of SOC.

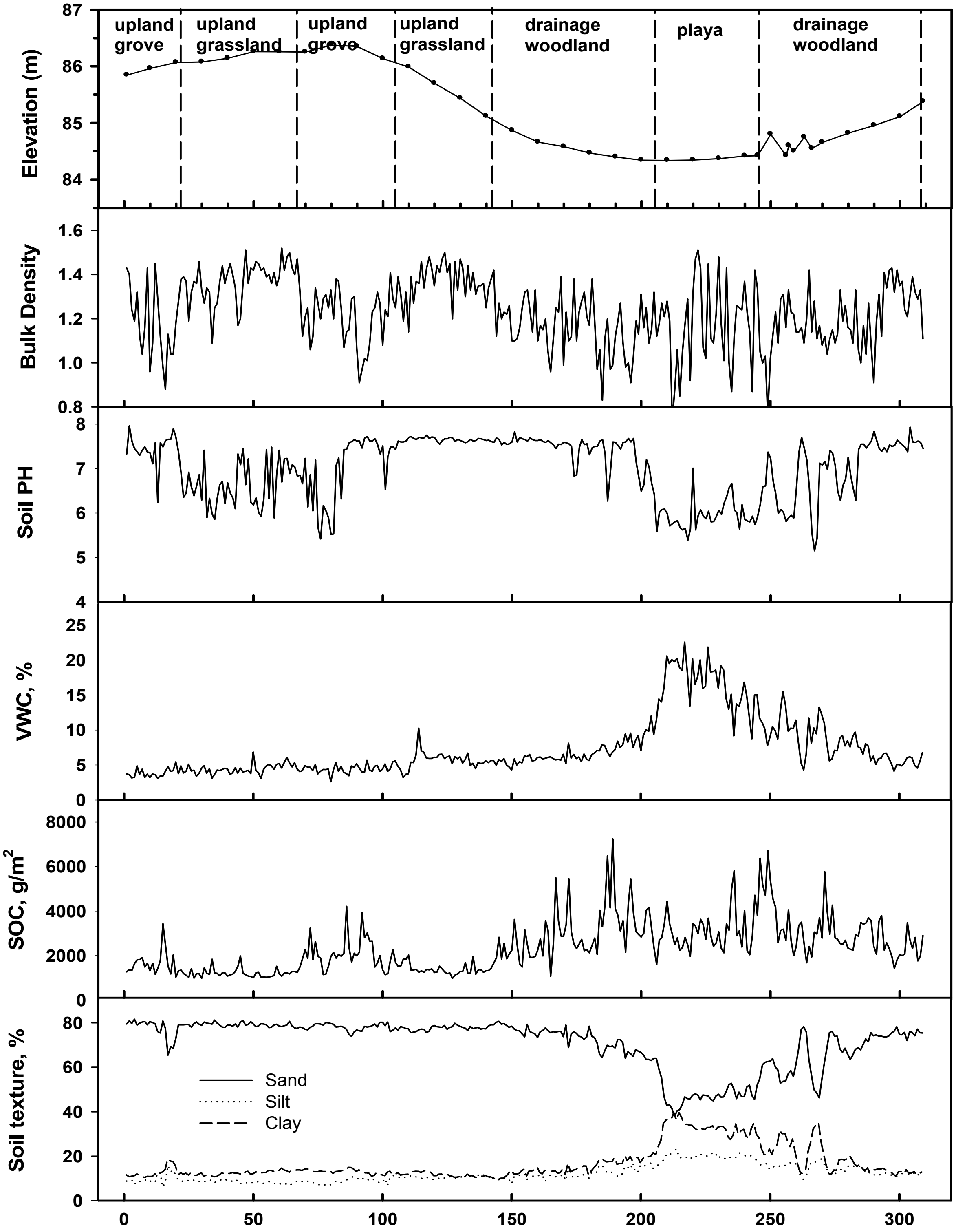

Figure 18: Elevation and environment variables along the transect. VWC is soil volumetric water content; SOC is soil organic carbon.

A total of 12 tree species with a basal diameter > 8 cm were found in the 12-meter wide belt along the topoedaphic gradient (Table 6). The numbers of tree species appearing in clusters, groves, drainage woodlands, and playa are 5, 11, 11, and 7 respectively. Among these tree species, *Acacia farnesiana* and *Zanthoxylum fagara* appeared in all 4 woody plant communities while *Acacia rigidula*, *Bernardia myricaefolia*, *Ephedra antisyphilitica*, and *Parkinsonia aculeata* only appeared in one of the plant communities (Table 6). Five tree species have a density higher than 100 stems/ha. *Zanthoxylum fagara* had the highest density (183 stems/ha) among all tree species. *Prosopis glandulosa* had the largest average basal area at 543 cm^2 per stem.

Shrubs were sampled in a 2 m wide belt centered on the transect line and a total of 27 shrub species were present. All tree species also appeared in the shrub species list (Table 7). *Bernardia myricaefolia* and *Ephedra antisyphilitica* only occurred once while *Colubrina texensis*, *Celtis pallida* and *Zanthoxylum fagara* were abundant with multiple stems. Some species such as *Zanthoxylum fagara, Celtis pallida* and *Eupatorium* were found in all 4 plant communities. *Acacia rigidula, and Yucca treculeana* were only found in one of the plant communities. Species such as *Prosopis glandulosa*, *Diospyros texana*, *Parkinsonia aculeata*, and *Acacia spp.* are larger shrubs with average basal areas bigger than 6 cm^2 per stem. Other species like *Colubrina texensis*, *Eupatorium spp.*, *Lantana horrida* and *Salvia ballotaeflora* have a large number of stems with average basal area per stem smaller than 0.5 cm^2.

Prosopis glandulosa is the dominant overstory woody species in all woody plant communities (Archer et al. 1988), but different shrub species dominate in different plant communities. The dominant shrub species changed from *Colubrina texensis, Zanthoxylum fagara* in clusters and groves to *Celtis pallida*, *Diospyros texana* in the drainage woodland and playa (Table 7).

In order to detect the indicator species of each plant community, Dufrene and Legenre's (1997) method was used to calculate species indicator value. Significance of the indicator value was calculated through a randomized Monte Carlo simulation using PC-ORD. No tree species had a significant indicator value due to small numbers of tree species and there was little difference in tree species composition between different plant communities. Indicator species values of shrubs are shown in Table 8.

Table 6: Occurrence of tree species within a 6-m wide belt along the transect. N is number of trees; BA ($cm^2\ m^{-2}$) is basal area of trees.

Species	**Cluster**		**Grove**		**Woodland**		**Playa**	
	N	BA	N	BA	N	BA	N	BA
Acacia farnesiana	2	0.57	2	0.24	8	1.6	19	16.97
Acacia rigidula					2	0.49		
Bernardia myricaefolia			3	0.45				
Celtis pallida			5	0.66	37	3.78	22	6.61
Condalia hookeri	6	2.52	5	0.69	39	2.42		
Diospyros texana			3	0.34	50	2.11	5	0.51
Ephedra antisyphilitica			1	0.17				
Karwinskia humboltiana	2	0.62	4	0.34	1	0.1		
Parkinsonia aculeata							1	0.46
Prosopis glandulosa			22	9.61	34	13.16	4	12.38
Yucca treculeana			8	1.36	3	0.12		
Zanthoxylum fagara	2	4.18	21	4.22	37	2.71	8	1.33

Table 7: Occurrence of shrub species within the 2 m wide belt along the transect. N is the number of individual stems; BA ($\mathrm{cm}^2\ \mathrm{m}^{-2}$) is basal area.

Species	**Cluster**		**Grove**		**Woodland**		**Playa**	
	N	BA	N	BA	N	BA	N	BA
Acacia farnesiana					5	2.97	3	2.23
Acacia greggii	5	0.85						
Acacia rigidula					13	0.45		
Aloysia gratissima					257	0.69		
Asclepias spp.					5	0.01		
Bernardia myricaefolia					1			
Berberis trifoliolata	19	0.87	10	0.09	20	0.07		
Capsicum annuum					6			
Celtis pallida	6	0.05	109	4.49	571	13.98	8	3.64
Colubrina texensis	289	2.97	313	1.29	31	0.46		
Condalia hookeri	15	2.04	18	0.08	22	5.49		
Diospyros texana			12	0.24	140	4.65	8	2.18
Ephedra antisyphilitica					1	0.01		
Eupatorium spp.	12	0.08	42	0.15	80	0.11	1	0.08
Eysenhardtia texana	22	1.4						
Forestiera angustifolia	2	0.1	1	0.02	4	0.04		
Gymnosperma spp.			10	0.04	1	0.01		
Karwinskia humboltiana			113	3.08	184	0.76		
Lantana horrida	10	0.06	16	0.07	20	0.04		
Opuntia leptocaulis	3	0.31	7	0.15	15	0.04		
Parkinsonia aculeata							2	0.16
Prosopis glandulosa	1	0.35	17	16.05	20	30.4		
Salvia ballotaeflora					130	0.21		
Schaefferia cuneifolia	20	0.87	84	0.5	160	0.41		
Yucca treculeana			3	2.08				
Zanthoxylum fagara	85	5.28	169	4.87	143	3.12	4	1.26
Ziziphus obtusifolia			3	0.12	4	0.05	5	0.24

Table 8. Indicator species value (IV) of shrub species. Only species with significant indicator value were shown. Max Veg. is the vegetation type the maximum indicator value in.

Species	**IV**	**Max Veg.**
Colubrina texensis	65.5	Cluster
Aloysia gratissima	50	Woodland
Diospyros texana	41.4	Playa
Ziziphus obtusifolia	26.3	Playa
Acacia farnesiana	24	Playa
Eysenhardtia texana	23.1	Cluster
Prosopis glandulosa	23.1	Grove

CCA ordination

Canonical ordination of tree species had a total inertia of 4.167, of which 24.7% was explained by the first 4 axes. The first and second axes accounted for 12.5% and 7% of the total inertia respectively. CCA ordination diagrams of quadrats, tree species and environmental variables are shown in Figure 19 and Figure 20.

The first CCA axis was strongly and positively associated with environmental variables such as VWC and silt and clay content. However, it was negatively correlated with sand content and soil pH (Figure 19). The first axis suggests an elevation gradient with dry sandy quadrats on one end and moist clay quadrats on the other end. Quadrats of trees were well separated along this gradient with clusters and groves on one side and drainage woodlands and playas on the other side (Figure 20). The centroids of most tree species distributed closely along this gradient. Most species were located on the sandy drier side of the gradient while *Acacia farnesiana* and *Celtis pallida* were on the other side of the gradient.

The second CCA axis was strongly and positively correlated with SOC and TN. It was also weakly negatively correlated with soil bulk density (Figure 19), which is related to SOC and TN content. The second axis suggested a gradient of soil nutrients level. Quadrats of same plant community type were well spread out along this gradient depending on their difference in soil nutrient level and species composition (Figure 20). The centroids of tree species were well separated by this gradient with *Berberis trifoliolata* and *Yucca treculeana* on the nutrient poor end and species like *Celtis pallida*, *Diospyros texana* and *Acacia rigidula* distributed on the nutrient rich end of the gradient.

CCA ordination of shrubs in 2 m × 2 m plots along the transect line had a total inertia of 8.4, of which 13% was explained by the first four axes. The first two axes explained 9.3% of the variance in species composition data. CCA ordination biplot of species and environmental variables for the first two axes is shown in Figure 21 and the CCA ordination diagram of sample plots is shown in Figure 22.

Similar to the CCA ordination results for trees, the first axis of shrub ordination was strongly associated with soil texture (sand, silt and clay percentages) and soil volumetric water content. The centroids of most shrub species' distribution were close to the plot

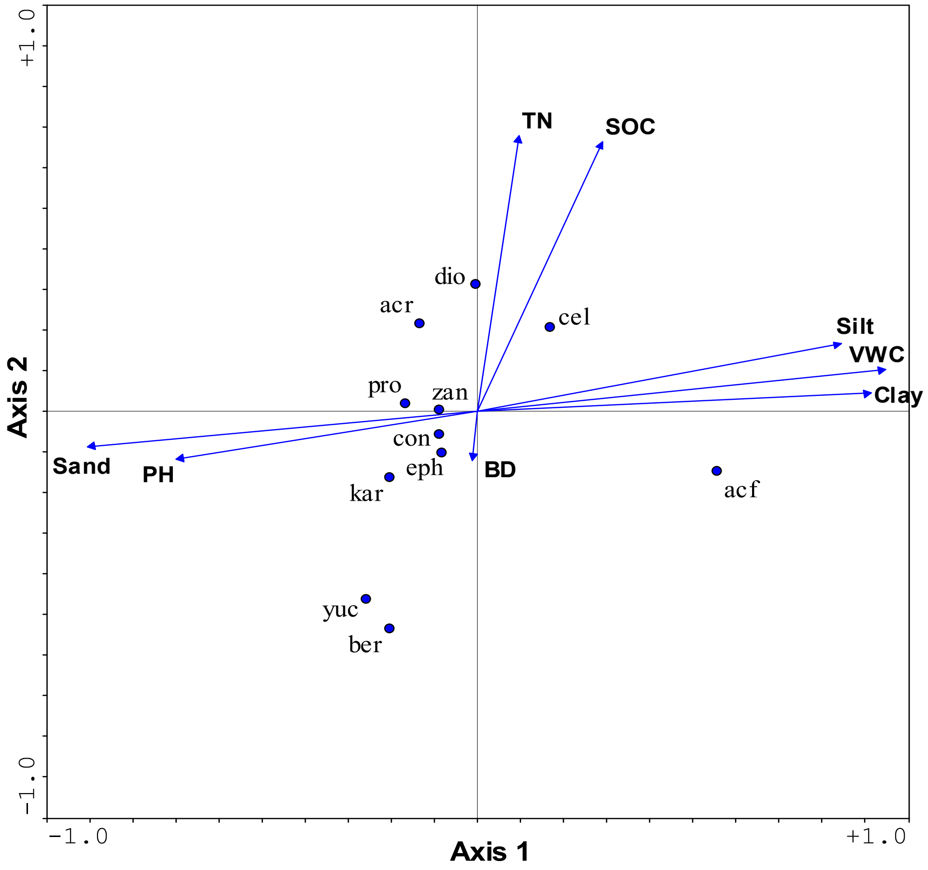

Figure 19. Canonical correspondence analysis (CCA) ordination of tree species and environmental variables. Dots indicate centroids of tree species distribution (acf is *Acacia farnesiana;* acr *is Acacia rigidula*; ber *isBernardia myricaefolia*; cel *is Celtis pallida*; con *is Condalia hookeri*; dio *is Diospyros texana*; eph *is Ephedra antisyphilitica*; kar *is Karwinskia humboltiana*; pro *is Prosopis glandulosa*; yuc *is Yucca treculeana*; zan *is Zanthoxylum fagara*). Arrows indicate environmental vector toward increasing values with longer arrows indicating broader range of variation in tree species distribution (BD is soil bulk density; PH is soil pH; Sand is particle percentage of sand in soil; Clay is particle percentage of clay; silt is particle percentage of silt; SOC is soil organic carbon; TN is soil total nitrogen; VWC is soil volumetric water content).

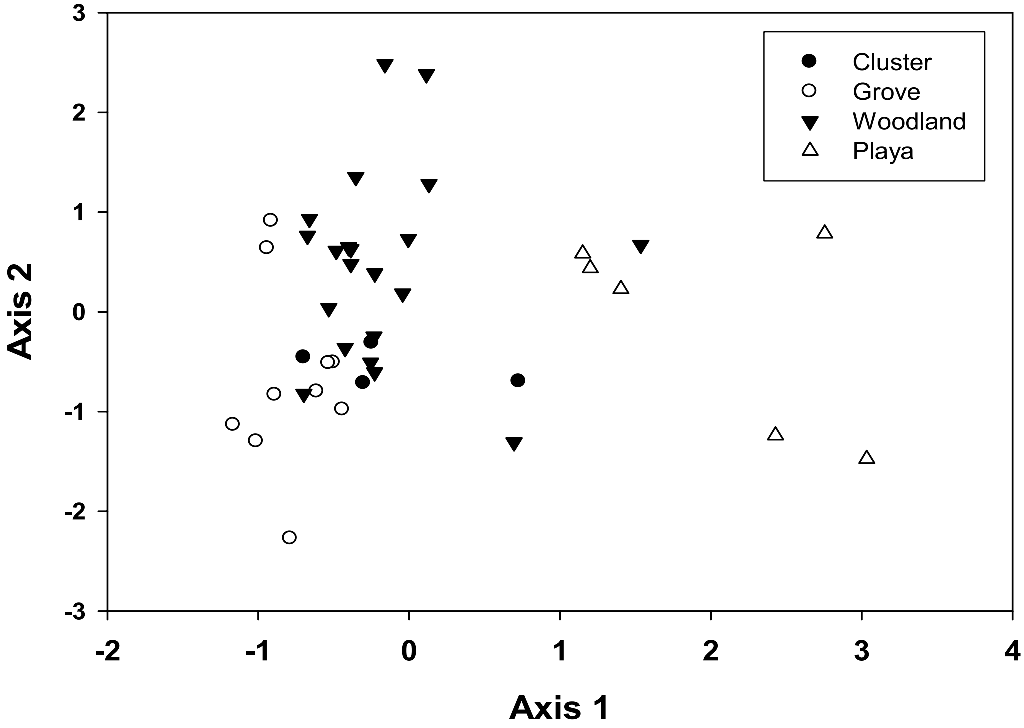

Figure 20. CCA ordination of 6 m × 6 m tree sampling quadrats on Axis 1 and Axis 2. Plant communities were shown in different symbols.

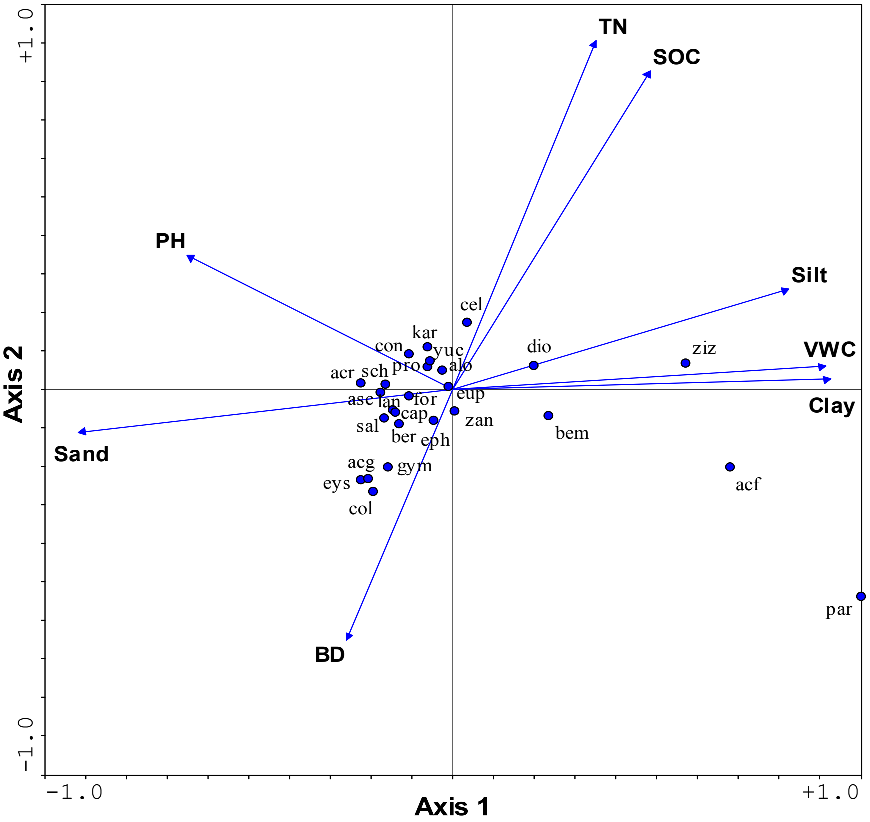

Figure 21. CCA ordination diagram showing the biplot of tree species and environmental variables. Dots indicate centroids of tree species distribution (acf is *Acacia farnesiana*; acg is *Acacia greggii*; acr *is Acacia rigidula*; alo is *Aloysia gratissima*; asc is *Asclepias spp.*; bem is *Bernardia myricaefolia*; ber *isBernardia myricaefolia*; cap is *Capsicum annuum*; cel *is Celtis pallida*; col is *Colubrina texensis*; con *is Condalia hookeri*; dio *is Diospyros texana*; eph *is Ephedra antisyphilitica*; eup is *Eupatorium spp.*; eys is *Eysenhardtia texana*; for is *Forestiera angustifolia*; gym is *Gymnosperma spp.*; kar *is Karwinskia humboltiana*; par *is Parkinsonia aculeata*; pro *is Prosopis glandulosa*; sal is *Salvia ballotaeflora*; sch is *Schaefferia cuneifolia*; yuc *is Yucca treculeana*; zan *is Zanthoxylum fagara*; ziz is *Ziziphus obtusifolia*). Arrows indicate environmental vector toward increasing values with longer arrows indicating broader range of variation in tree species distribution (BD is soil bulk density; PH is soil pH; Sand is particle percentage of sand in soil; Clay is particle percentage of clay; silt is particle percentage of silt; SOC is soil organic carbon; TN is soil total nitrogen; VWC is soil volumetric water content).

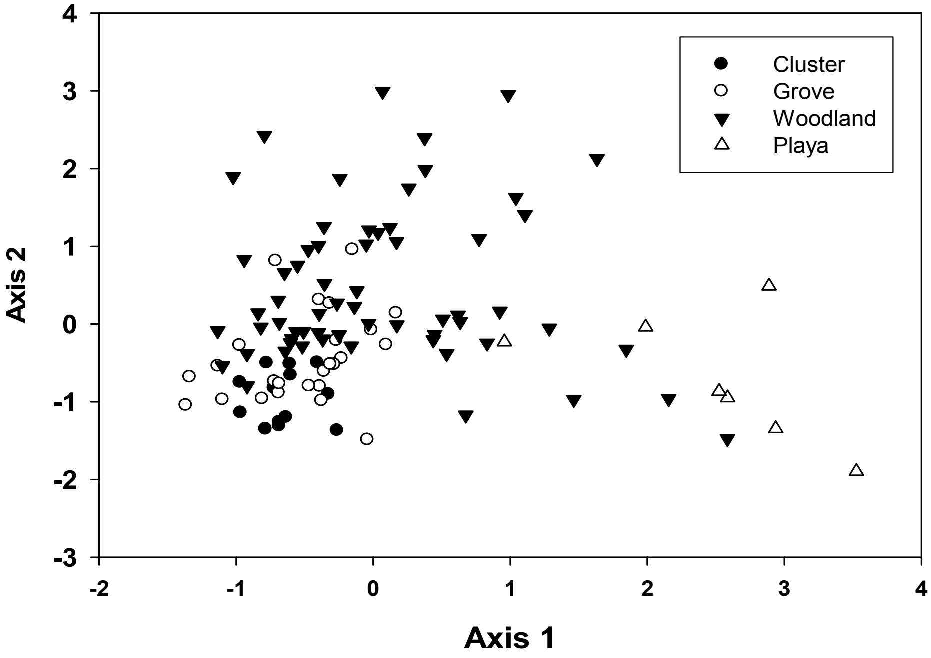

Figure 22. CCA ordination of shrub sampling quadrats on Axis 1 and Axis 2. Plant communities were shown in different symbols.

origin while species like *Parkinsonia aculeata, Acacia farnesiana* and *Ziziphus obtusifolia* were distributed at the end of this gradient. On the first axis, the sampling plots of shrubs change from groves, clusters to woodland and playa with considerable overlap between these plant communities (Figure 22).

The second axis of the CCA diagram was correlated with SOC, TN and soil bulk density. Soil pH was correlated with both the first and second axes. The centroids of shrub species did not spread out on the second axis as much as they did on the first axis. With increasing SOC and TN, the centroids of shrubs species changed from *Colubrina texensis*, *Eysenhardtia texana* to species like *Celtis pallida* and *Diospyros texana* (Figure 22).

Variance partitioning

Only the environmental variables that could independently explain a significant amount of variation in tree and shrub species composition were included in the variance partitioning. Soil bulk density and TN content were excluded because they did not significantly explain variation in tree species composition. Relative amounts of total variation explained (TVE) by the two groups of environmental variables for tree and shrub species composition are shown in Figure 23. For both tree and shrub species composition, a large portion of the variation was explained by landscape location related environmental variables (76.9% of total TVE for trees, and 58% of total TVE for shrubs), which indicated that these variables were playing a primary role in determining species composition and abundance. The group of soil nutrient related variables played a secondary role in determining tree and shrub species composition.

For variation in tree species composition, there was almost no shared explained variation (0.2%) between the two groups of environmental variables while 22.4% of the variation of shrub species composition was shared by the two groups of environmental variables (Figure 23). This suggested that soil nutrient level had a bigger influence on understory shrub species composition through interactions with landscape location related environmental variables than on overstory tree species composition.

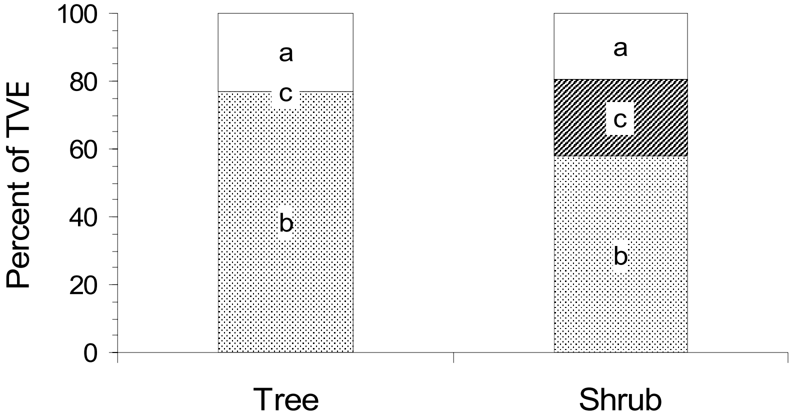

Figure 23. Percentage of variation of tree and shrub species composition (TVE is total variation explained) explained by groups of environmental variables. a represents landscape location related variables; b represents soil nutrients related variables; c represents intersection between a and b.

Discussion

Woody species composition

A total of 27 woody species were found along the transect, most of which were found in all woody plant community types (Table 6, Table 7). The abundant species in all woody plant communities were these common species though their dominance was different in each type of plant community. For example, *Zanthoxylum fagara* was more dominant in groves than in drainage woodland, while *Celtis pallida* was the opposite though both species were abundant in the two woody plant communities (Table 7). Several species were found in only one or two of the woody plant community types. Some of them occurred only when a specific combination of environmental factors was present. For example, *Parkinsonia* was found only in the playa because it thrives around watercourses and prefers clay soils. Some other species may have been limited by their dispersal abilities or competition with other species.

Previous studies at this site indicated that the number of woody species per cluster was strongly related to the size of *Prosopis* (Archer et al. 1988), which is an indicator of cluster age (Flinn et al. 1994). *Prosopis*, *Opuntia* and *Zanthoxylum* were the most common species that occured in clusters with two or three other species. As numbers of woody species in a cluster increased, other species such as *Condalia obovata*, *Diospyros texana*, and *Celtis pallida* became frequent. Shrubs such as *Berberis* and *Zizyphus* were found only in species-rich clusters. Many landscapes in this region with continuous woody cover appear to have developed from coalesce of clusters. If this process persists, the present two-phase landscape is likely to move toward a closed-canopy woodland (Archer 1995, Hibbard et al. 2003). By comparing woody species composition along this successional gradient, we should be able to enhance our ability to predict the future evolution of this landscape.

The woody plant community types along the topoedaphic gradient, from clusters to groves to drainage woodlands, suggested a gradient of succession stages. Although species composition was similar among clusters, groves and woodlands, there appear to be some subtle changes in their relative dominance during succession. The dominance of *Zanthoxylum* decreased from clusters to groves to drainage woodlands, while *Celtis* and *Diospyros* increased over succession (Table 6, Table 7). This shift of woody species dominance may be caused by interactions among woody species, interactions between woody species and herbaceous plants, and/or modification of microenvironment. Previous studies found that though *Prosopis* facilitated the establishment of other woody species during early stages, their presence did not enhance the growth of mature understory shrubs (Francopizana et al. 1995, Barnes and Archer 1996). Further studies have found that understory shrubs have a significant negative effect on *Prosopis* by competing for limited soil resources that can cause the demise of *Prosopis* in many cases by preventing its regeneration (Archer 1995, Barnes and Archer 1999). Tree-grass interactions in savannas are complex and they could be competition or facilitation for different systems (Scholes and Archer 1997). There is no single model that can fully account for the observed variety and persistence of tree-grass systems (House et al. 2003). Future studies are needed to fully understand how tree-grass interactions will affect woody species composition over succession. Invasion of woody plants into grassland affect every aspect of the ecosystem such as structure, microclimate, hydrology, soil and biogeochemistry. All these modifications could affect woody species composition in different ways.

Since indicator species are those that occur primarily in one group and are present in the majority of the sites of that group (Dufrene and Legendre 1997), species indicator values are helpful for detecting species that are common in one plant community group but not for detecting rare species. All significant indicator values for the shrub species are not strong, which suggest that there are few species that characterize a particular group (Table 8). This is consistent with the results that most woody species are either common species that occur in most plant community types or rare species that only occur in some sites within a plant community type (Table 7).

Spatial pattern of woody species

Ordination results indicated that tree and shrub species composition was influenced by both landscape position and soil related environmental factors. The first axis of CCA ordination showed a close correlation with soil texture and soil volumetric water content, which are known to be strongly determined by landscape position (Figure 19, Figure 21). Soil texture and soil water content had comparable strength of influence on species distribution of both tree and shrub species. The second axis of CCA ordination was related to gradients of SOC and TN, as well as soil bulk density. But soil bulk density showed a negative and weaker influence on woody species composition (Figure 19, Figure 21). Variance partitioning of environmental variables indicated that landscape location related to environmental variables (soil texture, soil water content) explained a larger portion of the variance in woody species composition than soil nutrients level related variables. This suggests that soil texture and soil water content, which are related to landscape position, play a greater role in determining woody species composition than soil nutrient levels.

Many environmental factors have been reported to influence the distribution of woody species in savannas. Some studies showed that soil geomorphic heterogeneity controls vegetation pattern in arid ecosystems (McAuliffe 1994, Bestelmeyer et al. 2006). Other factors like long-term climate change (Brown et al. 1997), disturbance regimes (Barton 1993), land management (Heaton et al. 2003), soil organisms (Kardol et al. 2006) and small mammal browsing (Weltzin et al. 1997) were also shown to affect the process of woody invasion. Environmental factors that determined the woody species assemblages differed for different spatial scales. Previous studies in our study site showed that, in uplands, the spatial distribution of patchy woody vegetation was controlled by the presence of an argillic horizon, a zone of clay accumulation at around 40-100 cm (Archer 1995). Soils under groves lack an argillic (Bt) horizon while soils associated with discrete clusters and herbaceous vegetation have a strongly expressed argillic horizon (Loomis 1989, Archer 1995). Another study conducted by Wu and Archer (2005) used a topographic wetness index to test effects of topography-based hydrology on woody vegetation and their dynamics. They found that surface hydrology influenced not only patterns of woody plant cover, but also their dynamics at the catena scale.

Other than abiotic factors, biotic interactions among woody species, between woody species and herbaceous plants could also influence woody vegetation composition and their dynamics. Modification of microclimate by *Prosopis* facilitates the establishment of other understory woody species in the early stages of succession (Archer et al. 1988, Franco-Pizana et al. 1996). Because root systems of *Prosopis* and understory woody species are distributed at different depths in soils (Watts 1993, Midwood et al.

1998), they could partition resources like soil moisture both spatially and temporally (Weltzin and McPherson 1997, Boutton et al. 1999). Hydraulic lift by *Prosopis*, which is influenced by edaphic factors, may also facilitate some understory shrubs (Zou et al. 2005). The facilitation of understory shrubs by *Prosopis* to other could convert into competition as woody patches expand and mature. Experiments showed that presence of *Prosopis* does not enhance the growth or activity of mature understory shrubs (Barnes and Archer 1996), but as understory shrubs increase in size and density, they could have a strong negative effect on *Prosopis* by competing for soil resources, which may cause the demise of *Prosopis* trees (Barnes and Archer 1999). Coexistence of trees and grasses may depend on different mechanisms (House et al. 2003, Sankaran et al. 2004, Wiegand et al. 2006) and their interactions could vary in both space and time (Scholes and Archer 1997).

Modified soil properties after woody invasion influence woody species composition over time. Modification of soil properties beneath woody plant canopies is well documented for a variety of arid and semi-arid ecosystems (Archer 1995, Schlesinger and Pilmanis 1998, Van Auken 2000, McCarron et al. 2003, Liao et al. 2006b, Thompson et al. 2006). Woody invasion has effects on soil texture, moisture, biogeochemistry, and microbial communities (Rossi and Villagra 2003, Liao 2004, Garcia et al. 2005). Studies on effects of woody encroachment on soil C and N pools showed contrasting results. Research in southern Texas and other places in North America indicated that encroachment of *Prosopis* increased near surface soil C and N pools (Archer 1995, Connin et al. 1997, Boutton et al. 1998, Gill and Burke 1999, Hibbard et al. 2001, McCarron et al. 2003, McCulley et al. 2004, Boutton et al. 2007). Other studies have found either decreased SOC pools associated with *Prosopis* invasion in northern Texas (Jackson et al. 2002) or no significant change of surface soil C and N pools with woody encroachment (Tiedemann and Klemmedson 2004, Hughes et al. 2006).

CCA results suggested that SOC and TN contents were not only affected by invaded woody plants, they also have effects on woody species composition (Figure 19, Figure 21). Other studies also suggested that effects of soil C and N on plant distribution and species turnover are noticeable (Burke et al. 1998, Schlesinger and Pilmanis 1998, Van Breemen and Finzi 1998). Interactions between invaded woody plants and soil could be changing and not necessarily to be monotonous (Ehrenfeld et al. 2005, Kardol et al. 2006). Another ordination study of upland clusters of different sizes suggested that species richness, diversity and the basal diameter of the central *Prosopis* are all positively and significantly correlated with a temporal cluster development gradient (Archer et al. 1988). Studies in our study site also indicated that soil C and N pools are positively correlated with stand age of woody patches (Liao et al. 2006b). This suggested a positive correlation of soil C and N contents with successional time. The second axis of the ordinations of tree and shrub species, which were positively correlated with soil C and N content, appeared to represent a temporal gradient of woody invasion (Figure 19, Figure 21). This suggested that succession time played a secondary role in affecting woody species composition.

Ordination of sample sites showed a clear pattern of woody plant communities along the first axis with cluster and groves on one end and playa on the other end (Figure 20, Figure 22). The first axis is related to landscape position related environmental variables, such as soil texture and soil moisture condition. But the separation of samples with similar soil texture and water condition along the second axis indicated that differences of SOC and TN content, which appears to represent a temporal gradient, played a secondary role in determining woody species composition. Ordination and variance partitioning suggested that, for this landscape, topographic gradient is more important than the differences of soil nutrient level in influencing woody species composition and abundance.

Summary

A total of 27 woody species were found in woody plant communities along a topoedaphic gradient in the Rio Grande Plains of southern Texas. Most species were common in all plant communities (cluster, grove, woodland, playa), though their abundance varied between plant communities. Species indicator values suggested no preferential association of common species with specific plant communities.

Ordination and variance partitioning results indicated that woody species composition was more influenced by soil texture and soil moisture level than SOC and TN. Soil texture and soil moisture are determined by landscape location. However, SOC and TN are related to the age of woody plant communities. Feedbacks from increased SOC and TN pools may be an important factor driving successional processes in this changing landscape.

The shift of dominance from herbaceous to woody plants has been reported in many arid and semi-arid ecosystems worldwide. Since 30-40% of the terrestrial surface is occupied by arid and semi-arid ecosystems, improved understanding on how environmental factors affect spatial distribution and succession of woody vegetation may have important implications for regional and global biogeochemistry and land management.

CHAPTER V
SUMMARY

Increased woody abundance in many grass-dominated ecosystems has been reported all over the world (Archer et al. 2001), and this vegetation change has been shown to influence both the magnitude and spatial heterogeneity of soil C and N. There is still no consensus on whether soil organic carbon storage increase, decrease or remain constant after woody invasion. Since grassland covers about 40% of the Earth's land surface, invasion of woody plants could have impacts on global biogeochemistry. However, new tools and approaches are needed to accurately quantify the effects of woody plant encroachment on soil C and N storage at landscape, regional and global scales.

In the Rio Grande Plains of southern Texas, woody plant species have encroached into grasslands over the past century. The present landscape consists of subtropical savanna parklands in the uplands and closed canopy woodlands in the low-lying drainages. Upland vegetation is comprised of discrete woody clusters (small woody patches comprised of a single *Prosopis* tree with understory tree and shrub species) and groves (large woody patches that formed by coalesce of several clusters) embedded in a grassland matrix.

The overall goal of this study was to improve our understanding of the spatial pattern soil organic carbon (SOC) and total nitrogen (TN) and their controlling factors in savanna landscapes and develop efficient sampling strategies for evaluating the effect of woody invasion on the SOC and TN pools at large scales. Specific objectives of this study were to: (1) Quantify the spatial pattern and uncertainty associated with SOC through conditional stochastic simulation and sampling experiments and develop efficient sampling strategies for quantifying SOC pattern in savanna landscapes; (2) Identify soil and vegetation factors and quantify their influences on spatial distribution of SOC and TN through examining their direct and spatial correlation and scaling; and (3) Determine the influence of biophysical variables related to landscape position and soil C and N on woody vegetation structure and possible feedback of woody invasion using canonical correspondence analysis (CCA).

Conditional sequential indicator simulation and simulation experiments were conducted to understand the spatial pattern and uncertainty in SOC distribution in relation to invasion of woody vegetation, and to develop efficient sampling strategies for effective estimation of soil C over large landscapes. Conditional sequential indicator simulation results indicated that woody encroachment into grassland increased both spatial heterogeneity and uncertainty of SOC, which in turn increased errors in estimating SOC storage. Sampling experiments showed that increased spatial uncertainty of SOC in woody patches reduced the effectiveness of complete random sampling in estimation of SOC storage. Stratified random sampling with higher density in woody patches substantially increased estimation accuracy. Other than spatial variability and uncertainty, strong patterns of SOC could also influence estimation accuracy. Incorporation of spatial pattern and uncertainty of SOC into sampling designs would increase the accuracy of the estimation of SOC storage. An efficient sampling strategy for quantify the spatial pattern of SOC in the upland landscape of La Copita was developed, including stratified random sampling in grassland (~50/ha density) and multiple groves (~100/ha density) plus structured samples along center-edge transects in multiple clusters (2-3/cluster). For similar arid and semi-arid landscapes undergoing woody encroachment, sampling strategies recommended include considerations of stratified random sampling with uneven densities based on SOC variability associated with landscape elements, structured sampling in landscape elements with strong spatial patterns in SOC, and preliminary assessment of spatial structures and appropriate sampling density. Quantitative understanding of the spatial structure of SOC and its relationship with vegetation structures and topoedaphic features developed based on these field assessment can be combined with remote sensing to enable effective estimation of SOC over large landscapes and regions to understand the implications and manage woody invasion.

In order to evaluate the relation ship between soil C and N and vegetation and soil attributes and their scaling, a 309 m transect was established along a topographic gradient running from an upland through a low-lying drainage into a playa. The transect passed through all 5 of the major vegetation types (grassland, cluster, grove, drainage woodland and playa). Modified t-test for correlation and cross-Mantel test were used to test the significance of direct and spatial correlations between SOC, TN and other vegetation and soil attributes. Results showed that SOC and TN were strongly correlated with litter and root biomass both quantitatively and spatially. Soil bulk density, shrub and tree basal area were also significantly correlated with SOC and TN, but with a lower correlation coefficient. Soil C: N ratio was significantly higher in playa than that in any other vegetation types, which was likely caused by the higher denitrification rate due to anaerobic conditions in the playa. Results of quadrat variance analyses showed that SOC, TN, litter, root biomass, shrub basal area and tree basal area had similar spatial scale, 40-45 m, which was about the average distance from center of woody patches to the center of their neighboring open grassland. These results suggested that litter and root related ecological processes are the dominant processes that affected both the magnitude and spatial distribution of SOC and TN. Furthermore, invaded woody vegetation has the most impact on the abundance and spatial pattern of litter and root biomass in the upland savanna landscape, hence exerts strong influence on the spatial distribution of SOC and TN in the landscape.

Canonical correspondence analysis (CCA) was conducted using the vegetation and soil data along the 309 m transect to identify factors that influence the spatial distribution of woody species and their assemblages along a topoedaphic gradient. A total of 27 woody species were found along the transect and most of them were common species for all four plant communities (cluster, grove, woodland, playa), though their abundance varied. Species indicator values suggested no preferential association of common species to specific plant communities. Ordination and variance partitioning results indicated that woody species composition was influenced more by soil texture and soil moisture than soil C and N. Soil texture and soil moisture level were determined by landscape location while soil C and N contents were affected by the invasion of woody plants. Landscape position related variables were the primary factor that determined the spatial distribution of woody species. Feedbacks of modified soil C and N pools on woody species composition could also influence successional processes in this changing landscape.

Findings of this study improve our understanding of the effects of woody invasion on the amount, spatial pattern, and uncertainty of soil C and N in savanna landscapes. These results will aid in the development of efficient sampling strategies for quantifying the spatial patterns and storage of soil C and N at larger scales, and will help evaluate the potential impacts of invaded woody vegetation on regional and global biogeochemistry.

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Publications

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