Remote sensing of vegetation characteristics and spatial analysis of pyric herbivory
in a tallgrass prairie

by

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B.S., Wuhan University, 2011
M.S., Kansas State University, 2013

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

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Abstract

Quantitative remote sensing provides an effective way of estimating and mapping vegetation characteristics over an extensive area. The spatially explicit distribution of canopy vegetative properties from remote sensing imagery can be further used for studies of spatial patterns and processes in grassland systems. My research focused on remote sensing of grassland vegetation characteristics and its applications to spatial analysis of grassland dynamics involving interactions between pyric herbivory and vegetation heterogeneity. In remote sensing of vegetation characteristics, (1) I estimated the foliar pigments and nutritional elements at the leaf level using hyperspectral data. The foliar pigments, chlorophylls and carotenoids, were retrieved by inverting the physical radiative transfer model, PROSPECT. The nutritional elements were modeled empirically using partial least squares (PLS) regression. Correlations were found between the leaf pigments and nutritional elements. This provided insight into the use of pigment-related vegetation indices as a proxy of the plant nutritional quality. (2) At the canopy level, I assessed the use of the broadband vegetation indices, normalized difference vegetation index (NDVI) and green-red vegetation index (GRVI), in detecting vegetation quantity (LAI) and quality (leaf and canopy chlorophyll concentrations). The relationships between vegetation indices and vegetation characteristics were examined in the physical model, PROSAIL, and validated by a field dataset collected from a tallgrass prairie. NDVI showed high correlations with LAI and canopy chlorophylls. GRVI performed even better than NDVI in estimating LAI. A new index GNVI (green-red normalized vegetation index) that combined NDVI and GRVI was proposed to extract leaf chlorophyll concentration. These findings showed the potential of using broadband vegetation indices from multispectral remote sensors to monitor vegetation quantity and quality over a wide spatial extent. In the spatial analysis, I examined interactions

between pyric herbivory and grassland heterogeneity at multiple scales from the remote sensing imagery. (3) At a coarse, watershed level, I evaluated effects of fire and large herbivores on the spatial distribution of canopy nitrogen. It was found that the interactive effects of fire and ungulate grazing were present in the watersheds burnt in spring, where a high level of ungulate grazing reduced vegetation density, but promoted canopy heterogeneity. Two grazer species, bison and cattle, were compared. Differences in the vegetation canopy between sites with bison and cattle were observed, which may be related to differences in the grazing intensity, forage behavior and habitat selection between the two grazer species. (4) At a fine, patch level (30 m), bison forage pattern was examined associated with canopy nitrogen heterogeneity. Bison preference for patches with high canopy nitrogen was evident in May. Later in June – September, bison tended to avoid sites with high canopy nitrogen. Vegetation heterogeneity showed significant influences on bison habitat selection in June. Bison preferred sites with low variance in canopy nitrogen, where the patch types were highly aggregated and equitably proportioned.

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Major Professor
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Chapter 1 - Introduction, Remote Sensing of Grassland Canopy Nutrients and Spatial Analysis of Pyric Herbivory

Fire and large herbivores, as well as topography, have great influence on formatting vegetation canopies in North American grasslands (Abrams 1988; Collins and Wallace 1990; Hartnett et al. 1996). The resulting vegetation resources in turn affect habitat selection and forage pattern of large herbivores (Allred et al. 2011a; Allred et al. 2011b; Anderson et al. 2005). Research into interactive processes among fire, large herbivores and vegetation is of special interest in grassland science, which is valuable for understanding grassland functions and formulating management plans.

Information about vegetation characteristics is fundamental to analysis of scale-dependent grassland dynamics. Traditional field sampling followed by laboratory chemical analysis of vegetation characteristics is expensive and time-consuming, which usually results in limited study area and sample size. The increasing use of air- and satellite-borne sensors provides a different means of vegetation survey, through which spectral data of grassland canopies over a large area can be captured effectively. Vegetation characteristics can be quantified by spectral analysis from the remotely sensed imagery.

1.1 Quantitative Remote Sensing of Vegetation

With the rapid development of remote sensing over the past few decades, spectral data from various multi- and hyper-spectral sensors have found a wide application in detecting biophysical and biochemical characteristics of vegetation (Santin-Janin et al. 2009; Wang et al. 2013; Zarco-Tejada et al. 2004). Multispectral data refer to a few discrete broad spectral bands. In contrast, hyperspectral data consist of hundreds of contiguous narrow bands, in which fine spectral features over the spectral profile can be observed and extracted. These fine hyperspectral

features are particularly useful when estimating vegetation nutritional elements, such as nitrogen, phosphorous and potassium (Mutanga et al. 2004; Ozyigit and Bilgen 2013).

Given the different formats of the spectral data, a variety of spectral analysis methods have been developed. These methods can be classified into two major categories: empirical and physical. The empirical method refers to model-building based on *in-situ* observations, whereas the physical method describes relationships between vegetation characteristics and spectral features mathematically based on simulations of the radiative transfer system.

1.1.1 Empirical Estimation of Vegetation Characteristics

Vegetation properties can be linked to spectral features readily through empirical models. For a small number of spectral predictive variables, multivariate regression is a commonly used method that selects the most suitable spectral predictors to fit a model of vegetation characteristics. In hyperspectral remote sensing, spectral data are typically high-dimensional, fine spectral bands which are usually highly correlated with each other (Landgrebe 2002). High correlations among a large number of predictive variables (hyperspectral bands) may lead to problems of multicollinearity and overfitting (Hawkins 2004; Kumar 1975) as conventional multivariate regression is used for vegetation characteristic modeling. Partial least squares (PLS) regression may address problems of multicollinearity and overfitting properly, and is therefore widely used in hyperspectral analysis. Through PLS regression the predictive variables and dependent variables are projected to a new space. The predictive variables are transformed into latent factors in directions associated with the maximum variance in the dependent variables. Thus the first few latent factors can explain most of variance in the dependent variables, and the dependent variables can be modeled by a reduced number of latent factors.

In empirical modeling of vegetation characteristics using spectral features, the predictive variables can be individual spectral bands or vegetation indices that combine two or more spectral bands to highlight specific features in the spectral profile. The simple ratio and normalized difference are commonly used forms of vegetation indices (le Maire et al. 2004), which provide a scale of the original reflectance and reduce much of the background effects. Among a large number of vegetation indices, the normalized difference vegetation index (NDVI) is probably most well-known, and considered the foundation for remote sensing of plant phenology. NDVI is formulated based on the opposite behaviors between the red and near-infrared regions in the reflected spectrum from plant leaves. The red radiative energy is absorbed by leaf chlorophylls and the near-infrared is reflected strongly due to the leaf cell structure. These particular spectral features are highlighted in NDVI, and have been widely used to track plant phenology changes in early studies (Ediriwickrema 2006; Lüdeke et al. 1996; Lee et al. 2002). More recently, NDVI has been found capable of estimating vegetation characteristics such as green biomass, canopy leaf areas and chlorophyll concentration in quantitative analyses (Boelman et al. 2003; Santin-Janin et al. 2009; Steltzer and Welker 2006; Vincini and Frazzi 2011).

Although empirical methods provide rapid estimates of vegetation characteristics using spectral data, they are not direct measurements of plant canopies. Reflected spectral data measured from the plant canopies can be affected by a number of factors, including atmospheric conditions, canopy configuration, leaf structure, soil type, as well as geometry of illumination and the sensor. Therefore, empirical relationships between vegetation characteristics and spectral features are varied across different measurement conditions, plant species and study sites. It is

important to understand factors that may affect plant reflectance before quantitative analyses of vegetation characteristics using reflectance spectral data.

1.1.2 Retrieving Vegetation Characteristics from Physical Models

1.1.2.1 Physical Modeling of Plant Radiative Transfer

As an alternative to empirical methods, vegetation characteristics can also be retrieved through inverting physical models of plant radiative transfer (Goel and Thompson 1984a, b). Physical models describe the interactive processes between radiation and vegetation mathematically. A system of remote sensing of vegetation usually includes five parts: the radiation source, atmosphere, vegetation, ground and the sensor. Physical models calculate radiation intercepted by the sensor (i.e., the reflectance) in terms of vegetation characteristics. In addition to vegetation characteristics, external factors such as radiation source, atmosphere and soil background are taken into account in determining vegetation reflectance. Compared to empirical methods, physical models provide a more systematic description of relationships between vegetation characteristics and vegetation reflectance, which are potentially more robust and universal across different measurement conditions, plant species and study sites.

A variety of vegetation radiative transfer models have been developed which are different in the scale of analysis and conceptual basis. At the leaf scale, physical processes of reflectance, absorption and scattering are simulated for a single leaf, in which the leaf structure is an important parameter in determining radiative transfer. Canopy-scale models incorporate leaf models, however, vegetation reflectance at the canopy level is largely dependent on canopy configurations.

In remote sensing of vegetation, PROSPECT is one of the most widely used leaf-level models due to its ease of use and general robustness. In the PROSPECT model, a compact leaf is

represented as a plate which consists of a stack of homogeneous layers. The leaf radiation regime is calculated from a small number of input parameters that characterize the leaf structure and leaf biochemical contents. The leaf structure parameter specifies the number of homogeneous layers in the leaf plate. The leaf biochemistry parameters include chlorophyll, carotenoids, water, and leaf dry matter contents (Feret et al. 2008; Jacquemoud and Baret 1990). With these input parameters, the PROSPECT model simulates the leaf reflectance and transmittance from 400 to 2500 nm with a spectral resolution of 1 nm.

The PROSPECT model is often coupled with the canopy model SAIL, referred to as PROSAIL (Jacquemoud 1993), to simulate the canopy radiation regime. The SAIL model is a turbid medium model in which the vegetation canopy is assumed to consist of plane parallel distinct layers. In each layer, small vegetation elements are randomly distributed. In the SAIL model, parameters that characterize the canopy configurations include the leaf area index (LAI) and leaf angle distribution (Verhoef 1984). Vegetation elements in the canopy layers can be simulated using the leaf reflectance and transmittance properties determined in the PROSPECT model. In this way, the PROSPECT model is linked to the SAIL model, which describes the canopy radiation absorption and scattering as a function of leaf structure, leaf biochemistry and canopy configurations.

1.1.2.2 Inversion of Physical Models

Physical models calculate vegetation radiative transfer properties from vegetation characteristics, which is referred to as the direct mode. Theoretically, vegetation characteristics can be retrieved by inverting the physical models (Jacquemoud et al. 1995). Commonly used model inversion techniques include the look-up table and artificial neural networks (Combal et al. 2002).

In model inversion, a spectral database is generated from a physical model by varying the input parameters. Each set of parameters corresponds to a specified spectrum. The look-up table is to search a spectrum in the simulated spectral database which has a minimum difference from the measured spectrum. Then the vegetation characteristics can be retrieved from the set of input parameters corresponding to the search result in the spectral database (Feret et al. 2008; Jacquemoud et al. 2009).

Artificial neural networks relate a set of input variables to output variables through one or more hidden layers of neurons with transfer functions. The weights of interconnections between neurons are determined by a training process. When retrieving vegetation characteristics, the neural networks are trained in the spectral database simulated from the physical model. The input variables are spectral features, and the output variables are vegetation characteristics of interest. The trained networks are then applied to the measured radiance for vegetation characterization (Combal et al. 2002; Trombetti et al. 2008).

1.1.3 Applications to Grasslands

Remote sensing has been widely used in estimating vegetation characteristics through spectral analysis at the leaf or canopy level (Curran et al. 1990; Jago et al. 1999). Generally, spectral analysis at the canopy level is more complicated than that at the leaf level. Reflectance received from vegetation canopies is largely affected by the structure and composition of the canopies. Even a relatively uniform canopy like crops can be structurally complex, consisting of living plant leaves, stems, standing dead materials, and other components. These elements with different absorption and scattering properties in the canopy, along with the soil background, produce a mixed reflectance signal received by the sensor. In a heterogeneous canopy, such as grass, the reflective materials are more diverse due to the various plant species and growth

forms, which result in an even more complexly integrated spectral response pattern (Ferwerda et al. 2005; Mutanga et al. 2004).

Among grassland canopies, the tallgrass prairie is especially complex in the canopy structure and species composition. Vegetation in a tallgrass prairie is dominated by tall grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Schizachyrium scoparium*. Forbs compose a small proportion of the total vegetation canopy but account for much of the species diversity. Grasses and forbs respond differently to disturbances by fire and large herbivores. Forb species that initiate in the early growing season can be largely removed by spring fires. This allows grass species to dominate the vegetation canopy. Grasses are more palatable than forbs, and therefore more preferentially grazed by large herbivores, while forbs may contain many secondary chemicals that deter ungulate grazing. Thus, an abundance of forb species can be often observed in the grazed areas at a later stage of the growing season. In a natural tallgrass prairie canopy, grasses and forbs are closely intermingled. There can be more than twenty plant species present in a single square meter, each with different leaf structures and growth forms. This may make it more difficult to retrieve vegetation characteristics from the canopy radiation signal.

Heterogeneous canopies in the tallgrass prairie are a major outcome of fire, ungulate grazing and topography. In the tallgrass prairie ecosystem, fire and grazing by large herbivores play an important role in shaping canopy structures, regulating species compositions and recycling soil nutrients (Collins and Smith 2006; Coppedge and Shaw 1998). Topography influences the soil properties, distribution of plant species, and herbivore habitat selection (Hartnett et al. 1996). Understanding the interactions between fire and ungulate grazing, as well

as topography effects are useful for perceiving the spatial distribution of canopy properties, and therefore revealing the biophysical rationales underlying the canopy spectral signal.

1.2 Spatial Analysis of Pyric Herbivory in Grassland System

1.2.1 Pyric Herbivory

Fire and large herbivores are critical components in North American grassland ecosystems (Collins and Wallace 1990; Hulbert 1986; Knapp et al. 1999). Fire has significant influence on above- and below-ground processes in grasslands. Generally, fire stimulates plant growth by removing the standing dead litter aboveground and increasing the light interception in the canopy (Anderson et al. 2007). Meanwhile, the soil temperature is increased by fire, which enhances the nutrition cycling belowground and potentially improves vegetation productivity (Seastedt and Ramundo 1990). In addition, fire is effective in keeping the prairie grasses from encroachment by woody species (Bragg and Hulbert 1976). Spring fires can suppress the growth of forb species, and allow the tall grasses to dominate the canopy (Collins and Gibson 1990).

Large herbivores, primarily the American Bison (*Bison bison*), are historically agents of disturbance in the tallgrass prairie (Hartnett et al. 1996). Grazing activities by large herbivores can reduce the standing dead materials in the canopy, and enhance plant abundance (Belsky 1986). In addition, ungulate grazing may reduce the palatable grass species, allowing forbs to flourish, which increases the species diversity (Collins et al. 1998). Large herbivores also play an important role in redistributing plant-available nutrients, and therefore promoting the nutrition cycling (de Mazancourt et al. 1998; Frank and Evans 1997).

It is interesting that fire and large herbivores are naturally interacting with each other through the vegetation canopy in the grassland ecosystem. Fire influences the forage site selection by large herbivores. It has been observed repeatedly that large herbivores prefer

grasslands burned by spring fires and avoid unburned, old patches (Allred et al. 2011a; Coppedge and Shaw 1998). Ungulate grazing activities may in turn influence the fire spread, severity and intensity through altering the fuel loading characteristics in the vegetation canopy (Strand and Launchbaugh 2014). The spatiotemporal interaction between fire and ungulate grazing is referred to as pyric herbivory, which results in a shifting mosaic of disturbance across the landscape (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009). Along with topography, pyric herbivory greatly promotes the vegetation heterogeneity in grasslands (Fuhlendorf et al. 2010). Studies on the vegetation heterogeneity associated with pyric herbivory and topography is essential to understand the ecological structure and functions in the grassland ecosystem, which are valuable for grassland conservation and management.

1.2.2 Spatial Analysis Methods

Prior to understanding the interplay between pyric herbivory and vegetation heterogeneity, it is necessary to study the spatial distribution of canopy properties and the movement pattern by large herbivores. The canopy vegetation status over a large spatial extent can be retrieved efficiently using remote sensing methods as discussed above. From the remote sensing imagery of vegetation canopies, the grassland heterogeneity can be measured at different spatial scales. As for the movement pattern by large herbivores, the Global Positioning System (GPS), which has developed rapidly in the past few decades, can record the spatiotemporal locations of herbivores accurately, which provide a new mode of modeling the herbivore movement.

1.2.2.1 Analysis of Grassland Heterogeneity from Remote Sensing Imagery

The image of canopy characteristics derived from the remote sensing data is typically a continuous numerical map. Spatial heterogeneity in the continuous map is featured by the scale

and intensity of spatial autocorrelation in the canopy characteristics (Li and Reynolds 1994), which can be measured using geostatistical techniques, such as variogram analysis (Curran 1988). A variogram calculates the variance of difference between vegetation characteristics at each pair of locations across the canopy. Through variogram analysis, the spatial autocorrelation distance and contrast in the canopy characteristics can be determined, which provide insight into the spatial structure and variability trends across the landscape.

The continuous data in the remote sensing imagery can also be converted into a categorical map by classifying the measured characteristic into discrete categorical levels, in which each level is considered a patch type. In the resulting categorical map, spatial heterogeneity can be measured by a variety of metrics, such as contagion, evenness, and patchiness (Li and Reynolds 1994). These metrics can be calculated either for a single specified patch type or for all the patch types as a whole, describing the composition and configuration of patches from multiple aspects. In terms of grassland heterogeneity, the spatial distribution of patches with high levels of vegetation quality or quantity is of special interest (Wallace et al. 1995). The quality and quantity of vegetation resources can be important factors that influence the forage pattern by large herbivores. Scale-dependent analysis of the linkage between vegetation resource distribution and ungulate grazing pattern is essential to understand grassland functions and address central questions in grassland science.

1.2.2.2 Forage Pattern and Resource Selection by Large Herbivores

Analysis of herbivore movement pattern and space use is a fundamental step prior to investigating resource selection and forage hierarchy in grasslands. A traditional method for modeling the animal movement pattern and space use is to calculate the minimum convex polygon that completely encloses the animal locations (List and Macdonald 2003). This method

is improved by a new model, referred to as the utilization distribution (UD), which calculates the probability density of animal's relative occurrence frequency in a two-dimensional space (van Winkle 1975). The kernel method is an approach to estimating the UD (Worton 1989). Classic kernel methods estimate the UD statically, assuming that all the animal relocations are unlinked. More recently, with the rapid development of GPS, spatial locations of animals can be recorded in time sequences with a high temporal resolution via GPS devices. This activates the interest of developing the movement-based kernel density methods that take into account the time dependence between the successive animal locations and calculate the UD based on the movement trajectory of the animal (Benhamou 2011; Benhamou and Cornélis 2010; Papworth et al. 2012).

The resulting UD estimation can be linked to factors such as fire, topography and vegetation for analysis of resource selection and forage strategy by large herbivores. The resource selection function (RSF) and resource utilization function (RUF) are commonly used methods in evaluating wildlife-habitat relationships (Long et al. 2009). In RSFs, the sampling sites are classified into used and unused sites. This binary variable of use status is related to the habitat factors through logistic regression. In RUFs, the continuous variable of space use summarized by the UD estimation is related to the habitat factors through multivariate regression. Theoretically, RUFs are more advanced than RSFs. However, methods for generating RSFs are more sophisticated than that for RUFs. This makes RSFs potentially more useful and reliable in realistic ecological applications, particularly in the case of large herbivores which tend to have large home ranges (Long et al. 2009).

In summary, the use of remote sensing and GPS provides a new approach for analyzing spatial patterns of vegetation heterogeneity and ungulate grazing in grasslands. Prior to the era of

remote sensing and GPS, the limited study area and sample size imposed by the limitations of traditional manual field measurements were not always able to represent spatial patterns in the entire landscape properly. With the development of remote sensing and GPS, the spatial distributions of animal and vegetation resources can be captured effectively. This new context allows quantitative examinations of wildlife-habitat relationships at multiple spatiotemporal scales.

1.3 Research Objectives

The overall purpose of my research is to assess forage quality in a tallgrass prairie using spectral analysis, and study the spatial patterns of forage quality and pyric herbivory associated with topography effects from the remote sensing imagery of canopy nutrient. More specifically, I have four objectives:

- Objective 1, to estimate foliar pigments and macronutrients at the leaf level across multiple tallgrass prairie species using hyperspectral reflectance data;

- Objective 2, to compare and evaluate two broadband vegetation indices, the normalized difference vegetation index (NDVI) and green-red vegetation index (GRVI), in detecting vegetation quantity and quality in a tallgrass prairie canopy;

- Objective 3, to evaluate effects of fire and large herbivore on the spatial pattern of canopy nitrogen at the watershed level across a tallgrass prairie topography from remote sensing imagery;

- Objective 4, to study interactions between bison forage and canopy nitrogen distribution at a fine, patch level.

My dissertation includes four manuscript chapters, corresponding to the four objectives outlined above. The first manuscript chapter (Chapter 2) is to assess vegetation quality in

tallgrass prairie canopies using hyperspectral analysis at the leaf level. The vegetation characteristics analyzed in this chapter included chlorophylls, carotenoids, magnesium (Mg), phosphorus (P), sulphur (S), potassium (K) and calcium (Ca). These foliar pigments and nutritional elements are important leaf properties that reflect the plant nutritional status. The leaf pigments, chlorophylls and carotenoids, were retrieved by inverting the PROSPECT model. The nutritional elements were estimated empirically using PLS regression. The physical model was not used in estimation of leaf nutritional elements, because the nutrients are not parameters of the PROSPECT model, and cannot be retrieved through physical model inversion. The correlations between leaf pigments and nutritional elements were examined, which provided insight into the use of pigment-related vegetation indices as indicators of the plant nutrition quality.

The second manuscript chapter (Chapter 3) examined the feasibility of using NDVI and GRVI as indicators of vegetation quantity and quality. In this chapter, vegetation quantity and quality were represented by LAI and leaf chlorophyll concentration, respectively. The relationships between the vegetation indices and vegetation characteristics were examined in the PROSAIL model, and then validated by field measurements collected in a tallgrass prairie. This chapter demonstrated the potential of using broadband vegetation indices from multispectral remote sensors to monitor vegetation quantity and quality over a wide spatial extent.

Chapter 2 and Chapter 3 were developed as an extension of my previous research which estimated canopy nitrogen in the tallgrass prairie using empirical methods (Ling et al. 2014). In Chapter 2 and Chapter 3, the physical models, PROSPECT and PROSAIL, were used in spectral analysis, through which the leaf and canopy vegetation characteristics were estimated in a more robust way with a physical basis. As the spectral analysis methods are validated and applied to remote sensing imagery, the spatially explicit distribution of canopy vegetation characteristics

can be retrieved, which is essential for further understanding the vegetation and pyric herbivory interactions in grasslands.

The third manuscript chapter (Chapter 4) reported a study involving remote sensing applications to grassland ecology, which evaluated effects of fire and large herbivores on the canopy nitrogen distribution across a tallgrass prairie topography from the remote sensing imagery. Vegetation canopy in the tallgrass prairie is a mosaic of watersheds with varying fire and ungulate grazing treatments. Comparing the spatial heterogeneity of canopy nitrogen at the watershed level revealed differences in effects of fire and ungulate grazing on formulating the grassland canopies.

The fourth manuscript chapter (Chapter 5) investigated interactions between bison forage and vegetation resource distributions at a finer spatio-temporal scale associated with the bison movement path and space use. Different from the coarse, watershed-level analysis in Chapter 4, an analysis at a finer scale within watersheds requires more finely resolved information on the spatiotemporal distributions of animal and vegetation resources. In Chapter 5, the bison forage pattern was modeled using the movement-based kernel density method from the GPS locations recorded every 30 minutes. Vegetation quality and heterogeneity were calculated from the remote sensing imagery of canopy nitrogen with a pixel size of 2 m. Space use of bison forage was related to canopy vegetation characteristics using methods of RSF and RUF.

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Chapter 2 - Hyperspectral Analysis of Leaf Pigments and Nutritional Elements in Tallgrass Prairie Species

Abstract

Knowledge of forage quality distribution is important for addressing critical research questions in grassland ecological science. There has been a widespread interest in mapping canopy vegetation characteristics from reflectance spectral data collected by remote sensors. In this study, foliar chlorophylls, carotenoids and nutritional elements across multiple tallgrass prairie species were quantified at the leaf level using hyperspectral analysis in the region of 470 – 800 nm, which was expected to be a precursor to further remote sensing of vegetation quality at the canopy level. A spectral standardization method was developed using a form of normalized difference, which proved effective for reducing the interference from the background effects in leaf reflectance measurements. Chlorophylls and carotenoids were retrieved through inverting the physical model PROSPECT 5. The foliar nutritional elements were modeled empirically. Partial least squares (PLS) regression was used to build the linkages between the high dimensional spectral predictive variables and the foliar biochemical constituents. The advantage of PLS was that the spectral features relevant to the leaf biochemistry can be selected and integrated effectively from a wide range of available spectral variables. Results showed that the retrieval of leaf biochemistry through hyperspectral analysis can be accurate and robust across different species. In addition, correlations were found between the leaf pigments and the nutritional elements. This provided insight into the use of pigment-related vegetation indices as a proxy of the plant nutrition quality.

2.1 Introduction

Interactive processes among fire, macro grazers and vegetation canopy are of special interest in grassland science (Allred et al. 2011a; Allred et al. 2011b; Anderson 1990; Anderson 2006; Anderson et al. 2007). It is essential to understand the spatial distribution of canopy characteristics over an extensive area in order to address critical research questions concerning the scale-dependent, hierarchical processes in grassland ecology (Bartlam-Brooks et al. 2013; Collins and Smith 2006; Wallace et al. 1995). With the development of multiple airborne and satellite sensors, there has been a widespread interest in mapping canopy characteristics through remote sensing analysis (Kawamura et al. 2008; Mutanga et al. 2004a; Ozyigit and Bilgen 2013; Trombetti et al. 2008). Compared to traditional field measurements, remote sensing provides a relatively effective method of collecting the spectral data over the vegetation cover. Remote sensing of vegetation properties is in essence spectral analysis, in which the spectral response pattern is linked to some property of the vegetation leaf or canopy.

Spectral analysis at the leaf level provides a preliminary step to further remote sensing of vegetation canopy characteristics. As leaf spectral analysis is validated at the canopy level, canopy characteristics can be mapped efficiently from the remotely sensed imagery, and details of spatial variability in the canopy characteristics can be retrieved reliably. This process provides fundamental information for the spatial analysis of grassland processes over a heterogeneous vegetation canopy.

Leaf spectral analysis is a fast and cost-effective method of detecting leaf pigments and foliar nutritional elements (Blackburn 2007; Carter and Knapp 2001; Mutanga et al. 2004a), especially compared to complicated chemical analysis in the laboratory. The visible and near infrared spectral region (400 – 2500 nm) is of interest in plant hyper-spectroscopy. The principle

underlying hyperspectral analysis in this spectral region is the absorption of energy by a variety of chemical bonds in organic matter, which results in distinctive spectral features. Leaf pigments and nutritional elements can be estimated from the spectral features due to their direct or indirect associations with the organic matter (Clark et al. 2003; Galvez-Sola et al. 2015; Goetz et al. 1985).

Hyperspectral data consist of hundreds of spectral bands which are usually highly correlated with each other (Landgrebe 2002). Vegetation biophysical/biochemical properties can be retrieved from these spectral reflectance values using a number of methods, including statistical ones. Multivariate regression is a widely used statistical method. However, when the conventional multivariate regression is used, the high correlations among a large number of predictive variables (spectral bands) may lead to problems of multicollinearity (Kumar 1975) and overfitting (Hawkins 2004), which impact the model prediction capability. Partial least squares (PLS) regression is a statistical method for modeling vegetation characteristics from the high-dimensional spectral features (Li et al. 2014; Ryan and Ali 2016; Yu et al. 2015) that is resistant to multicollinearity and overfitting. This technique is widely used in hyperspectral analysis. PLS may address the problems of multicollinearity and overfitting properly. The basic idea of PLS is to extract the latent factors from the manifest explanatory variables in the directions associated with the high variance of the dependent variables (Malthouse et al. 1997; Rosipal and Trejo 2002). In this way, the dependent variables can be modeled by a reduced number of PLS factors.

As an alternative to statistical methods, vegetation biophysical/biochemical characteristics can also be retrieved through inverting a physical radiative transfer model (Goel and Grier 1988; Goel and Thompson 1984a, b). Physical models simulate the interactive processes between the radiative energy and plant leaves in terms of the vegetation characteristics.

Physical models are typically of two types; leaf-level models, which simulate the reflectance, absorption and scattering within and from a single leaf, and canopy models, which simulate bulk reflectance from an entire vegetated canopy. At the leaf level, PROSPECT is one of the most widely used physical models. In the PROSPECT model, the leaf reflectance and transmittance are modeled using a small number of input parameters, including leaf mesophyll structure and leaf biochemical contents (Jacquemoud and Baret 1990). The leaf biochemical contents include chlorophyll, water, and dry matter contents. More recently, carotenoids have been separated from chlorophylls in the latest version PROSPECT 5, which allows more accurate estimations of plant photosynthetic pigments (Feret et al. 2008). Because process models are not as reliant on empirical information from the data, they have the potential to be a more robust method across different times, sites and plant species.

Physical models calculate the reflectance and transmittance from the vegetation characteristics in a direct mode. That is, the output from the model is a simulated spectral reflectance curve. When the goal is to use a measured reflectance curve to estimate leaf characteristics, the physical model must be inverted. Look-up tables and neural networks are two commonly used inversion methods (Combal et al. 2002). In the look-up table method, a database of spectra is generated by varying a range of input parameters sufficient to capture all possible valid solutions to the model. This database or look-up table is then searched for a specific set of vegetation parameters corresponding to a simulated spectrum that is closest to the radiance measurement (Feret et al. 2008; Jacquemoud et al. 2009). A possible problem when using a look-up table is that the measured spectra in practice may be shifted or stretched unexpectedly given the strong background effects. This increases the uncertainty of comparing the measured spectrum in direct with the simulations.

Neural networks are another numerical technique for model inversion. Neural networks relate a set of input variables to the output through one or more hidden layers of neurons with transfer functions. The weights of the interconnections between neurons are determined by an empirical training process. Vegetation indices that integrate two or more reflectance values and highlight specific spectral features are usually used as the input variables. The simple ratio and the normalized difference are commonly used forms of vegetation indices (le Maire et al. 2004), which provide a scale of the original reflectance and reduce much of the background effects. However, the number of input variables for networks is usually limited, and the architecture of networks needs to be defined before the training process. Unlike regression techniques, there is no mechanism to select the most suitable vegetation indices and network structure for building an optimal model in the network training algorithm. In addition, the resulting network weights are nondeterministic. Networks for the same inputs are usually trained with replicates, from which the average of the outputs is used as the final estimation result. This may impact the efficiency of the neural network modeling process.

The objective of this study was to estimate foliar pigments and macronutrients at the leaf level across multiple grassland plant species using reflectance spectral data. The foliar biochemical constituents analyzed included chlorophylls, carotenoids, magnesium (Mg), phosphorus (P), sulphur (S), potassium (K) and calcium (Ca). These foliar pigments and nutritional elements are important leaf properties that reflect the plant nutritional status. This study was part of a larger research project aimed at understanding the interplay between pyric herbivory and grassland forage quality in a tallgrass prairie. To address this objective, leaf biochemical properties were retrieved using either model inversion or empirical methods, depending on the specific property. Chlorophyll and carotenoid concentrations were retrieved by

inverting the PROSPECT 5 model. The macronutrients were estimated empirically using PLS regression, because foliar nutrients are not parameters of the PROSPECT 5 model, and cannot be retrieved through model inversion. In retrieval of the leaf biochemical contents, the spectral analysis focused on the visible and near infrared region ranging from 470 to 800 nm. This spectral region is of special interest in remote sensing of vegetation given the significant absorption feature in the red spectral domain.

2.2 Study Site

This study was conducted at Konza Prairie Biological Station (KPBS, Figure 2.1), a tallgrass prairie site near Manhattan, Kansas, USA (39°05′N, 96°35′W). The vegetation at the site consists of more than 80% of grasses and a minor proportion of forbs. Dominant grass species include *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Schizachyrium scoparium*; forbs include *Aster ericoides*, *Psoralea tenuiflora*, *Solidago missouriensis*, *Soldiago rigida*, *Liaris aspera*, *Vernonia baldwinii* and *Ambrosia psilostachya* (Collins and Calabrese 2012).

The site is divided into more than fifty watersheds, in which varying combinations of fire and ungulate grazing treatments are replicated at the watershed level for long term investigations into the interactive processes among fire, large grazers and vegetation communities. In addition, a variety of experiment plots are operated with different fire or nutrition treatments for multiple research purposes. The foliar samples were collected from several of these experimental plots, which are described below.

The Hulbert plots are managed to demonstrate the effects of fire on plant growth and species diversity. They consist of a number of subplots, each measuring 10 m × 25 m with a 5 m buffer, and are subjected to fire disturbances at intervals of one, two, four or twenty years. The

Belowground plots are another set of experimental plots, initially set up to investigate how varying combinations of fire, mowing, and fertilization affect both the above and below ground accumulation of biomass. The subplot of Belowground plots measures 12.5 m ×12.5 m. In addition, a fertilization plot was developed at a bison grazed site, watershed N4B, in 2014. The plot was arrayed in four lines, two controlled (without applications of nitrogen fertilization) and two fertilized that were alternately parallel arranged. Each line included five 2 m × 2 m subplots with a one meter buffer. In each fertilized line, 0, 12, 24, 48, and 96 grams of ammonium nitrate (NH_3NO_3) were applied to each of the five subplots, respectively, at the beginning of the growing season.
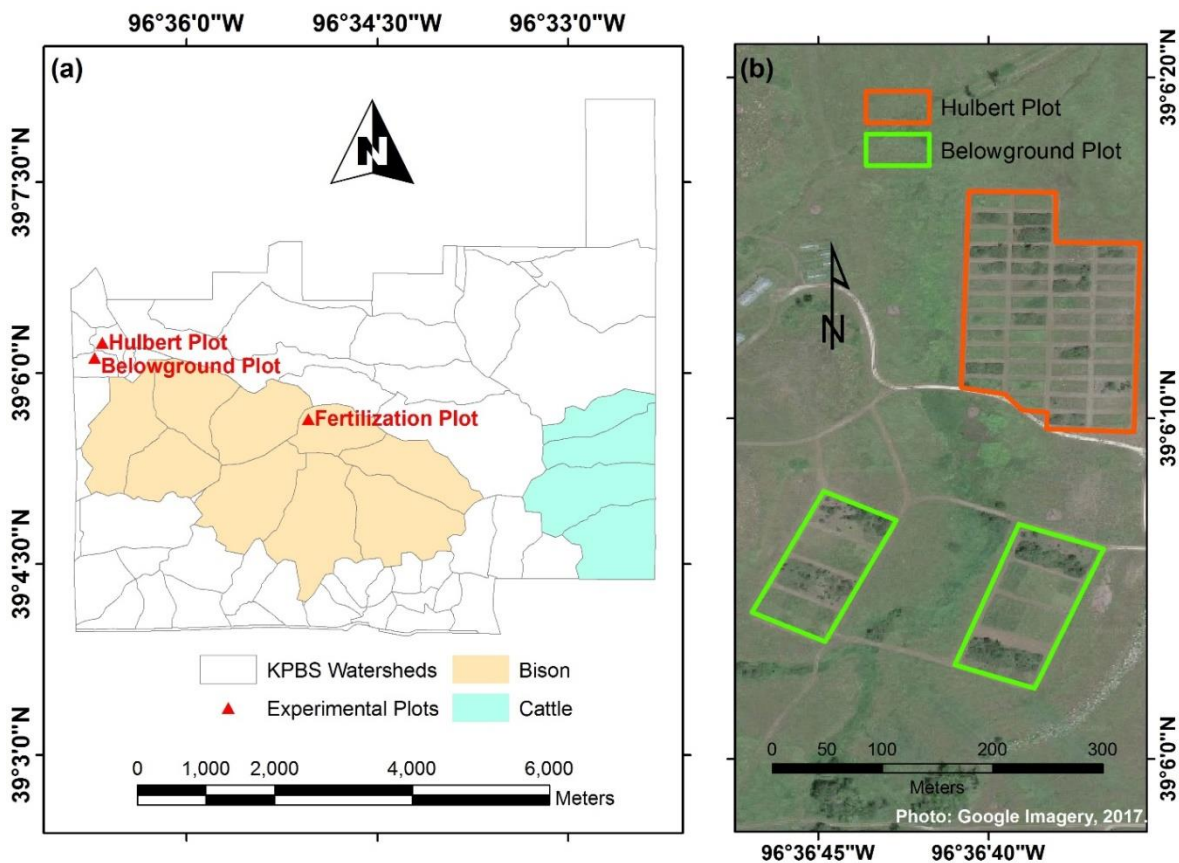
Figure 2.1 Study site at Konza Prairie Biological Station (KPBS). KPBS includes (a) more than fifty watersheds and (b) a variety of experimental plots, such as the Hulbert plot and Belowground plot.

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The treatments of fire and mowing have an immediate effect on the canopy structure. The fertilization additions affect the soil nutrient availability. All these treatments can influence the species composition in the canopy. The selection of these study plots allowed a wide range of foliar biochemical contents to be sampled.

2.3 Methods

2.3.1 Data Collection

The data collection was conducted multiple times across seasons during the years of 2014 – 2016 (Table 2.1). The leaf samples covered different treatments of fire, mowing and fertilization addition to make sure the foliar biochemical contents were in a wide range for spectral modeling. In 2014 – 2015, the grasses and forbs were collected separately from the fertilization plot and the Hulbert plots; in 2016, mixed grassland species were collected from the Belowground plots. The datasets embodied variations from time, site, plant species and measurement conditions, making it possible to evaluate the general robustness of the methodology in data analysis.

For each sample, around five grams of fresh leaves were randomly clipped from the canopy with a pair of scissors, and then divided into subsamples for measurements of reflectance, leaf pigments and nutritional elements. Hyperspectral reflectance data were measured using a leaf clip probe on an Analytical Spectral Devices (ASD) FieldSpec Pro portable spectrometer (Analytical Spectral Devices, Boulder, CO, USA). To determine chlorophyll and carotenoid concentrations (Wellburn 1994), the plant issues were dissolved in 80% acetone or in Dimethyl-Sulfoxide (DMSO), and then measured by a Spectronic 20 Genesys spectrometer (Spectronic Instruments Inc., Rochester, NY, USA). The subsamples for analysis of macronutrients were dried in an oven for 72 hours at 75°C, and then ground using a mortar and pestle. The resulting

dry foliar powders were analyzed for element concentrations using a Bruker Tracer III-SD X-ray

fluorescence spectrometer (Bruker, Kennewick, WA, USA). Each sample of the dry foliar

powders was measured three times, of which the average was used to reduce measurement errors.

The X-ray fluorescence method for quantification of leaf nutritional elements is relatively new in

plant analysis (Stephens and Calder 2004; Towett et al. 2016). In my study, the leaf nutritional

elements analyzed included Mg, P, S, K and Ca. These elements are important plant nutrients.

Their calibrations using the X-ray fluorescence measurement have been developed and proven

reliable in previous studies (Towett et al. 2016).

Table 2.1 Leaf sample datasets

Site	Fertilization Plot	Hulbert Plot	Belowground Plot
Date	July - September, 2014	June - September, 2015	July - September, 2016
Species (Sample size)	Forbs (20) Grasses (20)	Forbs (32) Grasses (32)	Mixed species (68)
Measurement			
Reflectance	ASD FieldSpec	ASD FieldSpec	ASD FieldSpec
Pigments			
Solvent	Acetone 80%	DMSO	-
Instrument	Spectronic 20 Genesys	Spectronic 20 Genesys	-
Nutritional elements	-	X-Ray Fluorescence	X-Ray Fluorescence

- : Not available

2.3.2 Spectral Standardization and Vegetation Spectral Features

The spectral analysis focused on the wavelengths of 470 – 800 nm. This spectral region

includes a significant absorption feature in the red spectral domain, which is associated with

photosynthetic pigments. A spectral standardization method was developed to reduce the

background effects in the leaf reflectance measurements. The background effects in

measurements of the grassland species can be significant, given that the narrow leaves may not cover the whole leaf clip probe face of the ASD spectrometer (Figure 2.2a). This irregular measurement may lead to a shift and stretch in the resulting spectrum (Figure 2.2b).
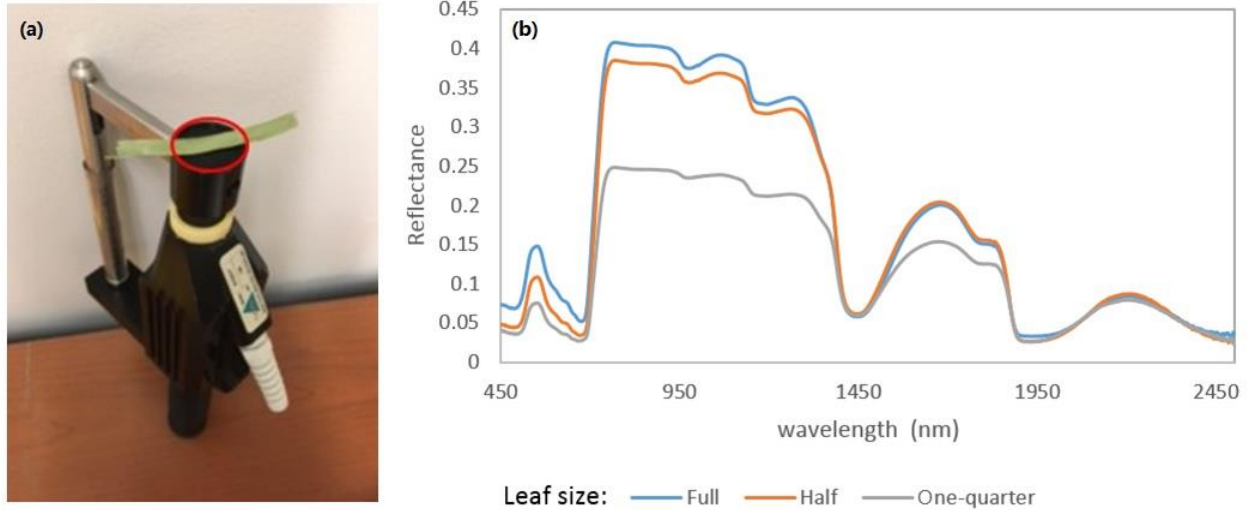
Figure 2.2 (a) ASD's leaf clip probe. Note that a narrow grassland leaf cannot cover the whole probe face. (b) The effects of leaf size on the measured reflectance spectra. The spectral signals can be shifted and stretched due to the background effects as the leaf cannot cover the whole probe face.

In spectral standardization, four feature points were located on the original reflectance spectrum, including the local minima in the blue and red regions, the local maximum in the green region and the turning point in the near infrared region (Figure 2.3). Based on these points, the original spectrum was scaled using a form of the normalized difference:

$$NDR_i = \begin{cases} \frac{R_i - R_b}{R_g - R_b}, & 470 \le i < g \\ \frac{R_i - R_r}{R_g - R_r}, & g \le i < r \\ \frac{R_i - R_r}{R_{nir} - R_r}, & r \le i < 800 \end{cases} \tag{2.1}$$

where NDR_i is the scaled reflectance with a normalized form at the wavelength i; b is the wavelength of the minimal reflectance in the region of $470 - 520$ nm; g is the wavelength of the maximum reflectance in the region of $520 - 600$ nm; r is the wavelength of the minimum

reflectance in the region of 600 – 720 nm; *nir* is the wavelength of the turning points in the

region of 740 – 800 nm at which the first derivative is equal to 0; R_i is the reflectance value at

the wavelength *i* nm.
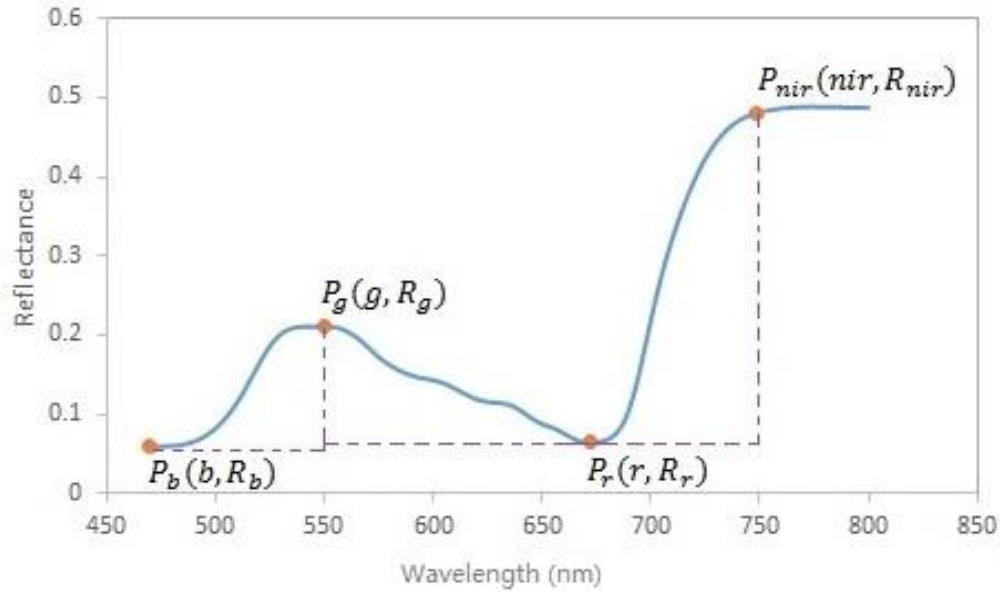
Figure 2.3 Feature points in spectral standardization. P_b **is the minimum point in the region of 470 – 520 nm;** P_g **is the maximum point in the region of 520 – 600 nm;** P_r **is the minimum point in the region of 600 – 720 nm;** P_{nir} **is the turning point in the region of 740 – 800 nm, where the first derivative is equal to 0.**

In this way, the original reflectance values in the visible and near infrared region were

transformed into a collection of normalized difference indices. A comparison between the

original reflectance and the scaled reflectance showed that the spectral response pattern to the

variation in the chlorophyll concentration was more evident in the scaled reflectance than that in

the original spectra (Figure 2.4). This suggested that the spectral standardization method was

feasible and efficient.

In addition to the normalized difference indices scaled from the original continuous

spectral curve, spectral features that characterize the shape of the spectral curve, such as the

slope (Lugassi et al. 2015), the red edge (Curran et al. 1990; Filella and Penuelas 1994; Munden

et al. 1994; Mutanga and Skidmore 2007; Schut and Ketelaars 2003), and the triangle

surrounding the red absorption trough (Hunt et al. 2013), are considered important indicators of

foliar biochemical contents. In this study, the absolute values of the slopes across the

wavelengths of $b - g$, $g - r$, $r - nir$, and distances across $b - r$, $g - nir$ on the scaled reflectance

spectral curve (Figure 2.5) were included in spectral analysis:

$$S_1 = \frac{1}{g - b} \tag{2.2}$$

$$S_2 = \frac{1}{r - g} \tag{2.3}$$

$$S_3 = \frac{1}{nir - r} \tag{2.4}$$

$$D_1 = r - b \tag{2.5}$$

$$D_2 = nir - g \tag{2.6}$$

where S_1, S_2, and S_3 are the spectral slopes; D_1 and D_2 are the spectral distance variables. On the

scaled reflectance spectral curve, the values at the wavelengths of g and nir are 1; the values at

the wavelengths of b and r are 0.
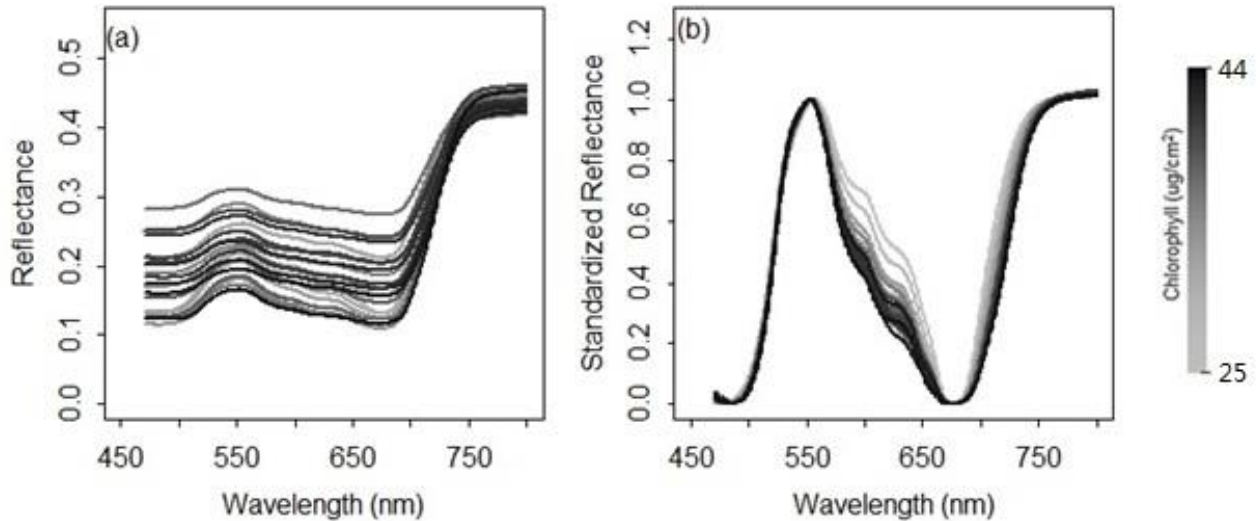
Figure 2.4 Comparison between (a) the original spectral measurements and (b) the standardized reflectance spectra for the grasses collected in 2015.
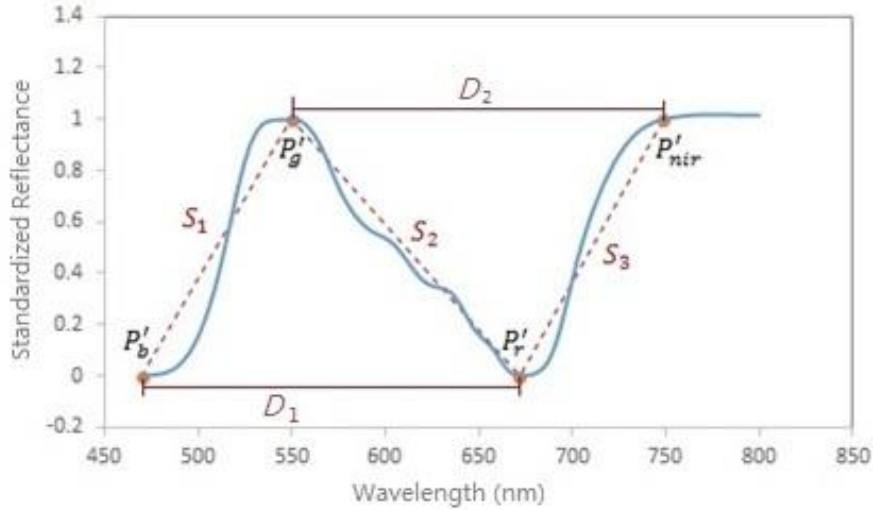
Figure 2.5 Spectral slopes and distances as variables potentially related to foliar biochemical contents. P_b', P_g', P_r' and P_{nir}' are the points on the scaled reflectance curve corresponding to the points P_b, P_g, P_r and P_{nir} on the original reflectance curve (Figure 2.4).

2.3.3 Retrieval of Leaf Pigments Using Process Modeling

Chlorophyll and carotenoid concentrations were retrieved by inverting the leaf radiative model PROSPECT 5 (Figure 2.6). A reflectance spectral database was simulated by varying the input parameters (Table 2.2), including chlorophylls (Cab), carotenoids (Ccx), water thickness (Cw), dry matter (Cm) and the leaf structure parameter (N). The output reflectance values at the wavelengths of $470 - 800$ nm were standardized using the form of normalized difference, from which the spectral slope and distance features were extracted (see Section 2.3.2). The resulting spectral variables, including $NDR_{470} - NDR_{800}$, $S_1 - S_3$, D_1 and D_2 (Eq. (2.1) – (2.6)) were related to chlorophyll and carotenoid concentrations in the original model parameterization through PLS regression. The resulting PLS models were then applied to the standardized spectral variables of the field measurements. The predicted chlorophyll and carotenoid concentrations from the PLS models were then compared with the laboratory chemical measurements for an assessment of the model performance. The model prediction accuracy was assessed by the root mean square error of prediction (RMSEP), the coefficient of variability (CV) and the index of agreement (d).

RMSEP incorporates the bias (BIAS) and the standard error corrected from the bias (SEPC); CV is a measure of variation in relation to the mean, which indicates the magnitude of the error (Feret et al. 2008); d is a standardized measure of the degree of model prediction errors (Willmott 1981):

$$RMSEP = \sqrt{\frac{\sum_{i=1}^{n}(y_i' - y_i)^2}{n}} \tag{2.7}$$

$$BIAS = \frac{\sum_{i=1}^{n}(y_i' - y_i)}{n} \tag{2.8}$$

$$SEPC = \sqrt{\frac{\sum_{i=1}^{n}(y_i' - y_i - BIAS)^2}{n}} \tag{2.9}$$

$$RMSEP^2 = SEPC^2 + BIAS^2 \tag{2.10}$$

$$CV = 100 \times \frac{SEPC}{\overline{y_i}} \tag{2.11}$$

$$d = 1 - \frac{\sum_{i=1}^{n}(y_i' - y_i)^2}{\sum_{i=1}^{n}\left(|y_i' - \overline{y_i}| + |y_i - \overline{y_i}|\right)^2} \tag{2.12}$$

where y_i is the measured value; y_i' is the predicted value; $\overline{y_i}$ is the mean of the measured values; n is the sample size. d varies between 0 and 1; a value of 0 indicates no agreement, and 1 indicates a perfect match.

PLS regression can be considered a supervised dimension reduction technique. It looks for a few of latent factors from a large number of manifest predictive variables to summarize the data with a consideration of correlations between the predictive variables and the dependent variables. PLS loadings reflect the importance of each predictive variable to the given PLS factor. As the number of the PLS factors increases in a prediction model, the model explanatory power increases. However, the model prediction accuracy may decreases as the model complexity increases, leading to the overfitting problem.
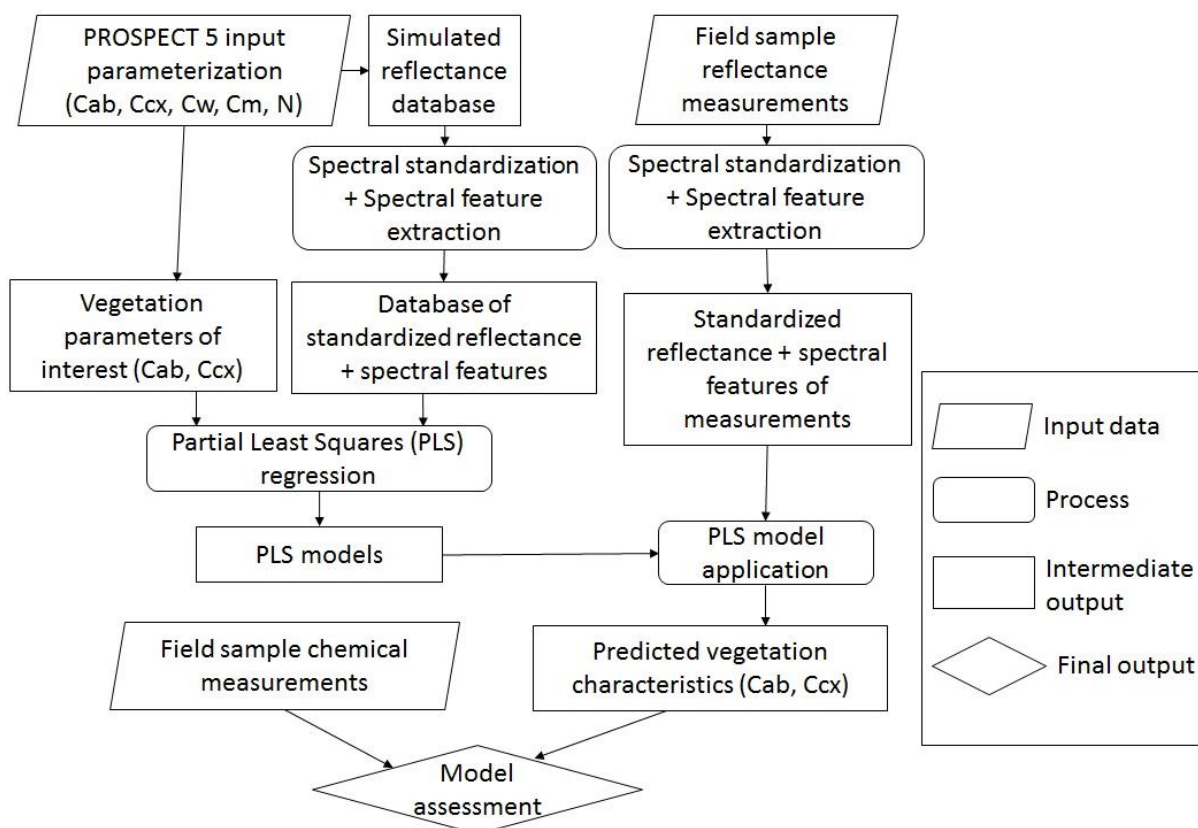
Figure 2.6 Overview of leaf pigment retrieval by inverting PROSPECT 5. The input parameters in PROSPECT 5 include chlorophylls (Cab), carotenoids (Ccx), water thickness (Cw), dry matter (Cm), and the leaf structure parameter (N). Concentrations of chlorophylls and carotenoids are of interest to be modeled.

Table 2.2 Input parameters and output in PROSPECT 5

Parameter	Range	Increment
Input		
Chlorophyll (Cab)	6 - 60 ug/cm^2	2 ug/cm^2
Carotenoids (Ccx)	2 - 16 ug/cm^2	2 ug/cm^2
Water thickness (Cw)	0.008 - 0.02 g/cm^2	0.004 g/cm^2
Dry matter (Cm)	0.005 - 0.02 g/cm^2	0.005 g/cm^2
Leaf structure parameter (N)	1.5 - 3	0.5
Output		
Reflectance	470 – 800 nm	1 nm

2.3.4 Leaf Nutrient Estimations

The foliar nutritional elements were modeled statistically from the standardized reflectance measurements using PLS regression. This procedure was not based on the PROSPECT model given that the foliar nutritional elements have not been calibrated as parameters in the radiative transfer process which the physical model describes. Around half of the samples were used for model development. The rest samples were used for model assessment. Both the modeling and assessment datasets were required to cover almost the full range of the sampled nutritional elements.

2.4 Results and Discussion

2.4.1 Leaf Pigment Retrieval

2.4.1.1 Laboratory Chemical Analysis

Descriptive statistics for the leaf pigment measurements (Table 2.3) showed that the chlorophylls ranged from 6.62 to 44.37 ug/cm^2, and the carotenoids ranged from 2.97 to 10.28 ug/cm^2 across all the samples. These values were in a reasonable range, compared to those reported by Combal et al. (2002) ,le Maire et al. (2004) and Feret et al. (2008). Datasets collected from different plots and species were slightly different in their statistical characteristics. The model robustness was allowed to be examined across different leaves with a wide range of leaf pigments.

Table 2.3 Descriptive statistics of the measured chlorophyll and carotenoid concentrations by laboratory chemical analysis.

	Fertilization Plot		Hulbert Plot	
	Forbs	**Grasses**	**Forbs**	**Grasses**
Sample size	20	20	32	32
Chlorophylls (ug/cm^2)				
Min	28.37	27.04	6.62	24.92
Max	39.59	38.24	43.37	44.37
Mean	31.89	32.06	33.03	35.55
Carotenoids (ug/cm^2)				
Min	8.20	8.602	2.97	7.91
Max	10.28	10.12	8.97	10.12
Mean	9.08	9.149	7.65	8.90

2.4.1.2 Adjustment of the Leaf Structure Parameter

In addition to chlorophyll and carotenoid concentrations, the leaf structure parameter has a significant effect on the spectral shape in the visible and near infrared region (le Maire et al. 2004). A systematic change in the spectral response pattern due to variations in the leaf structure parameter can be seen both in the original reflectance spectra simulated from PROSEPCT 5 and their corresponding scaled reflectance spectra (Figure 2.7). In the original parameterization, the leaf structure parameter N ranged from 1.5 to 3. The resulting predictions of chlorophylls and carotenoids were generally overestimated with the biases of 6.56 ug/cm^2 and 2.94 ug/cm^2, respectively (Figure 2.8a$_1$ and b$_1$). As N was adjusted within 1.7 – 1.9, the model biases were reduced, and the model prediction accuracy and the agreement statistics improved significantly (Figure 2.8a$_2$ and b$_2$). This indicated that a proper selection of the N range was important for accurate retrieval of leaf biochemical contents using the PROSPECT model.
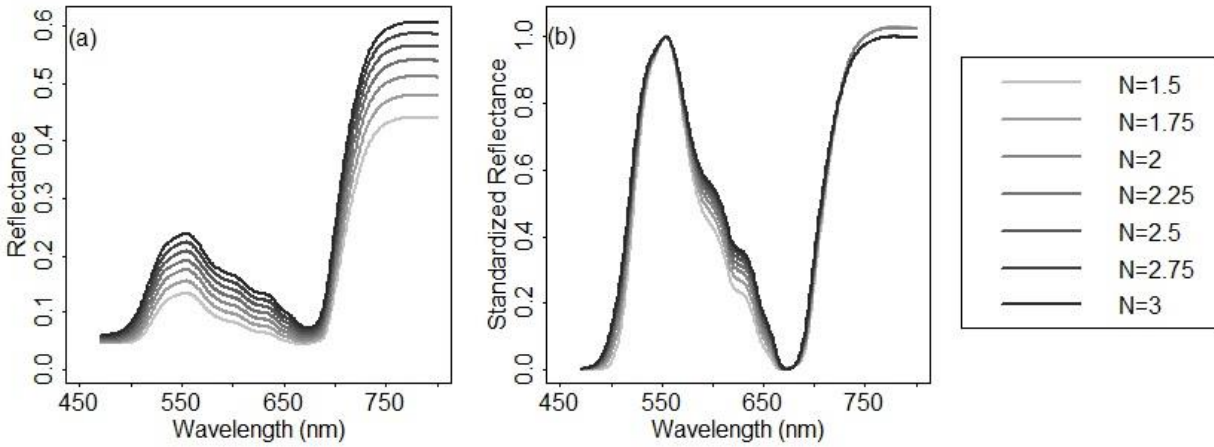
Figure 2.7 Spectral patterns varying with the leaf structure parameter N in (a) the reflectance spectra simulated from PROSPECT 5 and (b) their corresponding standardized reflectance spectra. In the reflectance spectral simulation, Cab=33 ug/cm^2, Ccx=9 ug/cm^2, Cw=0.014 g/cm^2, Cm=0.012 g/cm^2, and N varies between 1.5 and 3 with a step of 0.25.

2.4.1.3 Spectral Feature Selection by PLS Regression

For the leaf pigment retrieval models in this study, the first three factors were adequate to account for much of the variance in the data and led to relatively high prediction accuracy. The available predictors included the spectral variables $NDR_{470} - NDR_{800}$, $S_1 - S_3$, D_1 and D_2. $NDR_{470} - NDR_{800}$ were the continuous standardized reflectance data. $S_1 - S_3$, D_1 and D_2 were the slope and distance variables extracted from the standardized reflectance spectrum. These variables were different in characteristic, form and magnitude. Their importance to the corresponding PLS model was of interest. Therefore, the models developed from all the available predictors (Figure 2.8a$_2$ and b$_2$) were compared with those including only the continuous standardized reflectance variables (Figure 2.8a$_3$ and b$_3$). The PLS loadings were examined to see the contribution of each predictive variable to the PLS factors (Figure 2.9).

Results showed that the models including all the available predictors had higher prediction accuracy and agreement statistics than those including only the continuous standardized reflectance variables. With the slope and distance predictive variables included, high loadings occurred at the distance variables in the first two PLS factors, which accounted for more than 99% variance in the data (Figure 2.9a$_2$ and b$_2$). This suggested a significant influence from the distance spectral variables (D_1 and D_2) on predicting the leaf pigments. The distance variables were comparable with the leaf pigment spectral features, such as the red edge (Curran et al. 1990; Filella and Penuelas 1994; Munden et al. 1994; Mutanga and Skidmore 2007; Schut and Ketelaars 2003), and the red absorption triangle (Hunt et al. 2013), which were based on the positions of specific spectral points. The magnitude of the distance variables was far higher than that of the standardized reflectance variables. This can be a factor that influences the loading distribution pattern. However, it did not affect that the addition of the distance variables in this way as the predictors improved the prediction accuracy and model robustness.

The PLS loading distributions among the first 331 standardized reflectance variables were interesting. The loadings of the first PLS factors in Figure 2.9a$_1$ and b$_1$ were similar to that of the third PLS factors in Figure 2.9a$_2$ and b$_2$, respectively. This implied that the feature selection and integration among the standardized reflectance variables via such a loading pattern can be an important indicator of leaf chlorophylls and carotenoids.
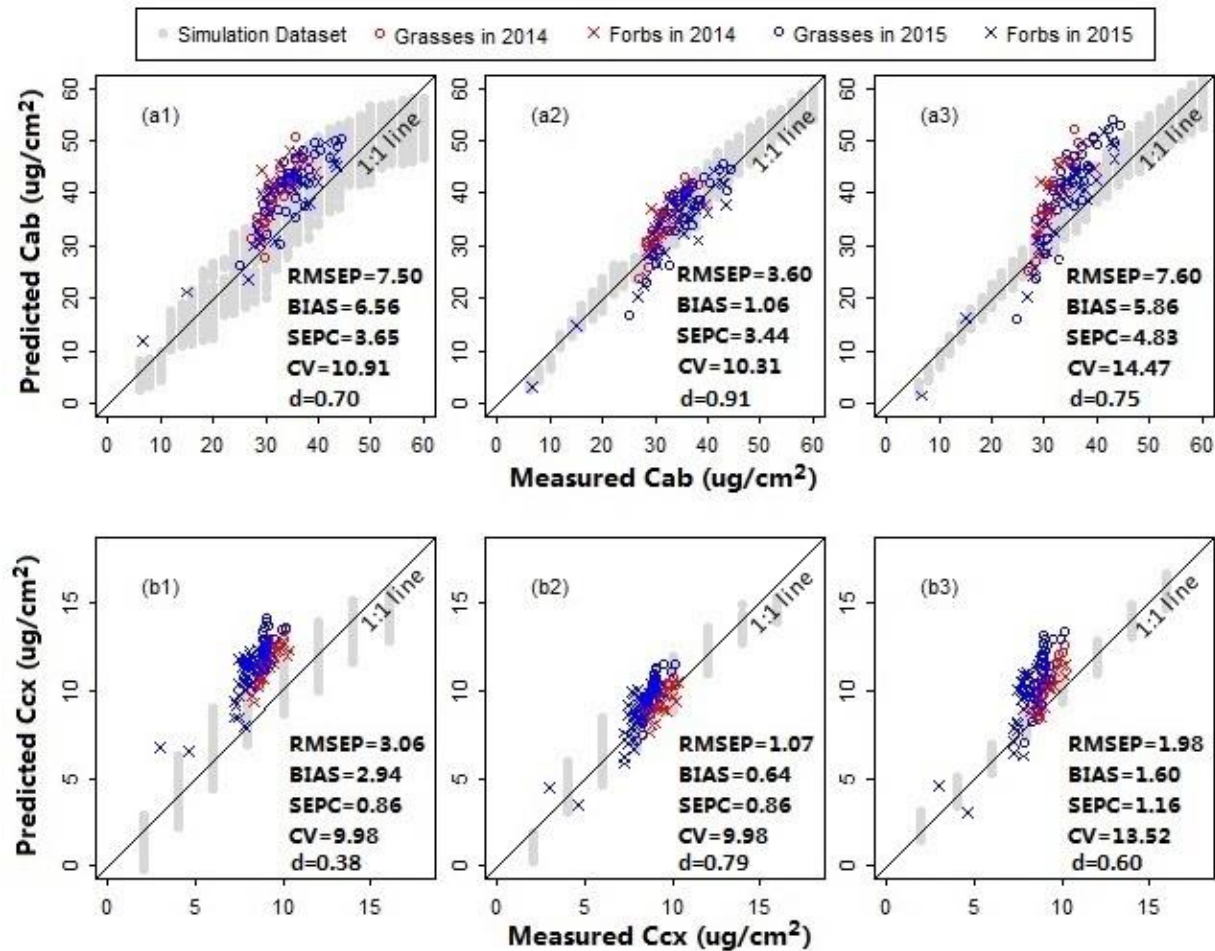
Figure 2.8 Model assessment for (a₁ – a₃) chlorophylls and (b₁ – b₃) carotenoids. Prediction accuracies of the models with different leaf structure parameter ranges and spectral variables were compared. For the models in plots a₁ and b₁, the leaf structure parameter N ranged from 1.5 to 3; the spectral variables $NDR_{470} - NDR_{800}$, $S_1 - S_3$, D_1 and D_2 were included as the manifest explanatory variables for the PLS regressions. In plots a₂ and b₂, N was adjusted within a range between 1.7 and 1.9; the spectral variables were the same with that in plots a₁ and b₁. In plots a₃ and b₃, N ranged from 1.7 to 1.9; the manifest explanatory variables included $NDR_{470} - NDR_{800}$, whereas the slope and distance spectral variables were excluded. The RMSEP, BIAS, SEPC, CV and *d* were calculated for the pooled samples collected from the fertilization plot in 2014 and the Hulbert plots in 2015. All the models were built using the first three PLS factors.
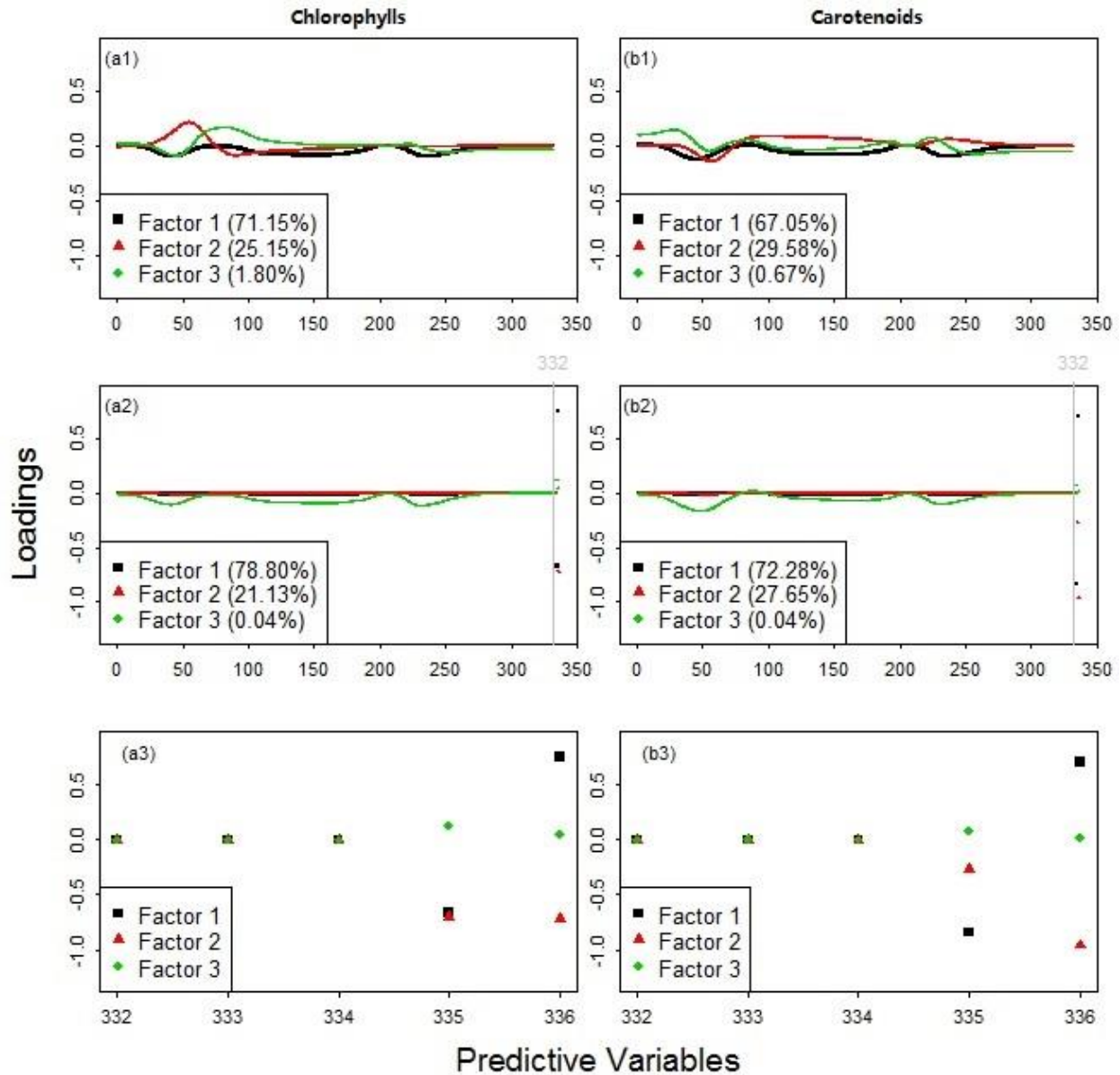
Figure 2.9 Predictive variable loadings for the PLS factors used to estimate ($a_1 - a_3$) chlorophylls and ($b_1 - b_3$) carotenoids. The models in plots a_1 and b_1 included 331 standardized reflectance variables, $NDR_{470} - NDR_{800}$, as the predictors. The models in plots a_2 and b_2 included all the available predictors, $NDR_{470} - NDR_{800}$, $S_1 - S_3$, D_1 and D_2. Plots a_3 and b_3 zoomed in on the loading distributions among the predictors $332 - 336$ (the slope and distance spectral variables, $S_1 - S_3$, D_1 and D_2).

2.4.2 Nutritional Element Estimation

2.4.2.1 X-ray Fluorescence Analysis

The foliar nutritional element concentrations were measured by an X-ray fluorescence spectroscopy. The studied elements included Mg, P, S, K, and Ca. These macronutrients are important for the constitution of the plant biomass. The samples were divided almost equally for modeling and validation. The descriptive statistics (Table 2.4) showed that the range and mean of the modeling dataset were consistent with that of the corresponding validation dataset. This suggested a proper selection of the empirical modeling and validation datasets.

Table 2.4 Descriptive statistics of the foliar nutritional element concentrations for the modeling and validation datasets. The number of the samples used in modeling and validation was slightly less than the foliar sample size in the field data collection due to the loss in the laboratory measurements and the outliers in the spectral modeling process.

Element	Modeling				Validation			
	Sample size	Min	Max	Mean	Sample size	Min	Max	Mean
Mg	62	0.119	0.257	0.173	56	0.122	0.262	0.177
P	65	0.033	0.172	0.091	61	0.047	0.169	0.094
S	64	0.040	0.154	0.087	56	0.045	0.144	0.087
K	65	0.363	2.256	1.102	56	0.377	2.324	1.115
Ca	60	0.255	1.966	0.790	56	0.281	1.847	0.788

2.4.2.2 Spectral Modeling by PLS Regression

The predictors for the PLS modeling of the plant nutrients included $NDR_{470} - NDR_{800}$, $S_1 - S_3$, D_1 and D_2. Comparisons between the measured and predicted nutrient concentrations in the best-performing models were shown in Figure 2.10. There were no evident patterns observed among the multiple plant species, which indicated that the models were robust across different species.

The model performance assessment was summarized in Table 2.5. In general, the RMSEP values for model-development were similar with that for model-validation; the bias values in the validation procedure were at the low levels. This consistency between the modeling and validation procedures verified the model prediction capability. The CV value was relatively low for the model of the element Mg, but high for the model of Ca, indicating the magnitude of the prediction error was low for Mg, but high for Ca. The d values were in a generally high level, indicating a good agreement between the predicted values and the measured values.

The nutritional element models generally required six to nine PLS factors to achieve the acceptably low prediction error when there was no evident modeling bias observed. Compared to the three PLS factors in the leaf pigment retrieval models, the increased number of factors in the nutrient models made the nutrient predictions more complex. This implied that the spectral modeling of the nutrient concentrations was more dependent on the fine spectral features of the hyperspectral signature (Mutanga et al. 2004a).

Table 2.5 Assessment of the PLS models for nutrient predictions

Element	Mg	P	S	K	Ca
Modeling					
Number of factors	8	9	6	7	8
RMSEP	0.0246	0.0226	0.0189	0.2877	0.2555
Validation					
RMSEP	0.0269	0.0249	0.0224	0.3282	0.3257
BIAS	0.0051	0.0040	0.0026	0.0044	0.0187
SEPC	0.0264	0.0246	0.0223	0.3282	0.3251
CV	14.9437	26.1488	25.5306	29.4423	41.2515
d	0.7352	0.6910	0.7597	0.8327	0.6865
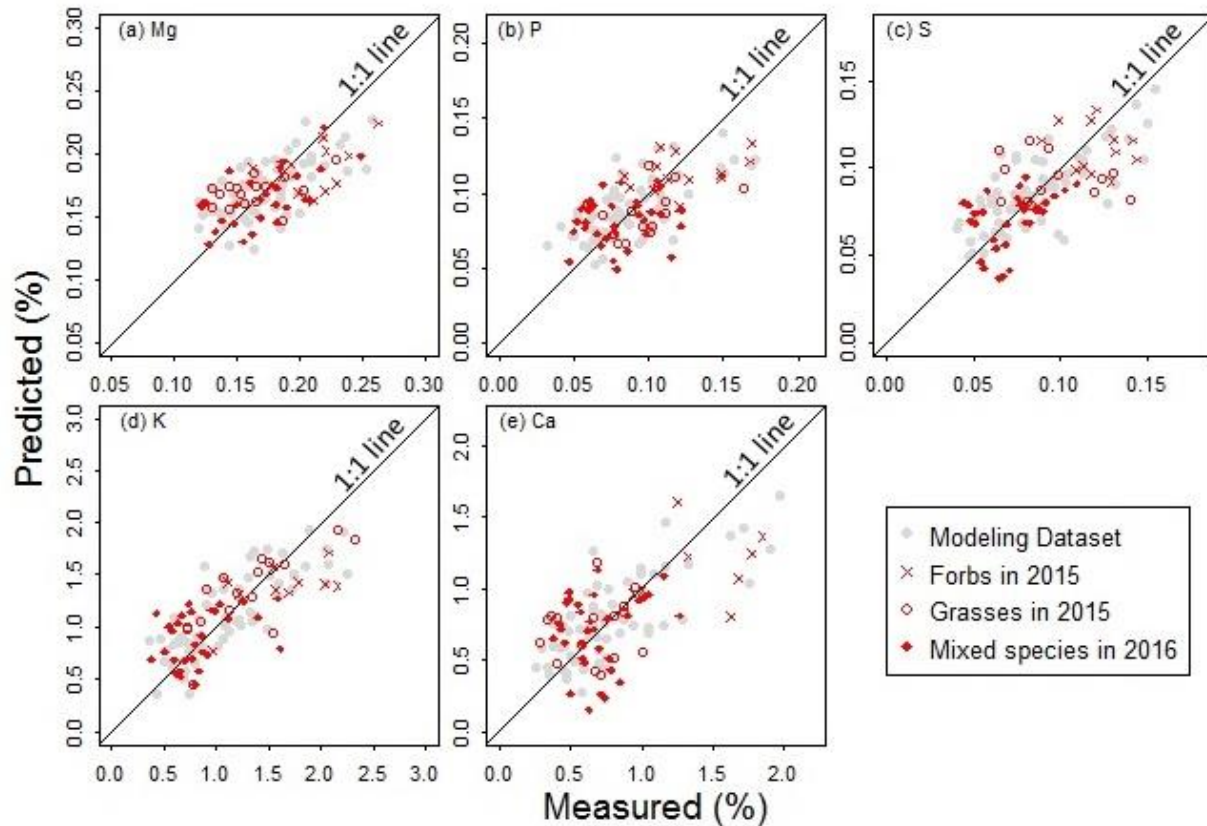
Figure 2.10 Comparisons between the measured and predicted nutrient concentrations for the elements (a) Mg, (b) P, (c) S, (d) K and (e) Ca. Samples used in analysis included the forbs and grasses collected from the Hulbert plots in 2015, and the mixed species collected from the Belowground plots in 2016.

2.4.3 Correlations between Leaf Biochemical Constituents

The correlations (Pearson's r) between leaf biochemical constituents were calculated for the Hulbert plot dataset, in which both the leaf pigments and the nutritional elements were quantified through the laboratory analysis (Table 2.6). The strong correlation between the chlorophylls and carotenoids was not surprising, which was consistent with the observations in previous studies that chlorophylls and carotenoids were co-varying in nature and statistically dependent (Feret et al. 2008). Most of the plant nutritional elements were significantly correlated. These macronutrients were collectively responsible for plant metabolic processes.

Therefore, it was understandable for the generally positive correlations between the leaf nutritional elements (Mutanga et al. 2004b).

Relationships between leaf photosynthetic pigments and nutritional elements were of interest. The chlorophylls were positively correlated with the element K. The carotenoids were negatively correlated with Mg and Ca. There were no other statistically significant correlations between the leaf pigments and the nutritional elements. However, the ratio of Cab:Ccx showed positive correlations with the elements P, S and K. This was consistent with the previous studies which showed that the ratio of Cab:Ccx can be an important index that reflected plant phenology and nutritional status (Feret et al. 2008; Yang et al. 2010).

Table 2.6 Correlations between leaf biochemical constituents

	Cab	Ccx	Cab:Ccx	Mg	P	S	K	Ca
Cab	1							
Ccx	0.80**	1						
Cab:Ccx	0.71**	0.18	1					
Mg	-0.10	-0.53**	0.23	1				
P	0.17	-0.19	0.35**	0.53**	1			
S	0.13	-0.23	0.32**	0.49**	0.60**	1		
K	0.32**	-0.12	0.50**	0.39**	0.63**	0.63**	1	
Ca	-0.12	-0.62**	0.27	0.79**	0.26	0.31**	0.20	1

**Significant at the 95% confidence level: p-value < 0.05

2.5 Conclusions

Results of this study showed that the hyperspectral features in the visible and near infrared region from 470 – 800 nm were useful for predicting the concentrations of leaf pigments and nutritional elements. Standardization of the spectral collection via normalized difference was shown to be feasible to scale the shift and stretch in the original spectral signals due to the

interference from the background effects. Four feature points were highlighted in the spectral standardization method, including the nadirs in the blue and red regions, the green peak and the turning point in the near infrared region. The positions of these feature points provided useful information for detecting leaf pigment concentrations.

Chlorophylls and carotenoids can be retrieved through inverting the physical model PROSPECT 5. PLS regression showed the capability of building the linkages between the high dimensional spectral variables and the vegetation parameters. The advantage of using PLS was that the spectral features relevant to the vegetation parameters of interest can be selected and integrated effectively from a wide range of available spectral predictive variables. In terms of the PROSPECT model, the leaf structure parameter N was proved important to affect the spectral response pattern in the region of 470 – 800 nm. A proper selection of the N range can reduce much of the bias in model validation and lead to a great improvement of model prediction accuracy.

Development of the PLS models for the leaf nutrients demonstrated that a reasonable selection of the modeling and validation datasets was critical to improving prediction accuracy of the empirical models. The nutrient models required more PLS factors to achieve an acceptable level of model accuracy than the retrieval of leaf pigments. It implied that spectral modeling of the nutrients was more complex and required more finely resolved spectral features.

It was promising to quantify leaf pigments and nutritional elements using the hyperspectral analysis method developed in this study. The model prediction accuracy was comparable with those reported by Feret et al. (2008) for pigment retrieval and Mutanga et al. (2004b) for nutrient estimation. This study provided a comprehensive assessment of the leaf biochemical status. More importantly, relationships between the leaf pigments and nutrients were

examined. It was found that the leaf photosynthetic pigments were correlated with part of the nutritional elements. The ratio of Cab:Ccx was informative to reflect the plant nutrition status. These findings provided insight into the use of most pigment-related vegetation indices as a proxy of the vegetation quality. In addition, the spectral models developed in this study were robust across different tallgrass prairie species. These results at the leaf level were of great value as a preliminary step to mapping the forage quality in a grassland canopy from reflectance data collected by airborne or satellite sensors.

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Chapter 3 - Evaluating the Use of Broadband Vegetation Indices as Proxies for Vegetation Quantity and Quality

Abstract

This study examined the use of broadband vegetation indices, the normalized difference vegetation index (NDVI) and green-red vegetation index (GRVI), in detecting vegetation quantity and quality. Leaf area index (LAI) provides a measurement of vegetation quantity. Leaf chlorophyll concentration, which relates to vegetation nutrient contents, is representative of vegetation quality. A spectral database was simulated by varying parameters over a wide range in PROSAIL model, including chlorophylls, carotenoids, LAI and soil moisture. In the PROSAIL-simulated database, NDVI showed high correlations to LAI and canopy chlorophyll contents. GRVI performed even better than NDVI in estimating LAI values. Given that canopy chlorophyll and LAI can be modeled by NDVI and GRVI, respectively, a new index GNVI (green-red normalized vegetation index) was proposed by combining NDVI and GRVI to extract leaf chlorophyll concentration. These empirical relationships between vegetation indices and vegetation characteristics determined in the PROSAIL-simulated database were then validated by a field dataset collected in a tallgrass prairie. The findings in this study showed the potential of using broadband vegetation indices from multispectral remote sensors to monitor vegetation quantity and quality over a wide spatial extent.

3.1 Introduction

Spectral analysis of vegetation quantity and quality has been an area of widespread interest in remote sensing (Asrar et al. 1992; Belluco et al. 2006; Gitelson et al. 1996; Sugiura et al. 2005). Compared to traditional field sample measurements, remote sensing provides a way in

which the vegetation status over a large area can be estimated with high accuracy and efficiency. Recently, an increasing number of multi- and hyper-spectral sensors have gone into service (Chen and Cihlar 1996; Cohen and Goward 2004; Coops et al. 2003; Remer et al. 2005). Hyperspectral sensors provide reflective spectral profiles with fine spectral characteristics, which can be used in quantitative analysis of biophysical and biochemical vegetation properties, such as biomass, chlorophyll concentration, and leaf nutritional element contents (Cho et al. 2007; Nguyen and Lee 2006; Zarco-Tejada et al. 2004). In contrast, multi-spectral sensors provide more generalized spectral signals. However, multi-spectral data are more easily accessible and less computationally complex. These advantages make multi-spectral sensors popular in the realm of remote sensing (Adam et al. 2010; Berni et al. 2009; Laliberte et al. 2011).

Broadband vegetation indices, which combine two or more multi-spectral bands to highlight specific spectral characteristics, are important means of analyzing vegetation properties in remote sensing (Vincini and Frazzi 2011; Wohlfahrt et al. 2010). Among innumerous broadband vegetation indices, the normalized difference vegetation index (NDVI) and green-red vegetation index (GRVI) are ones of the most widely used (Ishihara et al. 2014; Ishihara et al. 2015; Motohka et al. 2010). NDVI is considered the foundation for remote sensing of plant phenology. It is formulated based on the opposite behaviors of leaf reflectance in the red and near-infrared spectral regions (Kriegler et al. 1969; Rouse et al. 1974). The red radiative energy can be largely absorbed by vegetation, and near-infrared is reflected. However, other materials have similar reflectance in these spectral regions. These particular spectral features of a green leaf make NDVI useful in detecting the vegetation areas and their health status. NDVI is the most well-known index which was widely used to track the plant phenology changes in the early studies (Ediriwickrema 2006; Lüdeke et al. 1996; Lee et al. 2002). More recently, there has been

an increasing interest in the use of NDVI as an indicator to quantify the plant photosynthetic capacity. In these quantitative studies, NDVI was found to be correlated with the biophysical and biochemical characteristics of plant canopies, such as green biomass, leaf area index (LAI) and chlorophyll concentration (Boelman et al. 2003; Fan et al. 2009; Santin-Janin et al. 2009; Steltzer and Welker 2006; Yang et al. 2017).

GRVI is an index using a form of standardized difference which is similar to NDVI, but featured by the reflectance difference between the green and red spectral regions. This index has been used to qualitatively analyze the vegetation changes over seasons or canopy differences across ecosystem types (Ishihara et al. 2015; Motohka et al. 2010; Nagai et al. 2014). However, its feasibility to quantify vegetation characteristics has not been studied sufficiently.

The goal of my study is to evaluate the feasibility of NDVI and GRVI to quantitatively detect vegetation quantity and quality. More specifically, this study examined the relationships between the two broadband vegetation indices and the vegetation characteristics, including LAI, leaf chlorophyll concentration and canopy chlorophyll content. LAI is an indicator of vegetation quantity. Leaf chlorophyll concentration is positively related with part of leaf nutritional element contents, which can be considered a measurement of vegetation quality (Mutanga et al. 2004). The result of this study is important for improving the use of aerial or satellite remote sensing imagery to estimate vegetation quantity and quality.

To achieve this goal, the sensitivity of the two vegetation indices to variations in LAI and chlorophyll concentrations was examined and compared in a physical model of canopy reflectance, PROSAIL. PROSAIL is a combination of PROSPECT leaf optical properties model and SAIL canopy bidirectional reflectance model. It has been proven an effective and reliable radiative transfer tool by various laboratory and field experiments across different ecosystems

(Barman et al. 2010; Jay et al. 2017; Wang et al. 2013). As the theoretical analysis was done in PROSAIL, the determined relationships between the vegetation indices and vegetation characteristics were then validated by a field sample dataset collected in a tallgrass prairie. Thus, the feasibility of NDVI and GRVI to quantify vegetation quantity and quality was verified both theoretically and via observation.

3.2 Study Site

The field experiment was conducted at Konza Prairie Biological Station (KPBS, Figure 3.1), a tallgrass prairie site near Manhattan, Kansas, USA (39°05′N, 96°35′W). The vegetation at the site consists of more than 80% of grasses and a minor proportion of forbs. KPBS is divided into more than fifty experimental watersheds with varying combinations of fire and ungulate grazing treatments for long term studies on the interplays among fire, grazers and plant communities (Ling et al. 2014).

A fertilization plot was developed at a bison grazed site, watershed N4B, in 2014. The plot was arrayed in four lines, two controlled (without applications of nitrogen fertilization) and two fertilized. Each line included five 2 m × 2 m subplots with a one meter buffer. In each fertilized line, 0, 12, 24, 48, and 96 grams of ammonium nitrate (NH_3NO_3) were applied to each of the five subplots, respectively, at the beginning of the growing season. The plot was open to free-range bison in the watersheds. The fertilization additions and ungulate grazing were expected to enhance the canopy heterogeneity, allowing a wider range of vegetation characteristics to be sampled.
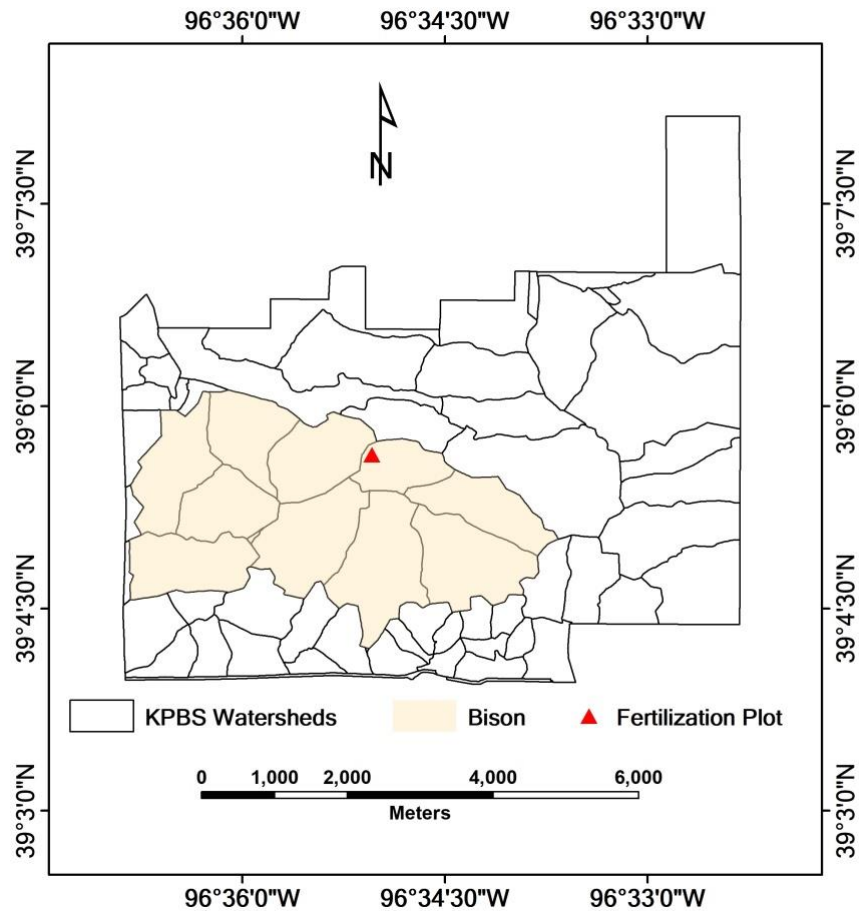
Figure 3.1 Study site at Konza Prairie Biological Station. The fertilization plot with varying nitrogen additions was arranged at a bison-grazed site, the watershed N4B.

3.3 Methods

3.3.1 Field Data Collection

Four data collection campaigns were conducted in the fertilization plot on 1 July, 24 July, 14 August and 20 September, 2014, respectively. In the field experiments, each 2 m × 2 m subplot was divided into four equal parts given the visual field of the sensors. In each quarter of a subplot, the destructive vegetation samples, the canopy reflectance and LAI measurements were collected, respectively (Figure 3.2). The plant samples were chopped into small pieces, dissolved in 80% acetone solvent and then measured by a Spectronic 20 Genesys spectrometer

(Spectronic Instruments Inc., Rochester, NY, USA) for the laboratory analysis of leaf

chlorophyll concentration. The canopy reflectance was measured using an Analytical Spectral

Devices (ASD) FieldSpec Pro portable spectrometer (Analytical Spectral Devices, Boulder, CO,

USA). LAI values were measured using an Accupar LP-80 line ceptometer (Decagon Devices,

Inc., Pullman, WA, USA). Then the measurements from the four subdivisions were averaged and

used as the measurement for the given subplot.
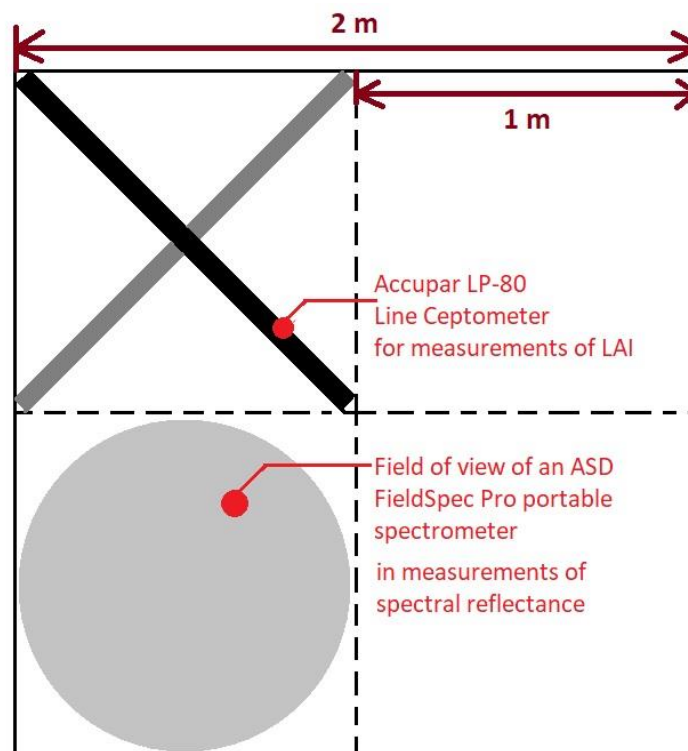
Figure 3.2 Field measurements of reflectance and LAI in a 2 m × 2 m subplot

3.3.2 Theoretical Analysis in PROSAIL Model

A database of reflectance is generated by varying the parameters of vegetation

characteristics in PROSAIL model. Then sensitivities of NDVI and GRVI to LAI, leaf

chlorophyll concentration and canopy chlorophyll content were examined respectively in the

PROSAIL-simulated database. NDVI and GRVI are defined by

$$NDVI = \frac{R_{NIR} - R_{red}}{R_{NIR} + R_{red}} \tag{3.1}$$

$$GRVI = \frac{R_{green} - R_{red}}{R_{green} + R_{red}} \tag{3.2}$$

where R_{NIR} is the averaged reflectance value in the near infrared spectral region (around 850 –

880 nm); R_{red} is the averaged reflectance value in the red spectral region (around 640 – 670 nm);

R_{green} is the averaged reflectance value in the green spectral region (around 530 – 590 nm). LAI

and leaf chlorophyll concentration are vegetation parameters included in PROSAIL model.

Canopy chlorophyll content is calculated by the product of LAI and leaf chlorophyll

concentration.

When setting the model parameters, two situations were considered: (1) varying LAI

values with a uniform soil background, and (2) varying soil backgrounds with a uniform LAI. In

the mode of varying LAI values with a uniform soil background, leaf chlorophyll concentration

was varied between 10 and 60 ug/cm^2 at an increment of 2 ug/cm^2; carotenoid concentration was

varied between 2 and 16 ug/cm^2 at an increment of 2 ug/cm^2; LAI values were varied between

0.5 and 3.7 at an increment of 0.4, with a mixed soil background consisting of 70% dry soil and

30% wet soil. Other parameters followed the default settings (Table 3.1). While varying the soil

background with a uniform LAI, parameter settings at the leaf level in PROSPECT model were

the same with those shown in Table 3.1. At the canopy level in SAIL model, the LAI value was

fixed at 2.1. Spectra of wet soil, dry soil and mixed soil (70% dry soil + 30% wet soil) were used

as backgrounds (Figure 3.3).

Table 3.1 Parameter settings for varying LAI values with a uniform soil background

Model	Parameter	Range
PROSPECT	Leaf mesophyll structure index	1.8
	Water content	0.014 g/cm^2
	Dry matter content	0.012 g/cm^2
	Chlorophyll content	10 – 60 ug/cm^2, by 2 ug/cm^2
	Carotenoid content	2 – 16 ug/cm^2, by 2 ug/cm^2
SAIL	Hot spot	0.01
	Solar zenith angle	25°
	Observer zenith angle	5°
	View azimuth angle	0
	LAI	0.1 – 3.7, by 0.4
	Leaf angle distributions	Spherical
	Background spectrum	70% dry soil + 30% wet soil
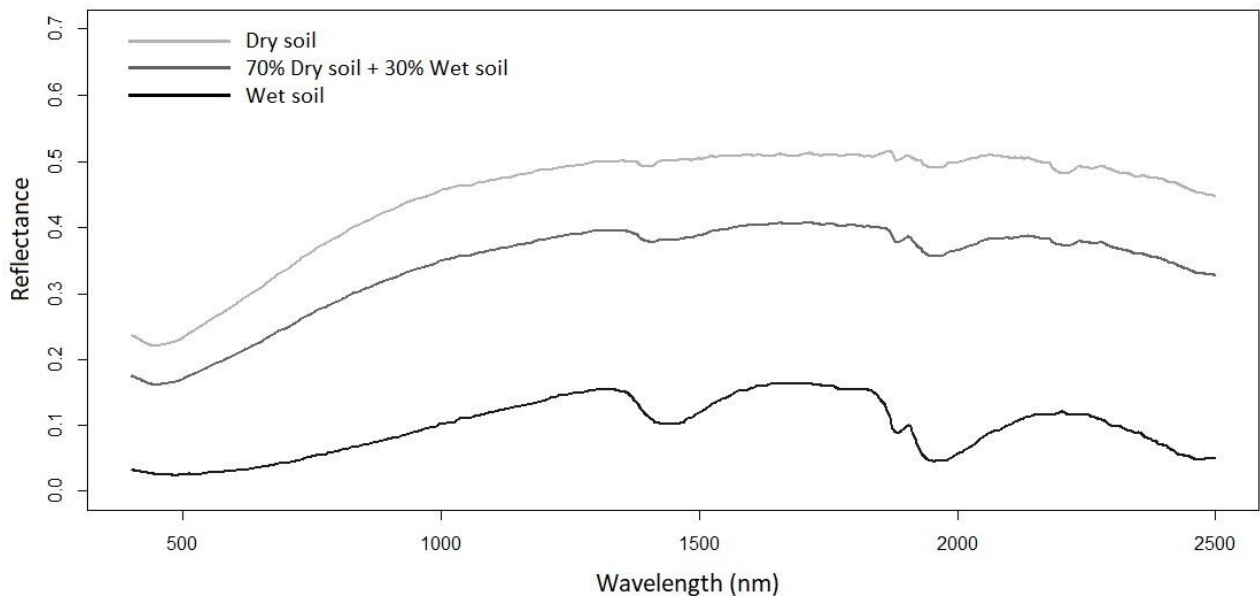
Figure 3.3 Three different soil reflectance spectra used in model settings

3.3.3 Validation by Field Experiment Data

The analytical methods developed in the theoretical analysis were applied to the dataset collected from field experiments. Thus relationships between the vegetation indices and the vegetation characteristics were examined in reality. Feasibility and reliability of NDVI and GRVI to estimate vegetation quantity and quality were evaluated.

3.4 Results and Discussion

3.4.1 Varying LAI Values with a Uniform Soil Background

3.4.1.1 Comparing NDVI and GRVI

The relationship between NDVI and leaf chlorophyll concentration with varying LAI values was shown in Figure 3.4a. For a given LAI value, there is a positively nonlinear correlation between NDVI and leaf chlorophyll concentration, which can be approximated by an exponential or power curve. As the LAI increases, the curve of NDVI-leaf chlorophyll shifts to a higher range of NDVI values. Separations between curves of NDVI-leaf chlorophyll are more compressed at the higher range of NDVI values. This can be explained by the NDVI saturation at the high LAI values (Pontailler et al. 2003).

Relationships between GRVI and leaf chlorophyll across varying LAI values are more complicated (Figure 3.4b). For a low range of LAI values (LAI ≤ 0.5), GRVI is negative or around zero. This characteristic of GRVI can differentiate green vegetation from other land cover types, which has been used to detect the early phase of leaf green-up and the middle phase of autumn coloring in plant phenology (Motohka et al. 2010).

For a given LAI value, scatter points in the plot of NDVI-leaf chlorophyll relationship are distributed along a "line". The band width indicating carotenoid variations has not been observed (Figure 3.4a). This implies that NDVI is insensitive to leaf carotenoid concentration.

Relationships between NDVI and leaf chlorophyll concentration are affected by LAI variations in this simplified case. Comparatively, for a given LAI value, scatter points in the plot of GRVI-leaf chlorophyll relationship are distributed along a "band". The band width indicates the variation in carotenoid concentration (Figure 3.4b). This reveals that GRVI is more sensitive to leaf carotenoids than NDVI.
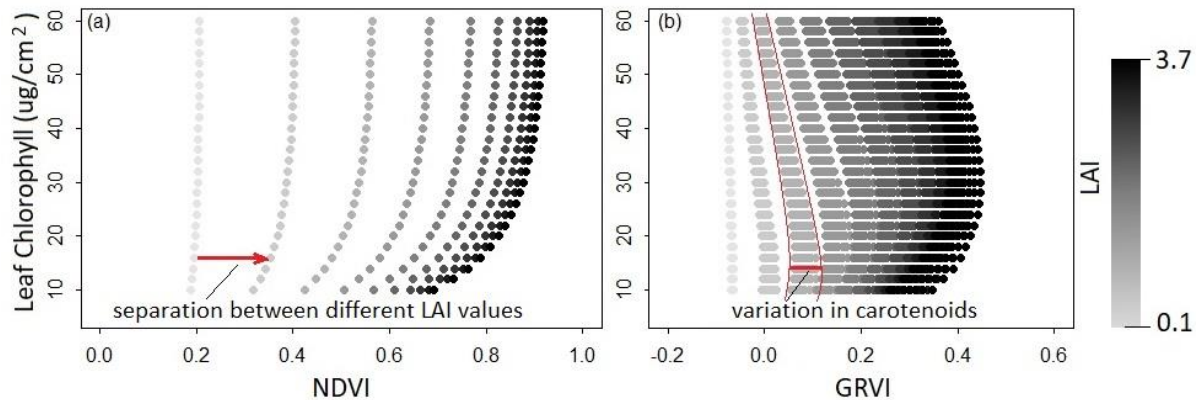
Figure 3.4 Relationships between vegetation indices and leaf chlorophyll concentration. The NDVI-leaf chlorophyll curve shifts across varying LAI values. The separation between curves decreases as the LAI increases. For a given LAI value, points in the plot of GRVI-leaf chlorophyll are distributed along a "band". The band width indicates the variation in carotenoid concentration.

Even if both the LAI and carotenoid concentration are specified, the relationship between GRVI and leaf chlorophyll is not deterministic. As the leaf chlorophyll increases, the GRVI value increases at first, but then decreases. Thus, a given value of GRVI may correspond to multiple values of leaf chlorophyll concentration. Factors of leaf carotenoids, leaf chlorophylls, and LAI all affect the value of GRVI. Given the multiple influential factors, it is difficult to use a single vegetation index, either NDVI or GRVI, to detect the leaf chlorophyll concentration.

Among the relationships between vegetation indices and LAI values, the NDVI-LAI relationship can be approximated by an exponential model, and the GRVI-LAI relationship can be simply approximated by a linear model (Figure 3.5). For convenience, samples with the GRVI

value less than or equal to 0 were excluded when fitting data to the empirical models. Compared to the NDVI-LAI exponential model, the GRVI-LAI linear model has relatively high coefficient of determination (R^2) and low root-mean-square error (RMSE). This indicated that GRVI performed better than NDVI as a predictor of LAI. Figure 3.6 examined relationships between vegetation indices and canopy chlorophyll contents. Results revealed that the relationship of NDVI-canopy chlorophyll can be predicted in an exponential model, whereas GRVI showed low correlation to canopy chlorophyll contents.
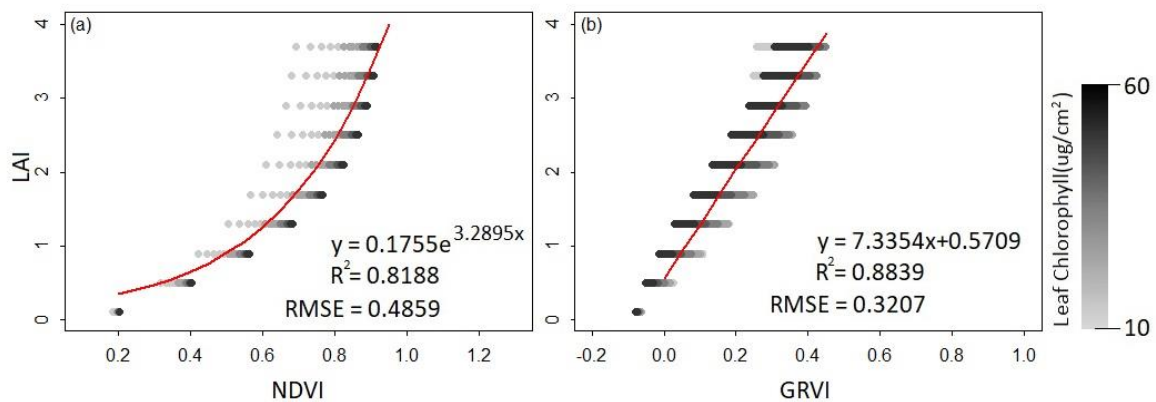
Figure 3.5 Relationships between vegetation indices and LAI values with varying values of leaf chlorophyll concentration.
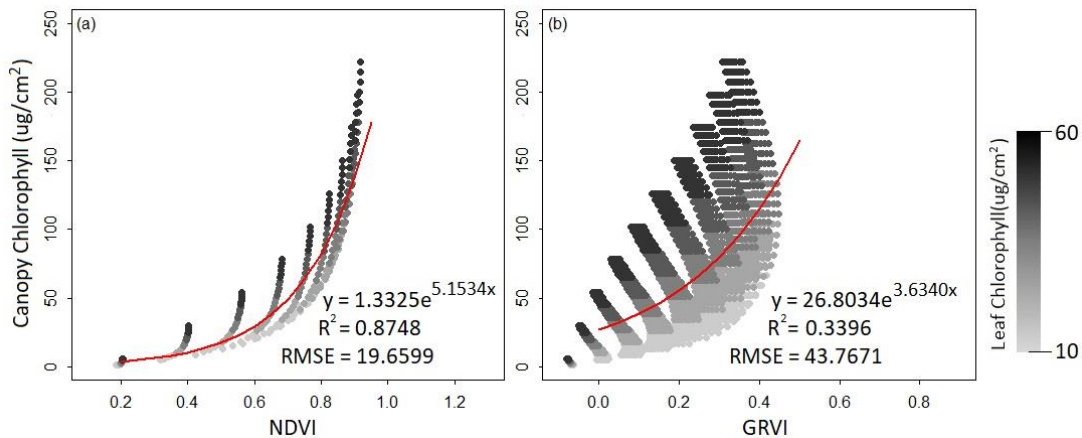
Figure 3.6 Relationships between vegetation indices and canopy chlorophyll contents. The canopy chlorophyll contents are determined by the product of leaf chlorophyll concentration and LAI.

3.4.1.2 Combining NDVI and GRVI

Given that LAI and canopy chlorophyll can be modeled by GRVI and NDVI, respectively, the leaf chlorophyll concentration may be estimated by combining GRVI and NDVI. A new vegetation index, GNVI, is proposed to extract the leaf chlorophyll concentration from canopy reflectance:

$$GNVI = \frac{e^{a \times NDVI}}{GRVI + b} \tag{3.3}$$

where a and b are empirical coefficients. In this case, $a = 5.1534$, and $b = 0.0778$, based on the empirical models determined in the previous analysis. Analysis of the relationship between GNVI and leaf chlorophyll showed that GNVI had a high correlation to leaf chlorophyll concentration (Figure 3.7). These results indicated that leaf chlorophyll concentration can be predicted by GNVI across varying LAI values $(0.1 - 3.7)$ using a linear model.
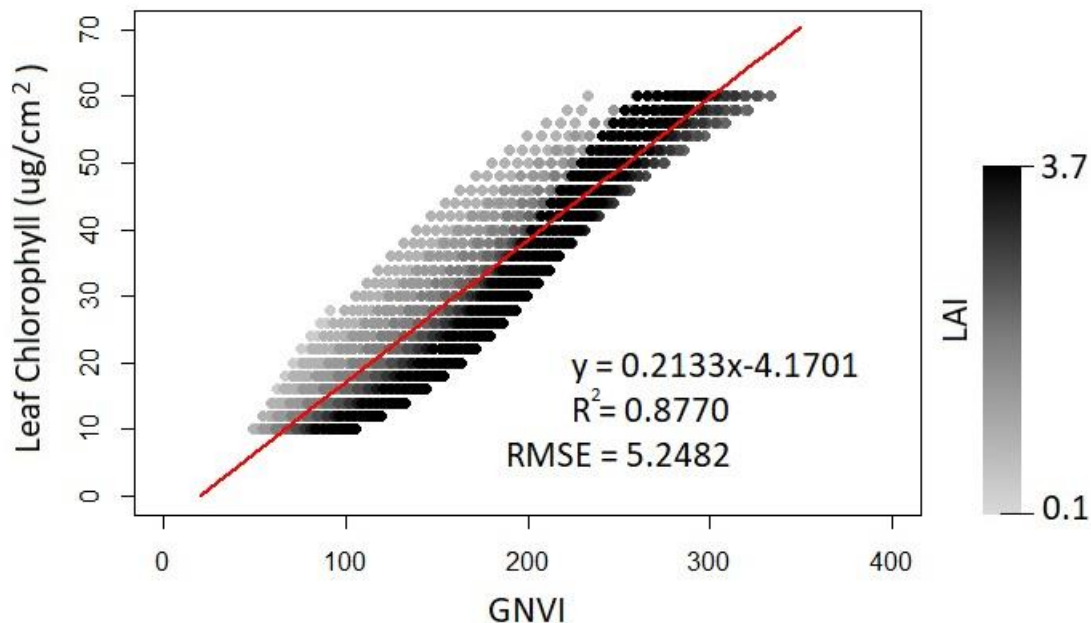
Figure 3.7 Use of GNVI as a predictor to leaf chlorophyll concentration

3.4.2 Varying Soil Backgrounds with a Uniform LAI

Canopy chlorophyll content is defined by the product of LAI and leaf chlorophyll content. When varying the soil backgrounds, the LAI value was fixed. Thus, the canopy chlorophyll content is proportional to the leaf chlorophyll concentration. Under these circumstances, variations in relationships between vegetation indices and leaf chlorophyll concentration due to the different soil backgrounds were observed (Figure 3.8). This indicates that the three vegetation indices, NDVI, GRVI, and GNVI, all are sensitive to the soil background to some degree. Across different soil backgrounds, GRVI had a low correlation to the leaf chlorophyll. NDVI and GNVI had acceptable model fitness and prediction accuracy as indicators of leaf chlorophyll concentration. GNVI performed even better than NDVI, with higher R^2 and lower RMSE. This indicates that GNVI is less sensitive to soil backgrounds than NDVI or GRVI. Estimation of leaf chlorophyll concentration using GNVI can be more robust and consistent across different soil backgrounds than using NDVI or GRVI.
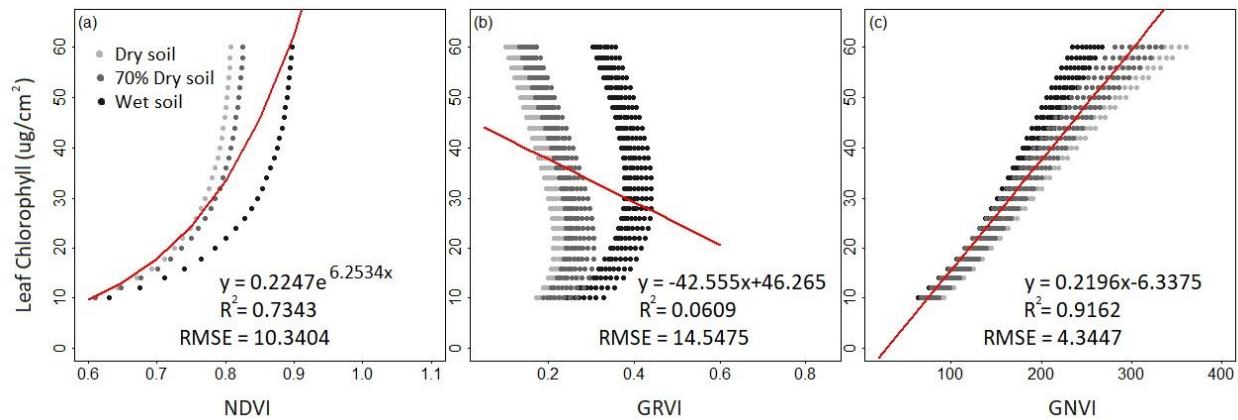
Figure 3.8 Relationships between vegetation indices and leaf chlorophyll concentration across varying soil backgrounds.

3.4.3 Validation

To validate these results, eighty field samples were collected across the growing season in 2014 from the Konza Prairie experimental site. Of these, thirty samples had GRVI values ≤ 0, and were therefore excluded from the validation procedure. The descriptive statistics for the remaining fifty samples were shown in Table 3.2. The variances in the field samples were much smaller than that in the PROSAIL-simulated dataset. The empirical coefficients determined in the PROSAIL-simulated dataset need to be adjusted to fit the field samples. Thus the relationships between the vegetation indices and vegetation characteristics were modeled empirically for the field samples using leave-one-out cross validation (Figure 3.9). The resulting empirical models had acceptable values of R^2 and RMSE, which verified the feasibility of NDVI and GRVI to estimate canopy chlorophyll contents and LAI values, respectively.

Table 3.2 Descriptive statistics for the field samples

	Min.	Max.	Mean	Standard deviation
Leaf chlorophyll (ug/cm^2)	24.900	42.070	32.950	3.910
LAI	0.440	1.020	0.710	0.170
Canopy chlorophyll (ug/cm^2)	12.120	40.020	23.580	7.210
NDVI	0.568	0.722	0.641	0.044
GRVI	0.015	0.146	0.072	0.042

The empirical coefficients in the new vegetation index GNVI were adjusted accordingly (*a*=6.3072, and *b*=0.1731 in Eq. (3.3), based on the empirical models determined for the field samples, see Figure 3.9). The model fitness and prediction accuracy were acceptable in modeling the relationship between GNVI and leaf chlorophyll concentration (Figure 3.10). This showed the capability of GNVI to be an indicator of leaf chlorophyll concentration.
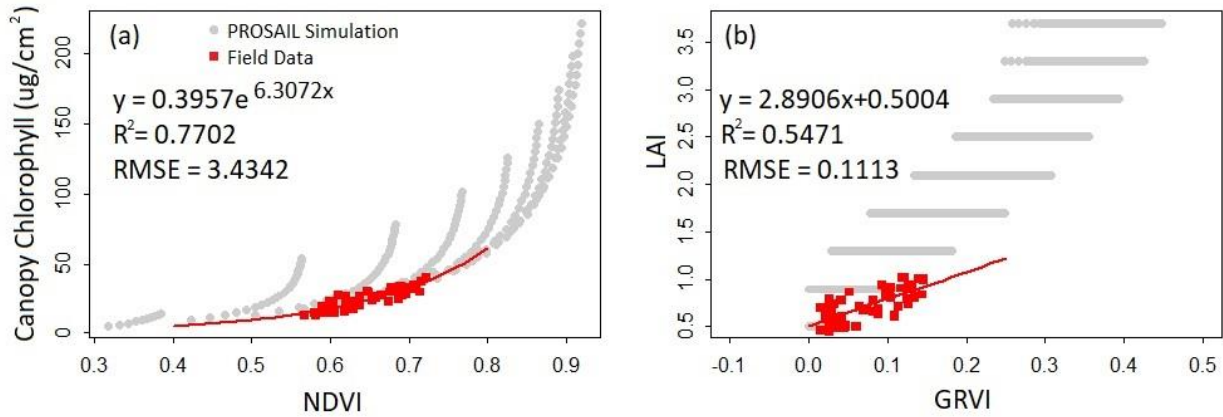
Figure 3.9 Leave-one-out cross validations for empirical modeling of relationships between vegetation indices and vegetation characteristics.
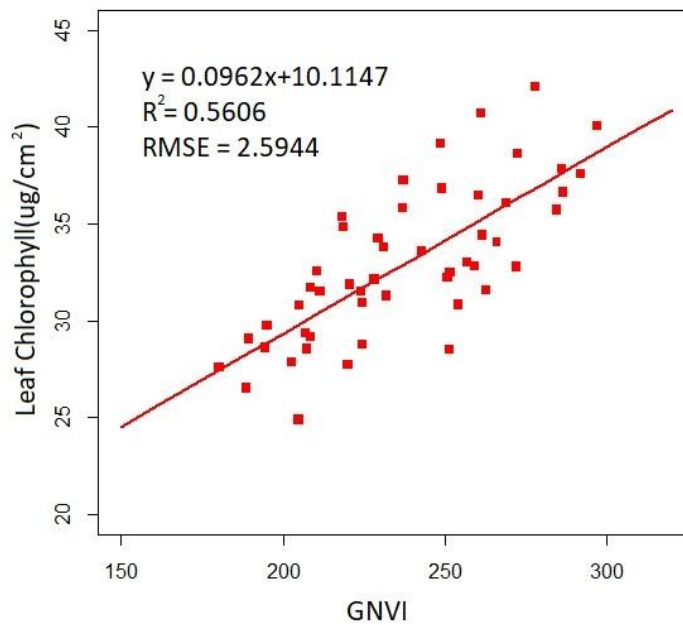
Figure 3.10 A linear model of the relationship between GNVI and leaf chlorophyll concentration for the field samples. In this case, *a*=6.3072, and *b*=0.1731 for determining GNVI values using Eq. (3.3).

3.5 Conclusions

Analyses in the physical model simulation and field samples showed positive results for

the use of multispectral vegetation indices to predict LAI and leaf chlorophyll concentration. LAI

provides a measurement of vegetation quantity. Leaf chlorophyll concentration, which relates to

vegetation nutrient contents, is representative of vegetation quality. Therefore, feasibility of the broadband vegetation indices to detect vegetation quantity and quality was evaluated. In the theoretical analysis based on PROSAIL model, NDVI showed a high correlation to LAI values, which verified the feasibility of NDVI to estimate vegetation quantity. This is consistent with the applications of NDVI to quantify canopy biophysical properties, such as LAI and plant biomass, in a wide range of previous studies (Boelman et al. 2003; Fan et al. 2009; Santin-Janin et al. 2009). Furthermore, NDVI has been proven an indicator of the canopy chlorophyll content, which is determined by the product of LAI and leaf chlorophyll concentration. This suggests that NDVI reflects combined information of vegetation quantity and quality, which can be used to quantify plant biochemical characteristics at the canopy level.

GRVI showed a capability to estimate LAI values across varying leaf chlorophyll concentrations, and performed even better than NDVI as a proxy for LAI values. The value of GRVI around zero indicates a low range of LAI values, which has been used as a site-independent threshold to detect plant phenology variations and land cover changes in a range of qualitative studies (Motohka et al. 2010; Nagai et al. 2014). In addition, the theoretical analysis of this study based on the PROSAIL-simulated database showed that GRVI is sensitive to carotenoids to some degree, whereas NDVI is insensitive to carotenoids. This suggested the potential of GRVI for detecting carotenoid-related characteristics in the canopy, such as the plant nutritional status (Yang et al. 2010).

Given that NDVI and GRVI can be used to predict canopy chlorophyll and LAI, respectively, a new vegetation index GNVI was proposed to extract leaf chlorophyll concentration from canopy chlorophyll contents using a combination of NDVI and GRVI (Eq.(3.3)). Methods that combine two or more vegetation indices to separate or synthesize

vegetation characteristics of interest are not unusual in remote sensing (Vescovo et al. 2012). The new index GNVI developed in this way showed high model fitness and prediction accuracy in estimating leaf chlorophyll concentration. This indicates that the broadband vegetation indices have the potential to extract vegetation characteristics at the leaf level and detect vegetation quality from the canopy reflectance.

In the theoretical analysis, disparities due to soil backgrounds can be observed in the vegetation indices, NDVI, GRVI and GNVI. However, the influence from soil backgrounds does not affect the general tendencies between vegetation indices and vegetation characteristics. This may be explained by the nature of the standardized difference index that highlights the difference in two spectral features which behavior diversely, and minimizes the background variation effects (Delalieux et al. 2008; Ferwerda et al. 2005).

A limitation of the new index GNVI is that it is sensitive to the empirical coefficients (a and b in Eq. (3.3)). It can be seen that in the validation procedure the leaf chlorophyll and LAI varied in a smaller range than that in the PROSAIL-simulated dataset. The empirical coefficients in GNVI were therefore adjusted to fit the field dataset. Determination of the empirical coefficients depends on the given field dataset or a simulation by a physical model with proper parameter settings.

In conclusion, this study compared the use of NDVI and GRVI in detecting vegetation characteristics. NDVI showed high correlations to LAI and canopy chlorophyll contents. GRVI performed even better than NDVI as an indicator of LAI. GNVI is a new index that combines NDVI and GRVI, which can be used to estimate leaf chlorophyll across varying LAI values. These findings are important for improving the use of broadband vegetation indices from multispectral remote sensors to detect vegetation quantity and quality over a wide spatial extent.

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Chapter 4 - Effects of Fire and Large Herbivores on Canopy Nitrogen in a Tallgrass Prairie: a Study from Spectroscopy Imagery

Abstract

Effects of fire and grazing by large herbivores on the vegetation cover in a seasonably variable environment with complex topography are of special interest in grassland science. This study focused on the analysis of variation in grassland canopy nitrogen associated with fire, ungulate grazing (e.g., bison and cattle), topography and vegetation phenology using remotely sensed hyperspectral images. These images provided accurate representations of the spatial variability in vegetation canopies, from which analysis of the grassland processes in a large spatial extent was allowed. Results in this study indicated that fire enhanced plant productivity, resulting in a more uniform distribution of canopy nitrogen. Fire effects interacting with ungulate grazing were most influential in the areas with shorter fire intervals. A high level of ungulate grazing reduced vegetation density, but promoted canopy spatial heterogeneity. Topography and phenology were important drivers that dominated the general tendency of the variation in canopy nitrogen. Effects of fire and grazing on the grassland canopy varied across topographic positions and seasons. Differences in the vegetation canopy between sites with bison and cattle were observed, which may be related to differences in the grazing intensity, forage behavior and site selection between the two grazer species. This study provided a preliminary understanding of spatial processes involving the interplay between vegetation and fire-grazing disturbances in a grassland ecosystem.

4.1 Introduction

Fire and grazing by large herbivores have historically played indispensable roles in determining and maintaining the canopy structure and species composition of vegetation communities in North American grassland ecosystems (Collins and Wallace 1990; Hulbert 1986). The effects of periodically recurring fires, involving above- and below-ground processes in grasslands, are complex (Evans et al. 1989; Neary et al. 1999). In general, fires stimulate plant growth through removing the standing dead litter aboveground and increasing the light interception in the canopy (Abrams et al. 1986; Anderson et al. 2007). The increased soil temperature in burned areas enhances the nutrition cycling belowground, and potentially improves plant productivity (Seastedt and Ramundo 1990). More specifically, fire effects on vegetation vary with factors such as plant species, seasons of the fire, and the time since the previous burn. Fire is effective for promoting the growth of prairie grasses by suppressing woody plant invasion (Anderson 1990; Bragg and Hulbert 1976). Winter fires during the period of plant dormancy may have little influence on plant abundance, whereas spring fires can reduce the forb species that have initiated growth before the burn, and thus increase the dominance and production of the matrix grass species (Collins and Gibson 1990). Moreover, spring fires tend to advance plant growth and speed up the phenological development (Svejcar 1990). The fire stimulus to grassland plants is dramatic but transitory. It is typically apparent for the first one or two years after the burn, and then it disappears as the community gradually reaches equilibrium (Loucks 1970). Frequent prescribed fires therefore become a commonly used practice in range management to maintain the grassland vegetation and enhance the forage quality.

Grazing by large ungulate herbivores is another critical component in grasslands (Archibald et al. 2005; Fuhlendorf and Engle 2001). Like fires, ungulate grazers can enhance

plant abundance, through reducing the standing dead materials in the canopy (Belsky 1986). In addition, plants have the capability to overcompensate for low levels of herbivory, which often results in higher vegetation production in the grazed sites than the ungrazed ones (de Mazancourt et al. 1998; McNaughton 1983). With regard to the effects on plant species, ungulate grazing reduces the palatable grass species, allows forbs to flourish, and increases plant species diversity (Collins et al. 1998). More importantly, large herbivores play a role in redistributing plant-available nutrients by their waste products. They promote nutrition cycling through reducing the microbial nitrogen immobilization (Frank and Evans 1997; McNaughton et al. 1997). Their grazing activities and forage patterns exert control over the spatial heterogeneity of grassland vegetation (Collins and Barber 1985).

The native ungulate grazers, American Bison (*Bison bison*), are the keystone species that affect the plant communities in the Great Plains of North America (Anderson 2006). Their distinctive behaviors, such as selective forage and wallowing, make them different from other large herbivores, the domestic cattle (*Bos taurus*) for example (Allred et al. 2011b). Bison select primarily graminoids (Plumb and Dodd 1993). This may reduce the dominant grasses and result in greater plant species evenness at sites grazed by bison than by cattle (Hartnett et al. 1996). The wallowing activities of bison disturb the soil conditions. The soil depressions created by bison wallowing may dramatically alter the plant species composition in the canopy (Collins and Gibson 1990; Trager et al. 2004). North America grasslands evolve with significant influences by bison and cattle. Comparison of these two species is of special research interest, and provides important implications for conservation and management of grassland ecosystems (Allred et al. 2011b; Coppedge and Shaw 1998; Senft et al. 1985).

Fire and large herbivores differ in mechanisms that affect the grassland vegetation. Interestingly, the two factors naturally interact with each other. Fire influences the forage site selection by large herbivores. For example, bison and cattle prefer recently burned grasslands (Allred et al. 2011a; Allred et al. 2011b). Grazing activities by large herbivores may alter the fuel load characteristics, and potentially influence the fire spread, severity and intensity (Strand and Launchbaugh 2014).

Interactions of fire and grazing (Archibald et al. 2005; Fuhlendorf et al. 2009), along with other factors such as climate and topography, contribute to complicated functions and processes in the grassland ecosystem. Their effects on plant productivity and grassland biodiversity have been substantially studied (Collins and Smith 2006; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2010; Hartnett et al. 1996; Koerner and Collins 2014). Most previous studies are based on data analysis from field measurements. For example, Augustine and Frank (2001) used plots with different sizes (4×4 m and 60×30 m) for field sampling. They studied the influences of the ungulate grazers on the spatial heterogeneity of soil nitrogen properties in a grassland system at a fine scale of $0.1 - 2$ m and a coarse scale of $5 - 30$ m, respectively. Wallace et al. (1995) mapped the 30 highest biomass points out of 225 field samples in a 30 m $\times$ 30 m plot every two meters, and compared their spatial pattern with the Poisson distribution to determine whether they were randomly distributed.

Traditional field data measurements can provide reliable and detailed ground references. However, these field measurement procedures are usually labor intensive and time consuming. The confined study plots and limited sample size in field measurements may result in unrealistic representation of the fire-grazing processes across large natural landscapes. More recently, with the development of remote sensing technology, spectral imaging has been widely used to

monitor the land surface in earth sciences (Jago et al. 1999; Knyazikhin et al. 2013; Kokaly et al. 2003). Compared to traditional field data measurements, spectral imaging provides a relatively effective way in which images in a range of spectral bands over a large study area can be taken immediately. The acquired multi- or hyper-spectral images can be used to extract biophysical and biochemical characteristics in the canopy, and map the canopy features at a large spatial extent (Martin and Aber 1997; Mutanga et al. 2005). This may attenuate the concern about the limited sample size by field measurements. In addition, the spatially intensive data, provided by the numerical maps from spectral imaging, make it possible to further explore the canopy spatial heterogeneity (Harris et al. 2003; Lobo et al. 1998).

The principal goal of this study was to evaluate the effects of fire and large herbivores on canopy nitrogen in a tallgrass prairie using hyperspectral imaging. The nitrogen content within vegetation canopies is an important index of grassland forage quality. Investigating the spatial distribution of the canopy nitrogen associated with the fire and herbivory activities throws light on critical questions concerning interactions between the forage nutrient pattern and grazer behaviors in grassland science. This study examined the variability in canopy nitrogen across a tallgrass prairie mosaic created by a variety of fire-grazing treatments along with the topographic and seasonal influences. To be specific, the effects of the fire interval (i.e., the time since the previous burn), the native grazer (i.e., bison) and the domestic grazer (i.e., cattle) on the content and spatial heterogeneity of canopy nitrogen were compared at different topographic positions over the growing season.

4.2 Methods

4.2.1 Study Area

This study was conducted at Konza Prairie Biological Station (KPBS, Figure 4.1), a

tallgrass prairie of 34.87 km^2 in the Flint Hills near Manhattan, Kansas, USA (39°05'N,

96°35'W). The site is dominated by a continental climate with warm, wet springs, hot summers

and dry, cold winters. The vegetation at the site is dominated by C4 perennial grasses,

intermingled with a minor proportion of C3 forbs and a few of C3 grasses. The soil conditions

vary with the topographically complex landscapes. In general, the lowland soils are thick, silty

clay loams. The upland and hillside soils are much shallower and rockier.
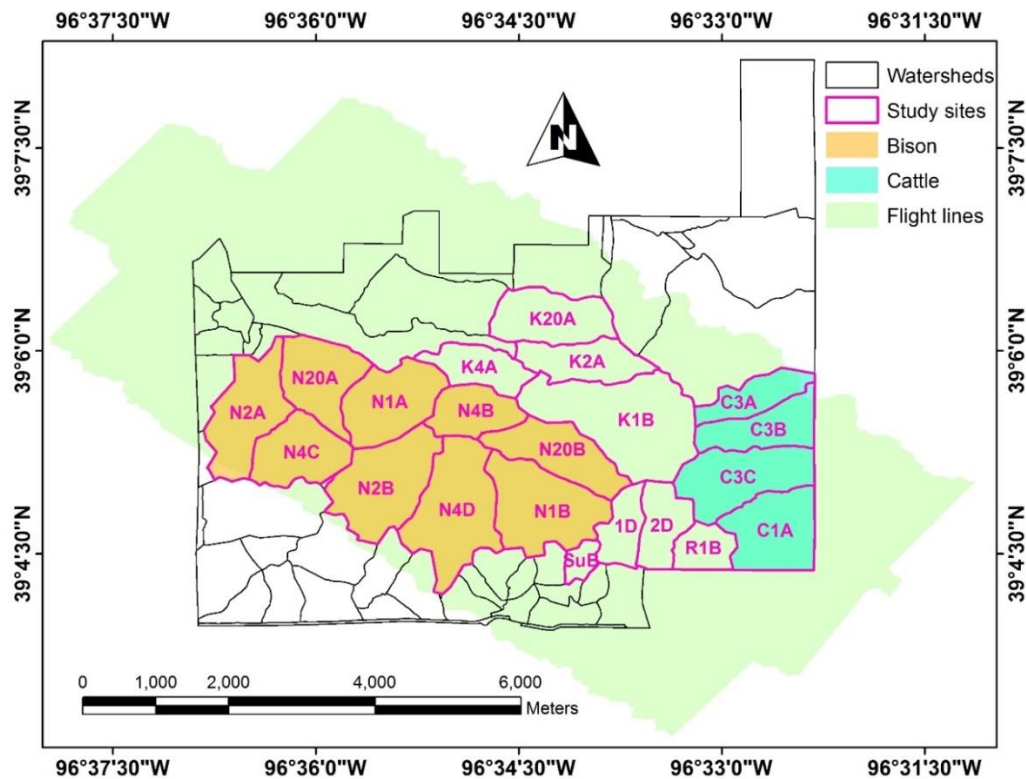
Figure 4.1 Study area at Konza Prairie Biological Station (KPBS). The site is topographically complex, and subject to a variety of fire-grazing treatments, resulting spatially variable vegetation canopies. Twenty-one out of totally more than fifty KPBS watersheds were selected for analysis in this study, with an area of 17.13 km².

KPBS is divided into more than fifty watersheds, each subject to a treatment combined by fire and ungulate grazing. Fire treatments vary with fire frequencies (1, 2, 4, 10 and 20 years). Grazing treatments include bison, cattle and non-grazing. The various combinations of fire and grazing treatments allow investigations into effects of the fire alone and the interactions of fire and ungulate herbivory in grasslands. In this study, twenty-one watersheds (with an area of 17.13 km^2) were selected for data analysis given the coverage of the aerial images, in which nine were grazed by bison, four were grazed by cattle and eight were ungrazed.

4.2.2 Data Collection and Preprocessing

Hyperspectral imagery covering the twenty-one watersheds was collected on four dates (26 May, 29 June, 2 August, and 26 September) spanning the 2011 growing season, using an AISA Eagle camera mounted on a Piper Warrior aircraft operated by the Center for Advanced Land Management Information Technology (CALMIT) of the University of Nebraska-Lincoln. The aircraft was flown at an altitude yielding a spatial resolution of 2 m × 2 m. The fire history records and the digital elevation model (DEM) of the study area were provided by the NSF Long Term Ecological Research Program at KPBS.

The fire interval for each watershed was calculated by the days between the dates of the previous burn and the image capture. Based on the DEM and the derived slope data, each watershed was divided into four types of topography, including drainage bottoms, lowlands, uplands and hillslopes (slope > 10°, determined by a natural break). The resulting topographic divisions were shown in Figure 4.2. The gallery forest pixels on imagery were removed before analysis. Canopy nitrogen contents in grasslands were retrieved from hyperspectral imaging statistically (Ling et al. 2014). In addition, the continuous values of canopy nitrogen on each image were classified into five groups from low to high levels using natural breaks (Evans 1977).

The spatial heterogeneity (Li and Reynolds 1994) of different canopy nitrogen levels can be

quantified from the resulting categorical maps (Figure 4.3).
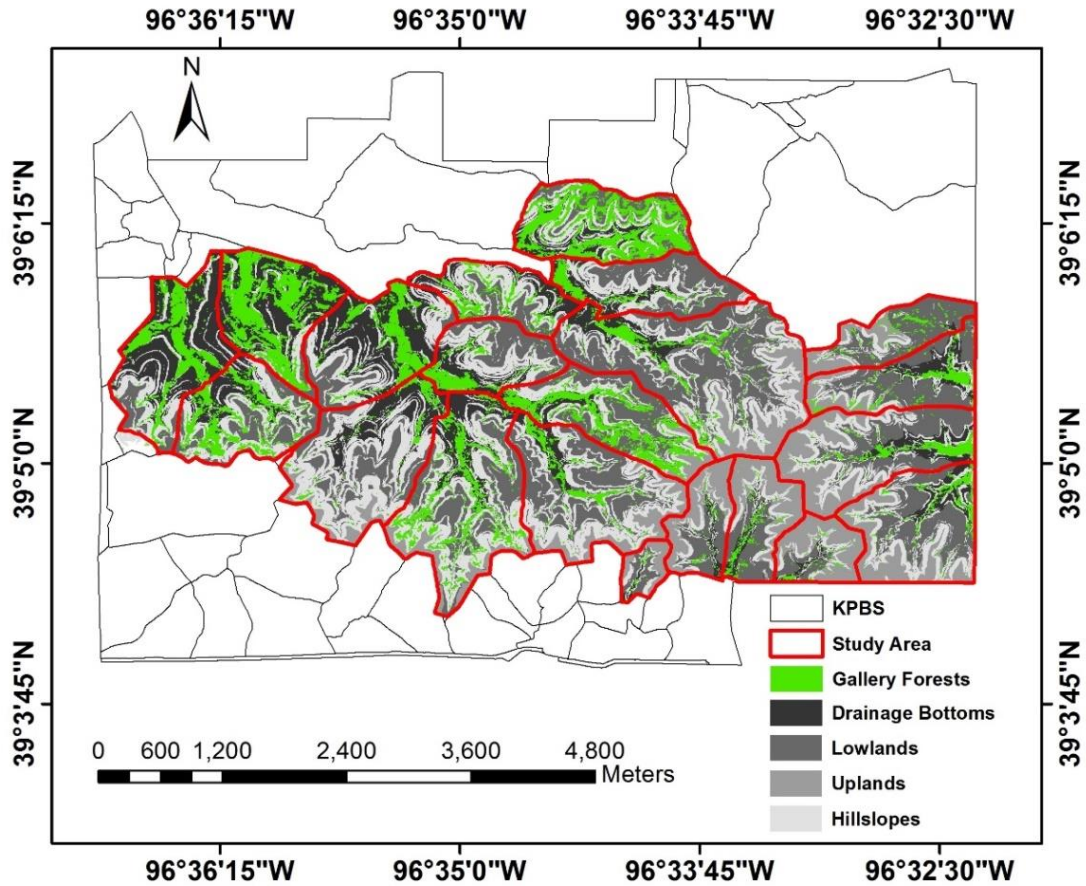
Figure 4.2 Topographic division of the study area. The hillslopes are the transition zones between the flat lowlands and the flat uplands.
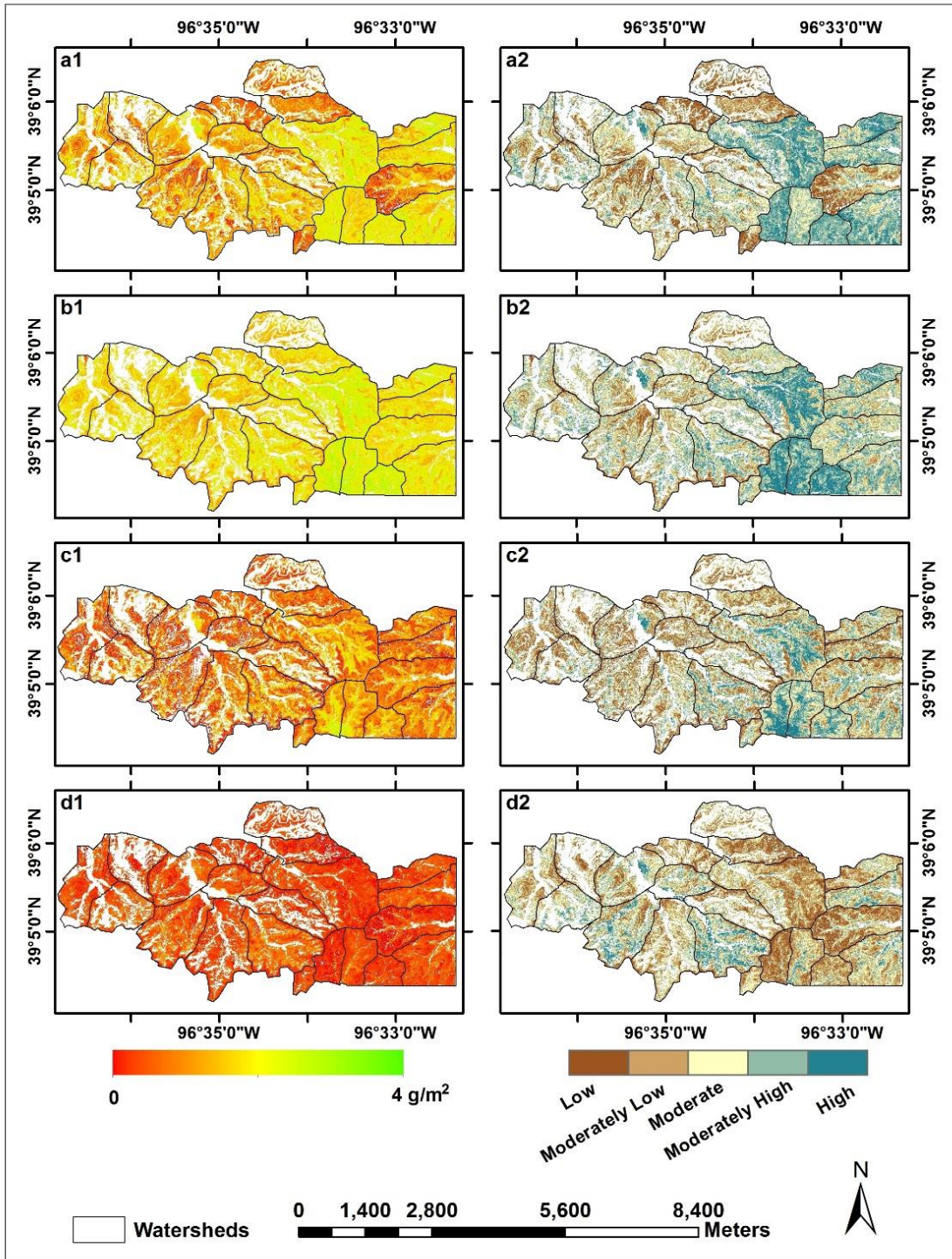
Figure 4.3 Continuous canopy nitrogen maps for (a₁) May, (b₁) June, (c₁) August, (d₁) September, and categorical maps with five canopy nitrogen levels from low to high for (a₂) May, (b₂) June, (c₂) August, (d₂) September.

4.2.3 Data Analysis

On the continuous canopy nitrogen imagery, the mean and standard deviation of canopy nitrogen were calculated in the zone defined by the topography type in each watershed. The topographic divisions by watershed on the categorical maps were subjected to spatial heterogeneity analysis using the FRAGSTATS program (McGarigal and Marks 1995), from which the metrics of contagion, Simpson's diversity, and interspersion/juxtaposition index (IJI) for the high-nitrogen patches were calculated (Table 4.1). These metrics provided informative measurements of the canopy nitrogen spatial heterogeneity. The results allowed quantitative comparisons among fire-grazing treatments, topographic positions and seasons from different perspectives of canopy nitrogen properties.

Table 4.1 FRAGSTATS metrics measuring spatial heterogeneity

FRAGSTATS metric	Range	Description
Contagion	(0,100]	A measurement of aggregation; the value approaches 0 as the path types become more disaggregated and interspersed; a value of 100 indicates all patch types are maximally aggregated.
Simpson's diversity	[0,1)	A measurement of diversity; a value of 0 indicates no diversity; as the patch richness increases and the proportional distribution of area among patch types becomes more equitable, the value approaches 1.
Interspersion/Juxtaposition index (IJI)	(0,100]	A measurement of patch interspersion and juxtaposition; the value approaches 0 as the distribution of patch adjacencies becomes increasingly uneven; a value of 100 indicates all patch types are equally adjacent to all other patch types.

To study the effects of fire separately, the data for the non-grazing watersheds were gathered. The fire interval was considered as the independent variable. The variation of the canopy nitrogen contents with the fire intervals was studied. In addition, the fire treatments were classified into two levels, including the fire intervals within one year (burned in spring), and those greater than one year (unburned in spring of the current year). The differences in the canopy nitrogen properties between the two fire interval levels were analyzed using the two sample t-test.

For the combined treatments of fire and grazing, the data for different topographic divisions were analyzed separately. Factorial analysis of variance (ANOVA) was used to examine the presence of the fire-grazing interactive effect. In the cases with influential ungulate grazing effect, the canopy nitrogen properties between sites with bison and cattle were compared, which revealed differences between the two important ungulate grazer species in their effects on the grassland heterogeneity.

Variogram analysis (Bachmaier and Backes 2008) was used to determine the spatial structure of the continuous canopy nitrogen data. Theoretically, a variogram levels off after a certain distance (Figure 4.4). This distance is called the range, within which the samples are spatially autocorrelated. The value of the variogram at the range is called the sill. The range provides insight into the spatial scale of the sampled characteristic, and the sill indicates the contrast of the characteristic (Curran 1988; Woodcock et al. 1988). In this study, the range reflected the vegetation patch size within which the canopy nitrogen was homogeneous and varied in a small range. The sill reflected the variance of the canopy nitrogen among uncorrelated vegetation patches, which may result from the diversity in plant species and canopy structure.

The variogram is sensitive to the direction, whereas the topographic divisions of this study manifested highly anisotropic patterns. To reduce the effects from the topographic complexity, the regions with different topography types were analyzed separately. For each topographic division in a watershed, three patches, each enveloped by a convex hull, were randomly selected. The patch size allowed a variogram analysis within fifty meters, and all the pixels in the patch were included in analysis. Results of the patches with the same fire and grazing treatments were pooled and averaged. The range and sill of the variogram that characterize the spatial variability were examined and compared between different fire and grazing treatments (Harris et al. 2003).
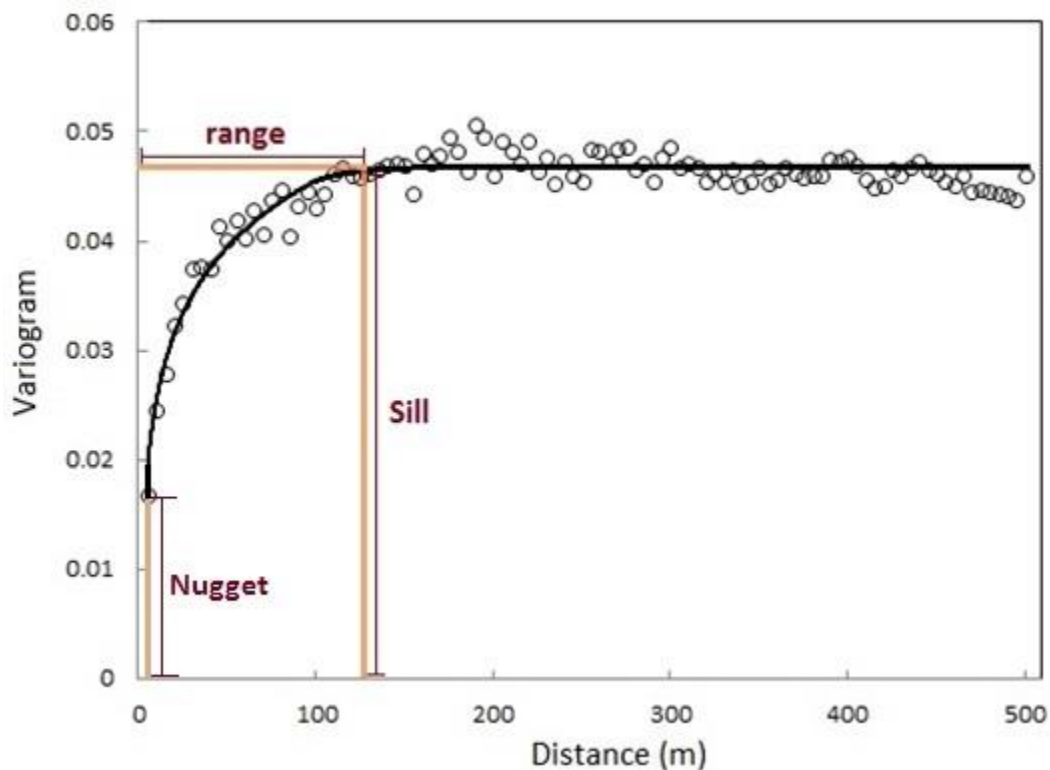
Figure 4.4 Variogram analysis for spatial variability. The variogram levels off after a certain distance. This distance is called the range, within which the samples are spatially autocorrelated. The value of the variogram at the range is called the sill. The nugget is the height of the variogram at the zero separation distance, which represents the measurement errors or the variation at a smaller distance than the sampling interval.

4.3 Results

4.3.1 Separate Effects of Fire on Canopy Nitrogen

The mean of canopy nitrogen contents at the watershed level over the non-grazing areas were plotted along with the days since the previous fire to study the fire effect separately from large herbivores (Figure 4.5). These plots suggested a general tendency that during May – August the canopy nitrogen with the fire intervals less than one year was higher than those with longer fire intervals. Differentiation associated with the topographic positions was most evident in August. In September, there was no apparent tendency observed in the variation of canopy nitrogen related with the fire intervals or topography.
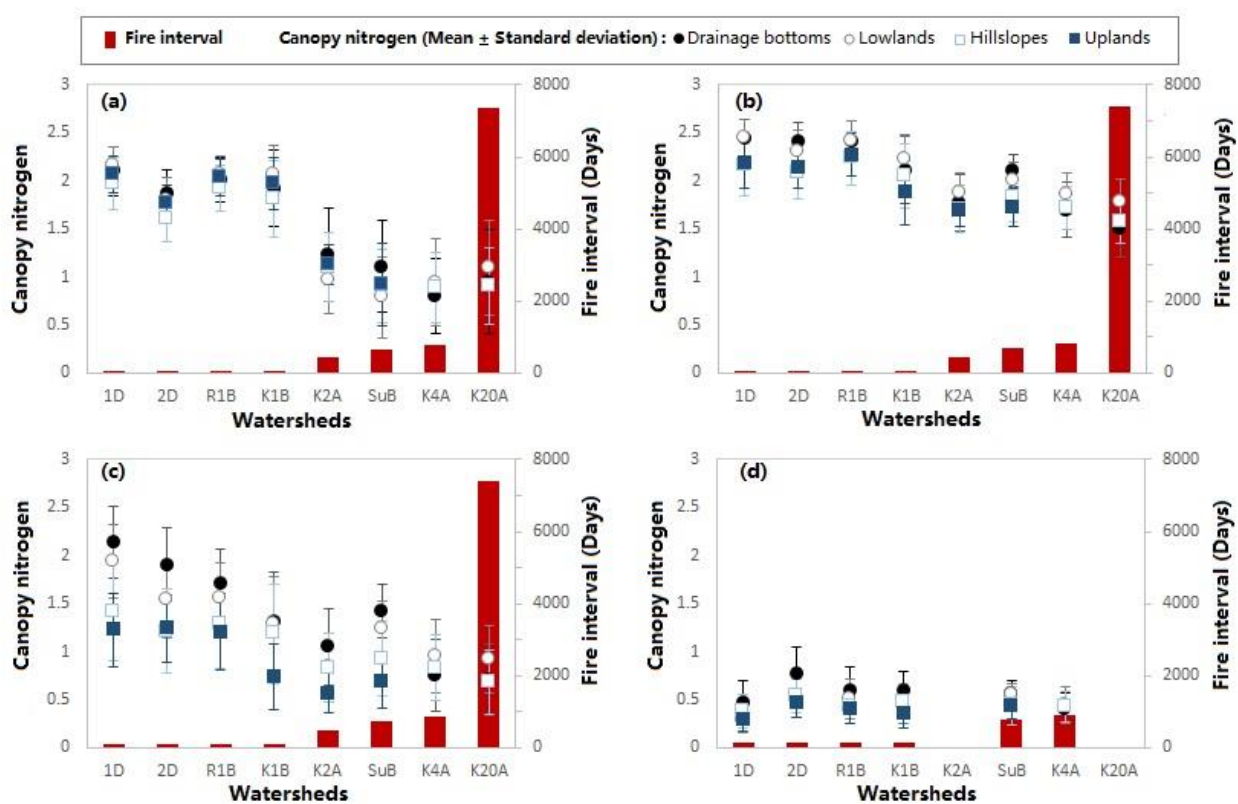
Figure 4.5 The mean of canopy nitrogen contents varying with the fire intervals over the ungrazed areas in (a) May, (b) June, (c) August, and (d) September. Watersheds 1D, 2D, R1B and K1B were burnt within one year; watersheds K2A, SuB, K4A and K20A had fire intervals greater than one year. In September, watersheds K2A and K20A were not included in analysis, given that the two watersheds were burnt shortly before the flyover, resulting in a fire interval of only one week.

Results of ANOVA showed that the interactive effects were seldom present between the fire interval and topography (Table 4.2). The two sample t-test examined the difference between burned (fire intervals within one year) and unburned (fire intervals greater than one year) sites from the perspectives of mean and standard deviation of canopy nitrogen, contagion and diversity of canopy nitrogen patches, and proportion and interspersion of high-nitrogen patches (Figure 4.6). Results showed that during May – August the canopy nitrogen contents were significantly higher in the burned areas, coincident with greater proportions of the high-nitrogen patches that were unevenly distributed and less interspersed. In September, differences between burned and unburned sites in the mean of canopy nitrogen and high-nitrogen distribution were insignificant.

The standard deviation was significantly lower in the burned areas than the unburned areas in May, which indicated relatively uniform canopies shortly after the fire treatments. The difference in canopy nitrogen standard deviation between burned and unburned sites became insignificant as the canopy was more developed in June. It is interesting that in August – September, the canopy nitrogen standard deviation in burned areas became significantly higher than in unburned areas. This suggested that fire enhanced the variance in canopy nitrogen at a later stage of growing season.

Differences in contagion and diversity between burned and unburned sites were statistically significant in May – June. The burned sites had higher contagion and lower diversity than the unburned sites. This indicated that fire effects resulted in more aggregation and uneven proportion distribution of canopy patch types in the early growing season.

Table 4.2 Analysis of variance *F* statistics for the canopy nitrogen properties responding to the interaction of the fire interval and topography.

Properties	May	June	August	September
Mean	0.9131	0.5701	0.8969	1.0099
Standard deviation	2.0911	1.6487	1.2974	3.0364
Contagion	1.2928	3.6203 †*	-	1.0384
Diversity	1.4088	3.347	2.5088	1.8052
% High N patches	0.9942	0.5250 †	0.6404 †	1.0991
IJI	1.7855	0.2572	0.5801	0.5700

Significant level: *** = 0.001, ** = 0.01, * = 0.05;

† : the responsive variables were logarithmically transformed to correct the problem of non-normality or heteroscedasticity;

- : the data violated the assumptions of normality or homoscedasticity.

One-way ANOVA across various topographic positions showed that during May – August differences in canopy nitrogen were not statistically significant, whereas significant differences in the mean of canopy nitrogen contents and the interspersion/juxtaposition index of the high-nitrogen patches were present in September (Figure 4.7). Tukey's honest significant difference (HSD) post-hoc test for the data in September showed that the mean of canopy nitrogen contents in the drainage bottoms was significantly higher than in the uplands (difference = 0.177, p-adj = 0.023); the interspersion/juxtaposition index of the high-nitrogen patches in the drainage bottoms was significantly lower than in the uplands and hillslopes (difference between drainage bottoms and uplands = -30.789, p-adj = 0.042; difference between drainage bottoms and hillslopes = -31.166, p-adj = 0.029). This suggested that the influences from the topography pattern on the vegetation canopies were more evident in the senescent season, but less so in the

growing season. The timing of senescence in the drainage bottoms was potentially later than that

in the uplands due to the different conditions of soil moisture, depth and temperature.
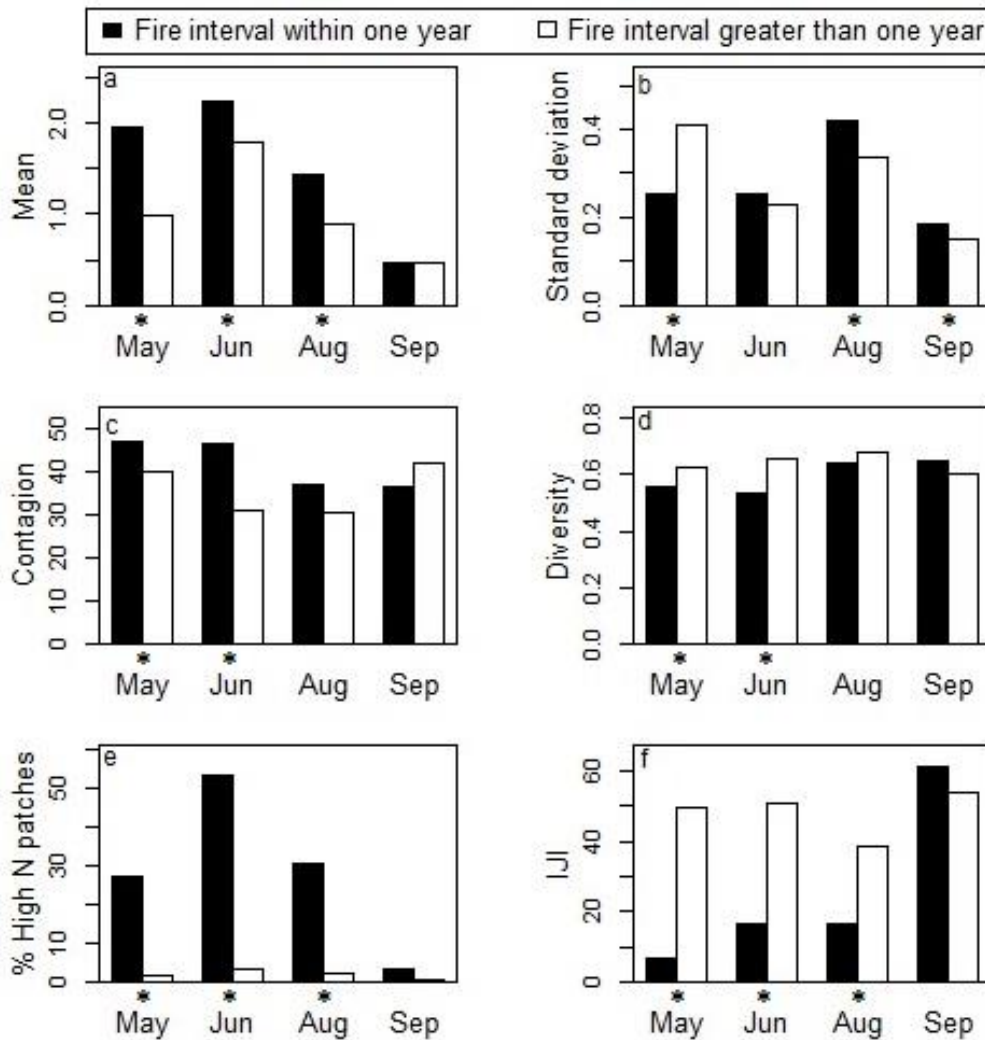
Figure 4.6 Two sample t-test for comparing difference between sites with fire intervals within one year and greater than one year from perspectives of (a) the mean of nitrogen contents, (b) standard deviation, (c) contagion, (d) Simpson's diversity index, (e) percentage of high-nitrogen patches and (f) interspersion/juxtaposition index (IJI) of the high-nitrogen patches (*= the difference is statistically significant at the 95% confidence level).
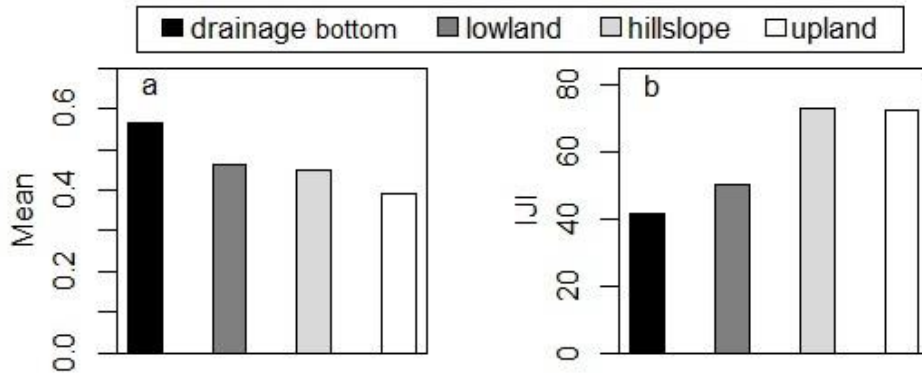
Figure 4.7 Statistically significant differences in (a) the mean of canopy nitrogen contents and (b) IJI of the high-nitrogen patches among various topographic positions in September.

4.3.2 Interactive Effects of Fire and Large Herbivores

Factorial ANOVA examines the significance of the main effects and their interaction term. If the interaction term is significant, the main effects cannot explain the influence on the dependent variable collectively. Results from ANOVA showed that the interactive effects of fire and grazing on the mean of canopy nitrogen contents and the interspersion/juxtaposition indices of the high-nitrogen patches were present in all three types of topographic positions during May – August. In September, the interactive effects were seldom present (Table 4.3).

The post-hoc analysis (Figure 4.8) showed that during May – August the grazed areas had generally lower canopy nitrogen contents and higher interspersion/juxtaposition indices of the high-nitrogen patches than the ungrazed areas when the fire intervals were within one year. In September, it was the opposite way that lower nitrogen contents and higher IJI were observed in the ungrazed areas. When the fire intervals were greater than one year, the differences between grazed and ungrazed areas were almost insignificant during June – September; however, at the beginning of the growing season in May, the grazed areas had generally higher nitrogen contents and lower IJI than the ungrazed areas. The insignificant difference in canopy nitrogen

between grazed and ungrazed sites with fire intervals greater than one year suggested a less

influential effect of grazing disturbance.

Table 4.3 Analysis of variance *F* statistics for the canopy nitrogen properties responding to the interaction of the fire interval and grazing type.

	Mean	Standard deviation	Contagion	Diversity	% High N patches	IJI
May						
Drainage bottom	12.08 **	2.66	0.26	0.94	3.79	6.84 *
Lowland	31.68 ***	5.85 *	0.51	0.56	10.13 **	37.69 ***
Hillslope	13.14 **	0.05	1.61	0.93	5.67 *	10.58 **
June						
Drainage bottom	15.55 **	0.89	14.01 **	10.59 **	41.66 ***	26.49 ***
Lowland	32.23 ***	1.22	29.01 † **	-	65.16 ***	17.63 ***
Hillslope	29.24 ***	0.78	2.05	0.42	13.77 † **	19.59 ***
August						
Drainage bottom	9.98 **	0.66	0.03	-	3.11	28.15 ***
Lowland	15.09 **	0.06	2.66	1.25	15.82 ***	20.50 ***
Hillslope	16.82 ***	4.94 *	2.60	2.62	10.65 **	13.70 **
September						
Drainage bottom	0.49	0.95 †	14.06 **	7.03 *	1.85	0.83 †
Lowland	2.28	0.26	0.00	-	1.43	0.40
Hillslope	1.19	5.93 † *	2.25	7.24 *	1.78	1.75

The uplands were not included in analysis given the insufficient non-grazing treatments with fire intervals greater than one year;
Significant level: *** = 0.001, ** = 0.01, * = 0.05;
† : the responsive variables were logarithmically transformed to correct the problem of non-normality or heteroscedasticity;
- : the data violated the assumptions of normality or homoscedasticity.
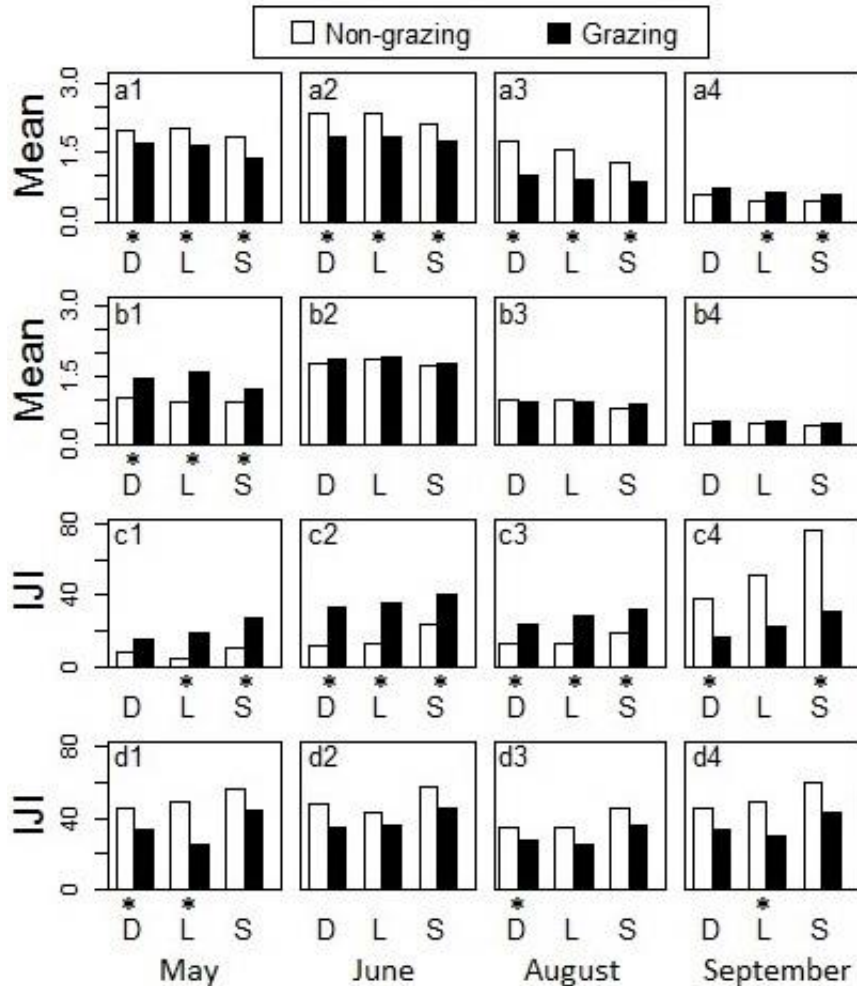
Figure 4.8 Differences in the mean of canopy nitrogen contents and the interspersion/juxtaposition indices of the high-nitrogen patches between non-grazing and grazing treatments. $a_1 - a_4$, the mean of canopy nitrogen contents in the areas burnt within one year; $b_1 - b_4$, the mean of canopy nitrogen contents with the fire intervals greater than one year; $c_1 - c_4$, IJI in the areas burnt within one year; $d_1 - d_4$, IJI with the fire intervals greater than one year. D=drainage bottom, L=lowland, S=hillslope. *= the difference was statistically significant at the 95% confidence level.

In the areas burnt within one year, where the grassland canopies were supposed to be more evidently influenced by grazing disturbances, the canopy nitrogen properties with the bison and cattle grazing were compared (Figure 4.9). In May, the bison-grazed areas had significantly lower mean of canopy nitrogen contents, coincident with generally higher IJI than the cattle grazed areas, whereas the cattle grazed areas were not significantly different from the ungrazed

areas. During June – August, the differences between bison and cattle grazing were insignificant overall except in the uplands, where the cattle had less evident influence on the grassland canopy than bison. In September, there was no significant difference detected.
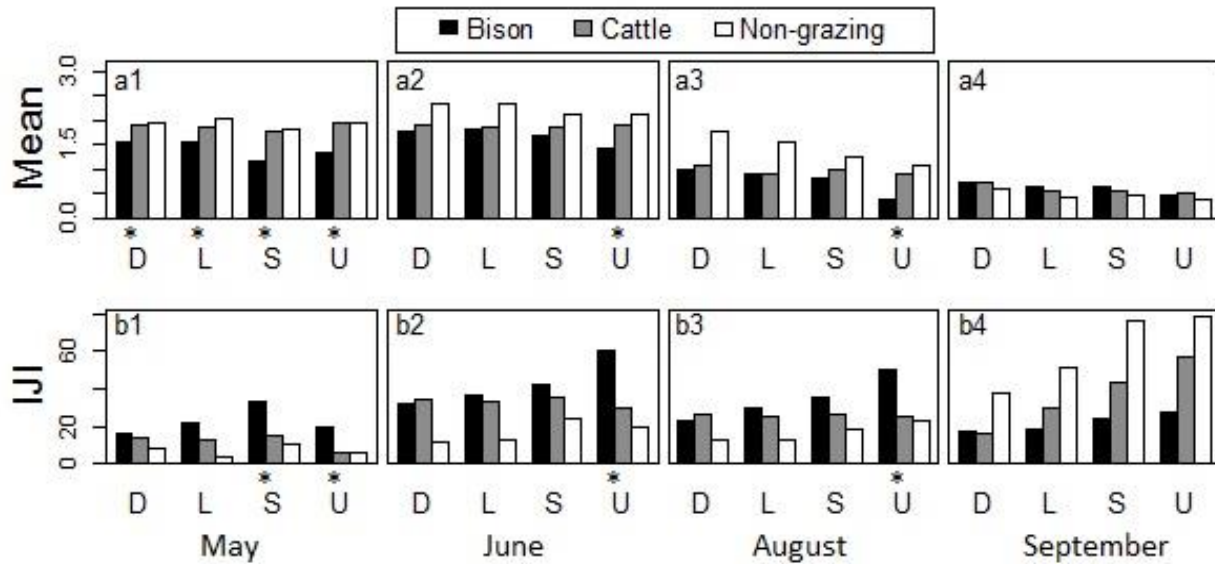
Figure 4.9 Comparison of grazing effects from bison and cattle on the canopy nitrogen across different topographic positions with fire intervals within one year. D=drainage bottom, L=lowland, S=hillslope, U=upland. *= the difference between bison and cattle grazed areas was statistically significant at the 95% confidence level.

4.3.3 Spatial Structure of Canopy Nitrogen Distribution

Results from the variogram analysis (Figure 4.10) revealed distinctive spatial structures of the canopy nitrogen across seasons. The average level of the sills reached to the highest in August, and dropped to the lowest in September. This fluctuation of the canopy nitrogen variance can be explained associated with the grassland phenology (Collins and Wallace 1990).

The differences in the variograms across topographic positions were noticeable. The sills were typically high in the hillslopes and low in the uplands. The ranges were generally greater in the lowlands than at other sites. Thus, there was a steeper, faster rising shape of the variograms for the hillslopes, whereas the variogram curves for the lowlands were gently rising at a longer

distance before leveling off. This suggested a greater contrast in the canopy nitrogen and a smaller patch size at the hillslope sites than at the lowland sites. The disparity in terms of different fire-grazing treatments was most evident at the lowland sites in May (Figure 4.10a$_2$), where the sill and range were generally greater when the fire intervals were longer than one year.

For the lowlands and uplands burnt within one year, the variograms were approximated using the spherical model (Woodcock et al. 1988), through which the nugget, sill and range were determined (Table 4.4). The sills and variance proportions were noticeably high for the bison-grazing treatments across seasons. This indicated that bison grazing created a more heterogeneous canopy, leading to greater canopy nitrogen variance than the cattle.

The sills and variance proportions for the cattle-grazed areas were slightly greater than that for the ungrazed areas in May. During June – August, the lowlands with cattle-grazing had lower sills and variance proportions than the ungrazed lowlands. However, in the uplands, the cattle grazed sites had higher sills and variance proportions than the ungrazed sites. In September, the difference between cattle-grazing and non-grazing was more evident in lowland than in uplands. The special patterns between lowlands and uplands across seasons may be related with cattle habitat selection. However, further explanations required more finely resolved information of cattle grazing density, movement pattern and space use.

In the growing season, from May to August, the ranges for the lowlands were generally greater than that for the uplands. During June – August, the ranges for the grazed sites were generally lower than that for the ungrazed sites. It can be implied that the factors of topography and ungulate grazing both had evident effects on the vegetation patch size.
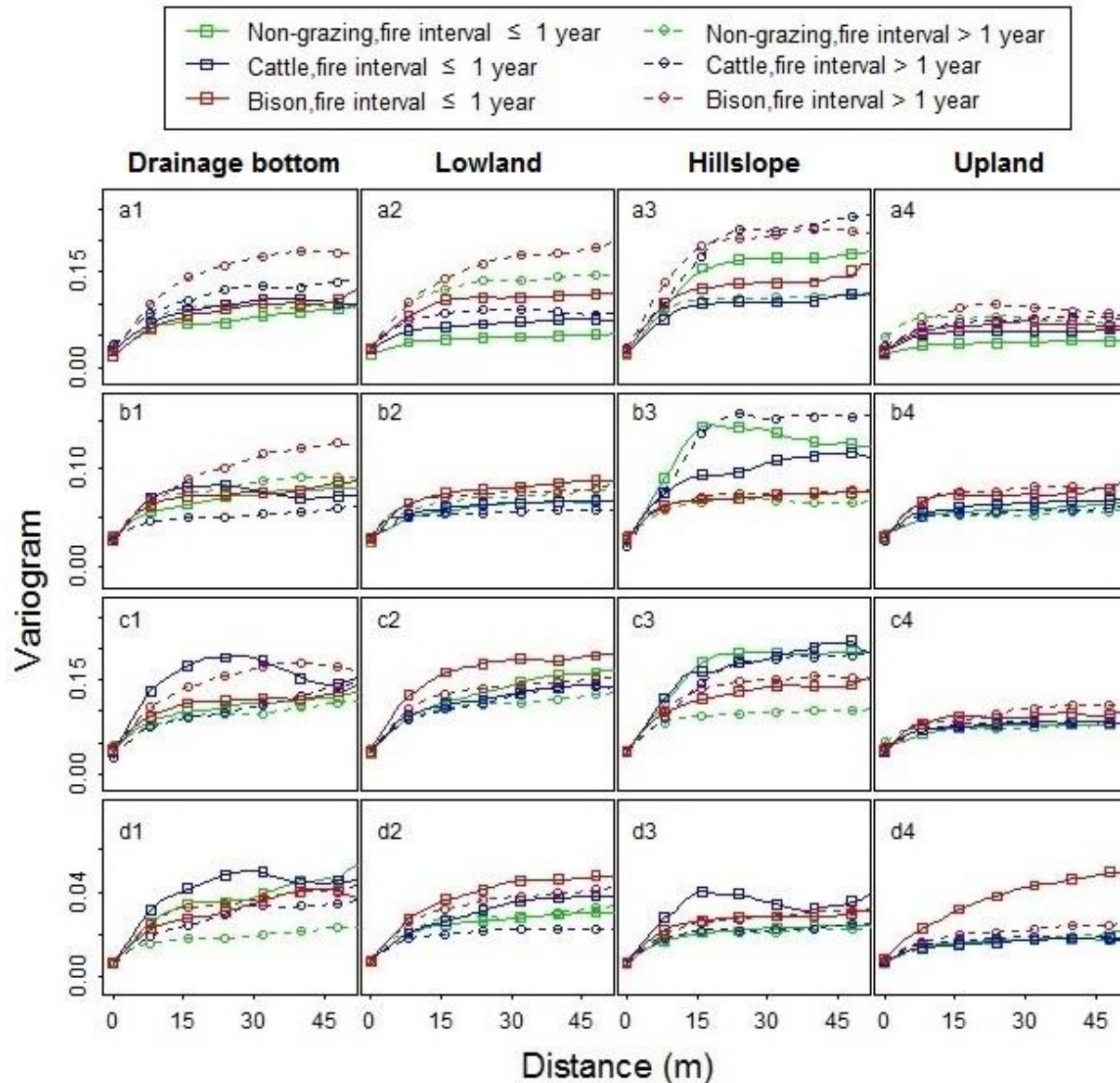
Figure 4.10 Variogram analysis for the spatial patterns of canopy nitrogen with a variety of fire-grazing treatments across different topographic positions over the growing season. The four columns of the plots from the left to right were corresponding to the drainage bottoms, lowlands, hillslopes and uplands, respectively. The four rows from the top to bottom were for May, June, August, and September, respectively.

Table 4.4 Variogram analysis of the canopy nitrogen in lowlands and uplands burnt within one year, where the effects of non-grazing, cattle and bison on the spatial structures of canopy nitrogen were compared.

Month	Topography	Treatment	Model	Nugget	Sill	Range	Proportion
May	Lowland	Non-grazing	$2\gamma(h) = \frac{7h}{3000}\left(1 - \frac{h^2}{972}\right) + 0.019$	0.019	0.047	18	0.591
		Cattle	$2\gamma(h) = \frac{43h}{40000}\left(3 - \frac{h^2}{400}\right) + 0.028$	0.028	0.071	20	0.609
		Bison	$2\gamma(h) = \frac{79h}{14000}\left(1 - \frac{h^2}{1323}\right) + 0.031$	0.031	0.110	21	0.720
	Upland	Non-grazing	$2\gamma(h) = \frac{19h}{32000}\left(3 - \frac{h^2}{256}\right) + 0.020$	0.020	0.039	16	0.472
		Cattle	$2\gamma(h) = \frac{17h}{16000}\left(3 - \frac{h^2}{256}\right) + 0.024$	0.024	0.058	16	0.583
		Bison	$2\gamma(h) = \frac{19h}{16000}\left(3 - \frac{h^2}{256}\right) + 0.026$	0.026	0.064	16	0.592
June	Lowland	Non-grazing	$2\gamma(h) = \frac{h}{1100}\left(3 - \frac{h^2}{484}\right) + 0.026$	0.026	0.066	22	0.611
		Cattle	$2\gamma(h) = \frac{9h}{10000}\left(3 - \frac{h^2}{400}\right) + 0.028$	0.028	0.064	20	0.567
		Bison	$2\gamma(h) = \frac{51h}{32000}\left(3 - \frac{h^2}{256}\right) + 0.028$	0.028	0.079	16	0.642
	Upland	Non-grazing	$2\gamma(h) = \frac{7h}{2500}\left(1 - \frac{h^2}{675}\right) + 0.029$	0.029	0.057	15	0.495
		Cattle	$2\gamma(h) = \frac{33h}{28000}\left(3 - \frac{h^2}{196}\right) + 0.031$	0.031	0.064	14	0.510
		Bison	$2\gamma(h) = \frac{11h}{7000}\left(3 - \frac{h^2}{196}\right) + 0.030$	0.030	0.074	14	0.594
August	Lowland	Non-grazing	$2\gamma(h) = \frac{31h}{20000}\left(3 - \frac{h^2}{1600}\right) + 0.033$	0.033	0.157	40	0.789
		Cattle	$2\gamma(h) = \frac{13h}{8500}\left(3 - \frac{h^2}{1156}\right) + 0.035$	0.035	0.139	34	0.748
		Bison	$2\gamma(h) = \frac{73h}{22000}\left(3 - \frac{h^2}{484}\right) + 0.036$	0.036	0.182	22	0.802
	Upland	Non-grazing	$2\gamma(h) = \frac{13h}{12000}\left(3 - \frac{h^2}{324}\right) + 0.038$	0.038	0.077	18	0.499
		Cattle	$2\gamma(h) = \frac{23h}{14000}\left(3 - \frac{h^2}{196}\right) + 0.035$	0.035	0.081	14	0.569
		Bison	$2\gamma(h) = \frac{27h}{14000}\left(3 - \frac{h^2}{196}\right) + 0.037$	0.037	0.091	14	0.592
September	Lowland	Non-grazing	$2\gamma(h) = \frac{h}{2000}\left(3 - \frac{h^2}{484}\right) + 0.008$	0.008	0.030	22	0.733
		Cattle	$2\gamma(h) = \frac{3h}{6400}\left(3 - \frac{h^2}{1024}\right) + 0.007$	0.007	0.037	32	0.802
		Bison	$2\gamma(h) = \frac{39h}{56000}\left(3 - \frac{h^2}{784}\right) + 0.007$	0.007	0.046	28	0.841
	Upland	Non-grazing	$2\gamma(h) = \frac{11h}{40000}\left(3 - \frac{h^2}{400}\right) + 0.007$	0.007	0.018	20	0.616
		Cattle	$2\gamma(h) = \frac{11h}{38000}\left(3 - \frac{h^2}{361}\right) + 0.007$	0.007	0.018	19	0.601
		Bison	$2\gamma(h) = \frac{41h}{96000}\left(3 - \frac{h^2}{2304}\right) + 0.009$	0.009	0.050	48	0.817

$2\gamma(h)$ is the variogram; h is the separation distance; Proportion = (Sill - Nugget)/Sill.

4.4 Discussion

4.4.1 Fire, Grazing and Vegetation Canopy

Fire has an immediate effect on the species composition in the canopy, which decreases the species diversity dramatically. The stimulus of spring fires on the vegetation productivity is most influential within the first year following the burn, and in decay shortly thereafter as the species diversity increases and the system approaches an equilibrium (Collins 1990; Loucks 1970). In this study, I observed that during May – August when the canopies were photosynthetically active, the watersheds with short fire intervals within one year had apparently high canopy nitrogen contents and large proportion of high-nitrogen patches. Meanwhile, the significantly higher contagion indices and lower diversity indices at the sites with shorter fire intervals during May – June suggested that canopy patches were more aggregated with uneven proportional distributions in the more recently burned grasslands.

Results of this study showed that the interactive effects of fire and ungulate grazing on canopy nitrogen were present during May – August, but not in September, suggesting that the grazing effects on the vegetation canopy were dependent upon the fire interval and varied across seasons. This was consistent with the pyric herbivory observed repeatedly in previous studies that during the growing season ungulate grazers prefer areas burned in the spring of the current year (Allred et al. 2011a; Fuhlendorf et al. 2009), whereas in the dormant season their grazing is more evenly distributed and may shift to the unburned areas (Raynor 2015).

In the cases of fire intervals within one year, the canopy nitrogen at the ungrazed sites was found to be significantly high in May – August, but low in September, compared to that at the grazed sites. The contrast between the growing season and the dormant season suggested that the effects of ungulate grazing on the vegetation canopy varied across seasons. In the cases of

fire intervals greater than one year, it was interesting that the grazed sites had significantly higher canopy nitrogen than the ungrazed sites in May, contrary to the situation with shorter fire intervals. This suggested that in the early growing season the higher grazing intensity at sites with shorter fire intervals reduced the canopy density, whereas the low level of grazing disturbances at sites with longer fire intervals improved the vegetation production (McNaughton 1983; McNaughton et al. 1997). During June – September, the differences between ungulate grazing and non-grazing were insignificant, suggesting that at this time the grazing disturbances became less influential on the canopy nitrogen distribution at sites with the longer fire intervals.

It is of interest to compare the grazing effects of bison and cattle in grassland ecology. Previous studies reveal that bison differ from cattle in their selections of forage species and grazing sites (Knapp et al. 1999). For example, bison prefer graminoids exclusively, whereas cattle have a greater proportion of forbs in their diets. Woody species, which usually occur in the drainage bottoms, are avoided by bison, but preferentially selected by cattle (Allred et al. 2011b). The distinctive forage strategies and physical activities between bison and cattle may result in different canopy structure and species composition in the plant communities.

In my study, the differences between bison and cattle in their effects on the canopy nitrogen were analyzed at sites with shorter fire intervals, where the ungulate grazing effects were supposed to be more evident. It was found that the sites with bison had lower canopy nitrogen contents and more interspersed high-nitrogen patches than sites with cattle in May across a variety of topographic positions. This overall difference in the canopy nitrogen properties may be explained by the ungulate density and grazing intensity (Afzal and Adams 1992; Augustine and Frank 2001) in addition to the distinctive forage behaviors between bison and cattle. During June – August, differences in the grazing effects between bison and cattle

were generally insignificant, except in the uplands where the canopy with cattle was significantly different from that with bison, but similar to that without ungulates. It can be inferred that the uplands were less disturbed by cattle, indicating differences between the two ungulate species in their preferences for habitats related to the topography factor.

4.4.2 Use of Remote Sensing Imagery

It has been widely recognized that remote sensing imagery with multi- or hyper-spectral data has advantages over traditional methods of mapping specific land surface characteristics for a large spatial extent. Traditional methods require a large number of field samples, which are labor-intensive and time-consuming. The spatial interpolation schemes are then used to estimate values between the sampled points and fill the gaps over the whole study area. However, the interpolation schemes may themselves be a source of error. Unlike traditional methods, remote sensing imagers can capture the spectral data over an extensive area efficiently. Related spectral features can be extracted and used to map the land surface characteristics of interest from the remotely sensed spectral image. The detailed spatial variability in reality is therefore well retrieved.

Remote sensing imagery provides quantitative and continuous measurements across the land surface. The basic statistics are allowed to be calculated from the image for different, specifically defined zones, such as the mean and standard deviation of the canopy nitrogen with various fire-grazing treatments in this study. More importantly, the image with the exhaustive data that vary continuously over the landscape permits analysis of spatial autocorrelation using geostatistical techniques. The variogram analysis of this study showed comparisons between bison and cattle from the perspective of their grazing effects on the spatial structure of canopy nitrogen. It was noted that in the lowlands and uplands with shorter fire intervals, the bison

grazed sites had evidently high sills and variance proportions across seasons, compared to the ungrazed or cattle-grazed sites. This was consistent with the comparisons in the interspersion of the high-nitrogen patches, indicating that the differences between bison and cattle in their grazing intensity, forage strategy and site selection may be important factors accounting for canopy heterogeneity across different topography positions in a seasonally variable environment.

The results from the remotely sensed imagery in my study were partly in agreement with the findings by Augustine and Frank (2001) from the field measurements that the influences of grazers on the plant communities were associated with the topography gradient at a coarse scale of 5 – 30 m. Their study also showed that the grazers promoted the spatial heterogeneity at a fine scale (0.1 – 2 m) through altering the vegetation canopy and diversifying the plant species. Unfortunately, in my study, analysis of spatial heterogeneity at a finer scale was limited by a 2 m spatial resolution of the remote sensor. On the remote sensing image, the details for the vegetation canopy within a 2 m × 2 m square were generalized, while the grassland plant species within a signal square meter can be of great diversity. This made the field measurements important and indispensable to the fine-scale analysis.

In addition to the surface pattern analysis based on the continuous data, the numeric images can be converted to categorical maps by classifying the canopy nitrogen into five levels from low to high, through which the high nitrogen patches were located readily in the whole study area. The spatial distribution of the patches with high forage quality or quantity is of special interest in grassland science. In a previous study, the field measurements by Wallace et al. (1995) showed that the high biomass points were almost following a random distribution at both the burned and unburned sites. In my study, the spatial distribution of the high nitrogen patches was measured by the interspersion/juxtaposition index. Results revealed differences in

forage distribution associated with the fire and grazing factors. During the growing season, the high nitrogen patches were less interspersed in the areas burnt within one year than that with longer fire intervals. In the cases of fire intervals within one year, the high nitrogen patches were more interspersed in the grazed areas than in the ungrazed areas.

4.5 Conclusions

My study analyzed the variation of canopy nitrogen in relation to factors of fire, ungulate grazing, topography and phenology. These factors collectively resulted in complex, variable vegetation covers. The separate effects of fire and the fire effects interacting with ungulates on grassland canopies have been studied repeatedly. Results of this study, consistent with those from previous studies (Collins and Wallace 1990; Loucks 1970), showed that fires greatly stimulated the plant productivity in the first year following the burn, resulting in the relatively uniform vegetation canopy. The interactive effects of fire and ungulates were most predominant in the areas with shorter fire intervals, where the spatial heterogeneity in the grazed canopy was great. Furthermore, the ungulate grazing effects varied with topographic positions and grazer species. The difference in vegetation spatial variability observed between lowlands and uplands grazed by bison and cattle extended the previous study of comparing the two herbivore species in Great Plains (Allred et al. 2011b). However, the comparison of bison and cattle in this study was at the watershed level, a relatively coarse scale. To dig deeper into details for difference in effects between the two grazer species on vegetation spatial heterogeneity, the grazing intensity at a finer spatial scale should be taken into account. This study, based on analysis from hyperspectral images, provided understanding of the grassland processes at a large spatial extent, which was expected to be meaningful as a baseline study for further modeling the grassland

dynamics involving interplay between vegetation variability, nutrition cycling and ungulate

grazing behavior.

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Chapter 5 - Investigating Interactions between Bison Forage and Vegetation Heterogeneity: the Use of Remote Sensing Imagery and GPS Relocations

Abstract

This study investigated interactive processes among fire, vegetation and bison forage in a tallgrass prairie topography. Vegetation canopy nitrogen distribution and bison locations were acquired using hyperspectral remote sensing and GPS techniques, respectively. Bison movement pattern was calculated from the GPS locations using a method of biased random bridge movement-based kernel density estimation. The resulting bison utilization distribution maps were linked with factors of fire, topography and canopy nitrogen characteristics, through which bison resource selection and vegetation responses to bison forage were studied. In bison habitat selection, fire is a watershed-level factor that plays a predominant role in affecting bison distribution. Bison preference for burned watersheds was found evident across seasons, which was especially strong during the early growing season in May. At a later stage in June – September, the use of unburned areas was continuously increasing. Topography is a landscape-level factor in bison resource selection. Bison avoided steep slopes and drainage bottoms. Lowlands were especially preferred in May – June, whereas the use of uplands was increased in August – September. Vegetation characteristics in canopy nitrogen are factors that affect bison resource selection at a finer scale. Results showed that bison preference for high canopy nitrogen patches was evident in May. Later in June – September, bison tended to avoid high-nitrogen sites. Vegetation heterogeneity showed significant influences on bison habitat selection in June. At this point of time, bison preferred sites with low variance in canopy nitrogen, where the patch

types were highly aggregated and equitably proportioned. As for vegetation responses to bison grazing, the proportion and spatial distribution of high-nitrogen patches showed different patterns between sites with high and low levels of space use by bison. A high level of herbivory was observed to reduce vegetation density and increase the evenness of high-nitrogen spatial distribution after the fire treatment initiated in May.

5.1 Introduction

Analysis of movement patterns is fundamental to understanding herbivore foraging strategy, which is important for improving management of grassland ecosystems (Coppedge and Shaw 1998; Senft et al. 1985). A traditional method for modeling the animal's movement pattern is to estimate the home range (Burt 1943; Jennrich and Turner 1969), where the animal moves during its everyday activities. The home range can be calculated simply by a minimum convex polygon that completely encloses the relocations of the animal (List and Macdonald 2003). This method has been improved by a more formal model: the utilization distribution (UD). The UD is defined as a probability density of the animal's relative occurrence frequency in a two-dimensional space (van Winkle 1975). The kernel method is commonly used in UD estimation (Calenge 2006; Worton 1989).

The classic kernel method estimates the UD statically, assuming that all the relocations are unlinked. More recently, spatial location of foraging animals can be tracked at a high temporal resolution using GPS devices. This activates the interest of developing a dynamic approach to estimating UD that takes into account the time dependence between successive relocations of the animal (Benhamou and Cornélis 2010). Then the movement-based kernel density method is developed and improved from the classic kernel method, through which the

UD is modeled based on the movement trajectories of the animal (Benhamou 2011). This method has been proven reliable and usable in most of current studies on the animal movement ecology (Papworth et al. 2012).

The resulting UD estimation can be linked to a set of continuous or categorical resource variables for analysis of resource selection. The resource selection function (RSF) and resource utilization function (RUF) are commonly used methods for modeling animal resource selection (Hooten et al. 2013; Long et al. 2009). In the method of RSF, the response variable is usually defined arbitrarily using a binary variable which contrasts the used and unused locations in the habitat. Logistic regression is then used to relate the habitat variable with the resource variables (Anderson et al. 2005; Mace et al. 1996). A limitation of this method is that the definition of the used and unused locations may not be accurate. In the method of RUF, a continuous variable summarized by the UD estimation is used as the response variable, which is related to the resource variables through a multiple regression (Bartlam-Brooks et al. 2013; Kertson et al. 2011; Marzluff et al. 2004). Both methods can be used to predict the relative probability of space use, or compare the influences from different resources on space use by an animal. RUF is theoretically more advanced than RSF. However, a study by Long et al. (2009) reveals that RUF is feasible for modeling resource selection within a small home range, whereas RSF is more advisable for large herbivores with a relatively large home range.

Grazing patterns of bison associated with forage resources are of special interest in North American grassland science. Ungulate grazing, interacting with other factors such as fire and topography, plays an important role in determining vegetation heterogeneity. In turn, the spatial pattern of canopy vegetation characteristics largely determines the habitat suitability for foraging herbivores. Studies of interactions between bison forage and vegetation heterogeneity are

valuable for understanding of grassland functions and conservation of grassland ecosystems. Before the era of GPS and remote sensing, a possible challenge for studies of grazing animal behavior is that the time-consuming manual field measurements of bison distributions and vegetation characteristics may not synchronize. This mismatch may lead to inappropriate evaluations of the response of grazers to the vegetation resources (Coppedge and Shaw 1998). With the development of GPS and remote sensing techniques, animal distributions can be located precisely by GPS at a high temporal resolution, while simultaneously the vegetation characteristics are monitored at a larger spatial extent by remote sensors. This new context allows quantitative examinations of interactions between bison grazing and vegetation characteristics at multiple spatio-temporal scales.

The objective of this study is to evaluate bison resource selection and vegetation responses at a fine spatial-temporal scale (within watersheds, associated with the bison movement path). Forage patterns associated with factors at a coarse landscape scale, such as fire and topography, have been studied sufficiently (Allred et al. 2011; Fuhlendorf et al. 2009; Raynor 2015). A finer spatio-temporal scale analysis requires more finely resolved information on distributions of animal and vegetation resources. In this study, the bison locations recorded every 30 minutes by the GPS devices were used for UD estimation. The canopy nitrogen maps derived from hyperspectral remote sensing imagery with a 2 m spatial resolution (Ling et al. 2014) were used for characterization of vegetation resource and habitat heterogeneity. Then interactions among bison forage, vegetation heterogeneity and topography were examined across seasons.

5.2 Study Area

This study was conducted at Konza Prairie Biological Station (KPBS, Figure 5.1), a tallgrass prairie in the Flint Hills near Manhattan, Kansas, USA (39°05'N, 96°35'W). The site is divided into more than fifty watersheds, each with a treatment combined by fire and ungulate grazing. Fire frequencies range from one to twenty years. Grazing treatments include grazing by American Bison (*Bison bison*), domestic cattle (*Bos taurus*) and non-grazing. These watershed-level experiments allow long-term investigations into interactive processes among fire, large herbivores grazing, and grassland vegetation communities. There are ten watersheds fenced and grazed by bison. In this study, nine out of the ten bison grazed watersheds were included in the analysis. One of the watersheds was excluded due to insufficient image coverage (Figure 5.1).
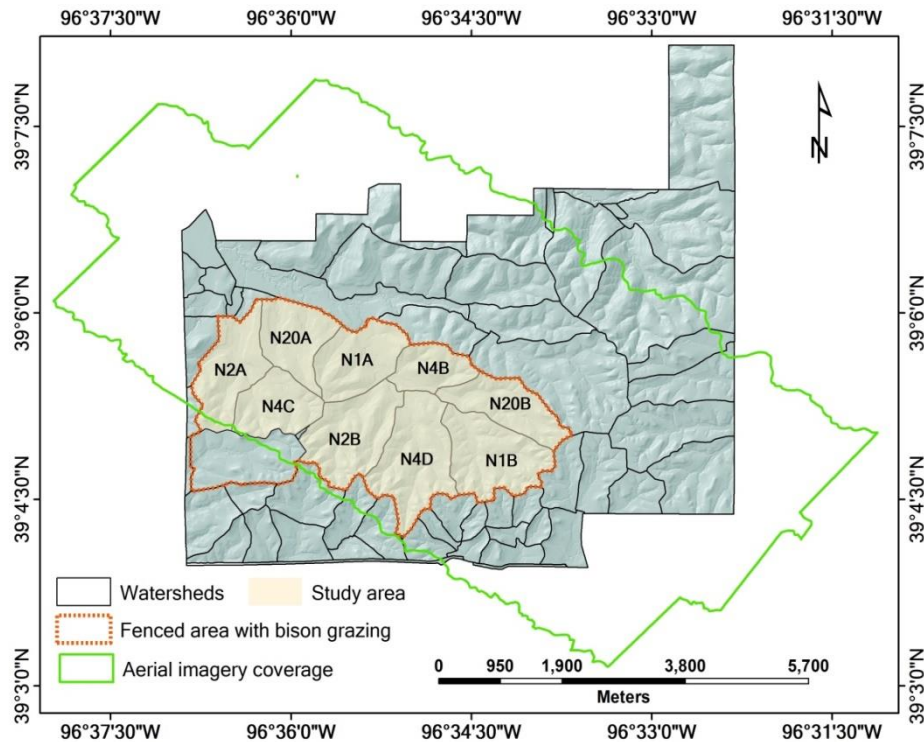
Figure 5.1 Study area at Konza Prairie Biological Station (KPBS). The site is divided into more than fifty watersheds with varying combinations of fire and grazing treatments. Nine out of the ten bison grazed watershed were included in analysis given the coverage of aerial imagery.

5.3 Methods

5.3.1 Data Collection

In this study, the bison live and move within the ten fenced watersheds (~1000 ha) at KPBS. The KPBS bison was established in 1987. The stocking rate is currently maintained at around 0.3 animals/ha. The sex ratio of mature females to mature males is around 4:1. Male bison are removed from the herd at the age of eight years old. Females may remain and stay in the herd until the age of fifteen.

Bison live in maternal herds; older females are more dominant in their herd. Fourteen older, matriarchal female bison in different herds were selected and collared with Telonics TGW-3700 GPS devices. Their spatiotemporal locations were recorded every 30 minutes in 2011. Each collared individual was followed by other $30 - 40$ members in the herd, and thus locations of the collared individuals were representative of presence of the entire herds at KPBS (Raynor 2015).

Hyperspectral imagery covering the study area was captured on four dates (26 May, 29 June, 2 August, and 26 September, 2011) using an AISA Eagle camera mounted on a Piper Warrior aircraft operated by the Center for Advanced Land Management Information Technology (CALMIT) of the University of Nebraska-Lincoln. The spatial resolution of the aerial imagery is 2 m $\times$ 2 m. Canopy nitrogen maps were derived from the aerial imagery using hyperspectral analysis (Ling et al. 2014). Fire history records and the digital elevation model (DEM) of the study area were provided by the NSF Long Term Ecological Research Program at KPBS (Figure 5.2).
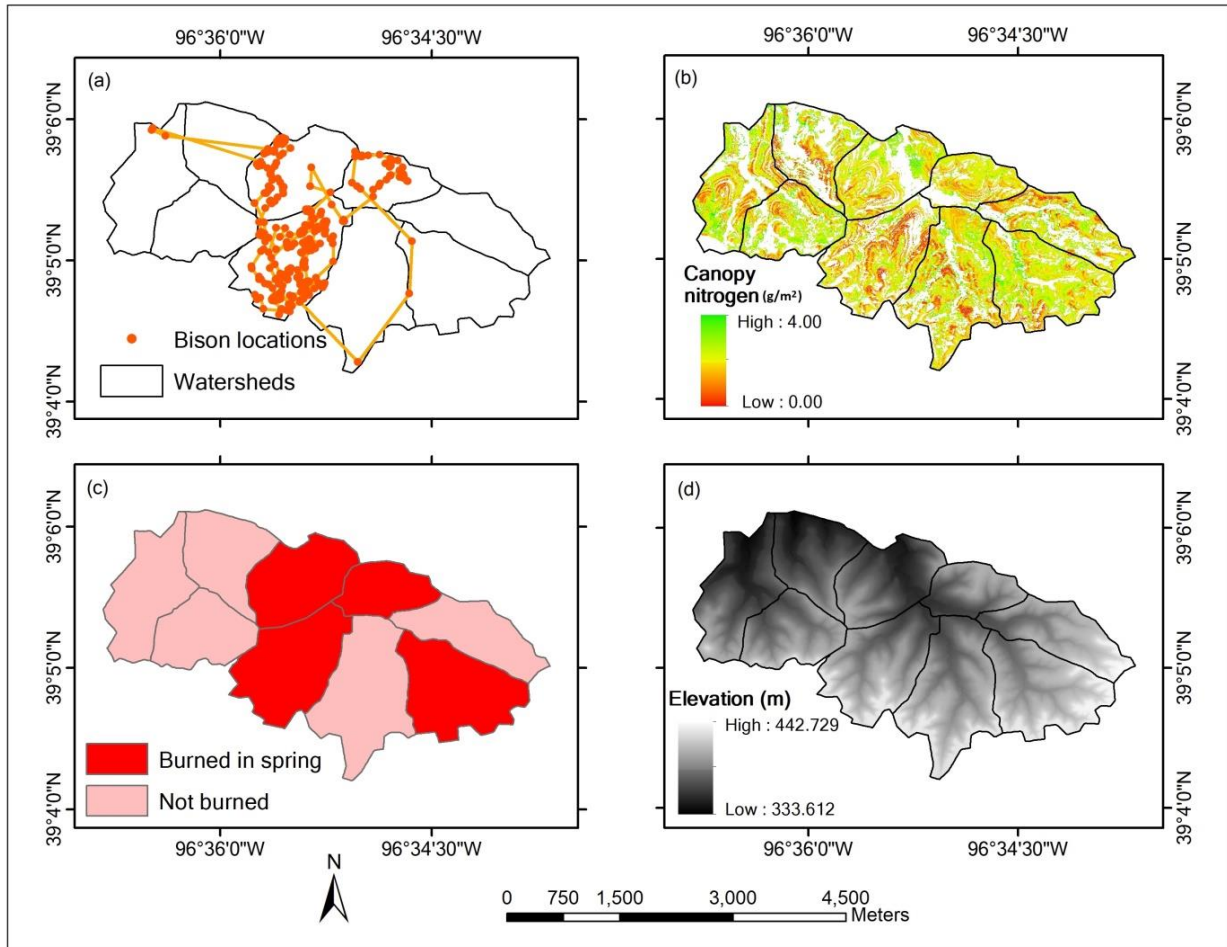
Figure 5.2 Data examples for analysis of interactions among (a) bison distribution (locations and movement trajectory of bison #026 during 27 May – 2 June, 2011), (b) vegetation heterogeneity (aerial imagery captured on 26 May, 2011), (c) fire history and (d) topography (DEM).

5.3.2 Data Analysis

5.3.2.1 Bison Forage and Habitat Selection

Bison locations recorded for a week after the aerial imagery capture were selected for UD estimations to study how the existing canopy nitrogen distribution attracted bison and influenced bison forage patterns. UD maps of bison individuals were calculated using a method of biased random bridge (BRB) movement-based kernel density estimation (Benhamou 2011). This method considers the animal movement path a succession of steps. A drift to change the strength

and direction from one step to the next is taken into account, which makes the BRB model

realistic in studies of animal movement (Calenge 2011).

The resulting UD maps with a spatial resolution of 10 m were then linked with factors

that may affect bison habitat selection. The factors analyzed in this study included fire,

topography, canopy nitrogen and vegetation heterogeneity. The kernel densities of space use by

bison in the burned and unburned areas were compared using a paired t-test. As for the

topography factor, there were four topography types defined in the study area, including drainage

bottoms, lowlands, uplands and hillslopes. Based on the DEM and the derived slope data of the

study area, the areas with slopes greater than 10° (determined by a natural break) were classified

as hillslopes. The lower flat areas (slope ≤ 10°) near to the gallery forest were classified as

drainage bottoms. The higher flat areas were classified as uplands. The intermediate flat areas

between drainage bottoms and uplands were classified as lowlands (Figure 5.3). The bison space

use in different topography positions were compared using one-way analysis of variance

(ANOVA).
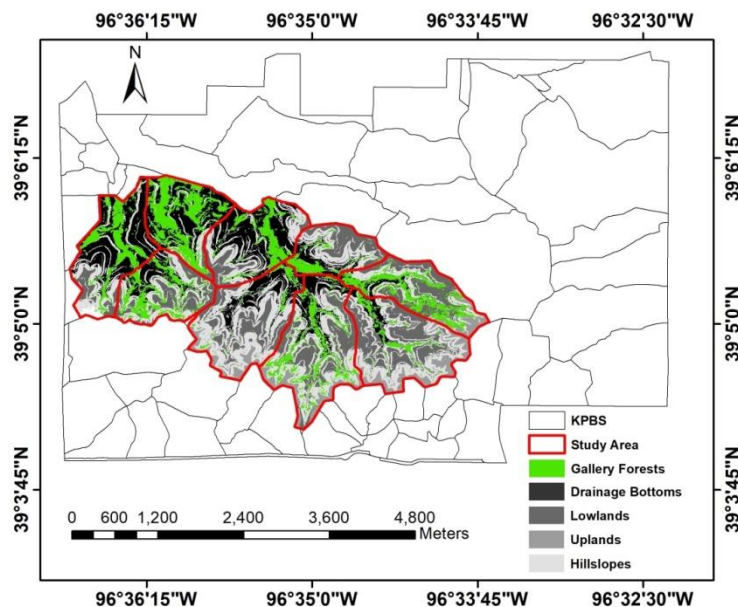
Figure 5.3 Topography divisions based on the DEM in the study area

At a finer scale (within watersheds, associated with the bison movement path and space use), factors that may affect bison habitat selection, including slope, elevation, canopy nitrogen and vegetation heterogeneity, were studied. Vegetation heterogeneity was measured by the standard deviation, contagion and Simpson's diversity (SIDI) of canopy nitrogen. In this part of analysis, the unburned watersheds were excluded to reduce the difference in vegetation characteristics caused by the fire influence. In addition, the drainage bottoms which were severely encroached by gallery forests were excluded in analysis.

Bison space use and topography factors (slope and elevation) were sampled for each individual every 30 meters along the movement trajectory. Vegetation characteristics were determined in a circular area with a diameter of 30 meters centered at each sample point, where the mean, standard deviation (SD), contagion (Contag) and SIDI of canopy nitrogen (N_{can}) were calculated. The mean and standard deviation of canopy nitrogen were determined in the continuous maps. The contagion and SIDI were calculated in the categorical maps using the FRAGSTATS program (McGarigal and Marks 1995; Simpson 1949).The categorical maps were determined by classifying the continuous canopy nitrogen values into five classes from low to high levels using natural breaks. Bison space use was linked with habitat selection influential factors using a logistic regression model in the method of RSF:

$$y = \frac{1}{1 + e^{-(\beta_0 + \beta_1 \times Slope + \beta_2 \times Elevation + \beta_3 \times N_{can} + + \beta_4 \times SD + + \beta_5 \times Contag + \beta_6 \times SIDI + \varepsilon)}} \qquad (5.1)$$

where *y* is a binary variable indicating the site use status; *e* denotes the exponential function; β_0 is the intercept; β_1, β_2, β_3, β_4, β_5 and β_6 are the regression coefficients for slope, elevation, and mean, standard deviation, contagion, SIDI of canopy nitrogen, respectively; ε is an error in the regression model. Results from RSF were compared with those from a multivariate regression model of the RSF method:

$$y = \beta_0 + \beta_1 \times Slope + \beta_2 \times Elevation + \beta_3 \times N_{can} + \beta_4 \times SD + \beta_5 \times Contag + \beta_6 \times SIDI + \varepsilon \qquad (5.2)$$

where y is a continuous variable denoting kernel density of space use by bison. In RSF and RUF, negative coefficients indicate that the corresponding predictive factors are avoided by bison. Positive coefficient indicates a preference for the given predictive factor. To compare the relative importance of the predictive factors, the regression analysis needs to be standardized; that is, the variances of dependent and predictive variables are 1. The absolute value of the standardized coefficient indicates its relative importance in resource selection.

In the method of RSF, the individual UD estimation was classified into five levels from low to high using a natural break. The sample point located in the areas with low to intermediate low levels of bison space use was defined as an unselected site, and its utilization status was assigned to 0. Animals tended to travel through these "unselected" sites, rather than stay and use the habitat resources. Other sample points with intermediate to high levels of bison space use were assigned to 1. The individual sample points were pooled when fitting the logistic regression model in RSF. In the method of RUF, the multivariate regression model that relates the bison space use to habitat selection variables was calculated for each individual animal. The mean of the resulting coefficients for individual animals was compared with 0 using a t-test. If the mean coefficient is significantly different from 0, the corresponding resource variable is selected or avoided by animals. Otherwise, the resource variable is insignificant in the process of resource selection.

5.3.2.2 Vegetation Responses to Bison Grazing

Bison locations recorded for a week before the capture of aerial imagery were selected for UD estimations to study vegetation responses to bison grazing activity. UD maps were calculated for individuals and then overlaid to form a summary map. The summarized UD map was classified into three levels from low to high using a natural break. The vegetation

heterogeneity was measured in the areas with low and high kernel densities of bison space use, respectively. To measure vegetation heterogeneity, metrics of contagion, SIDI and the interspersion/juxtaposition index (IJI) for high-nitrogen patches were calculated in the categorical canopy nitrogen maps using the FRAGSTATS program.

5.4 Results

5.4.1 Fire and Topography

At the watershed level, fire showed a predominant influence on habitat selection by bison. Paired t-test revealed that the kernel density of space use by bison in the watersheds burned in spring of the current year was significantly greater than that in the unburned areas across the growing seasons (Table 5.1). Preference for burned patches by large grazers is referred to as pyric herbivory, which has been observed repeatedly in previous studies (Allred et al. 2011; Fuhlendorf et al. 2009). Results in my study showed that the difference in bison space use between burned and unburned areas was greatest in May. This indicates that preference for watersheds with spring burns by bison is especially strong during the early growing season. The kernel density of space use by bison in the unburned watersheds continuously increased from May to September as the vegetation canopy was more developed (Figure 5.4).
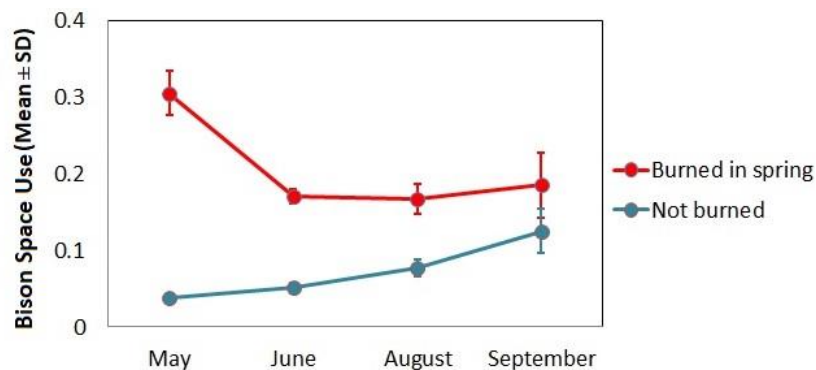
Figure 5.4 Kernel densities of bison space use in burned and unburned watersheds

Table 5.1 Paired t-test for comparing bison space use in burned and unburned areas

	May	June	August	September
Mean of differences	0.2678	0.120	0.090	0.060
t	34.494	46.173	16.004	4.388
p-value	<0.001	<0.001	<0.001	0.001

Topography is a landscape-level factor that influences habitat selection by bison. In this study, the kernel densities of space use by bison in the four topography positions within the watersheds burned in spring were compared (Figure 5.5). Results of one-way ANOVA showed that differences in bison space use across topography positions were statistically significant over the growing seasons (Table 5.2). Tukey's honest significant difference (HSD) post-hoc test revealed more detailed comparisons between topography types (Table 5.3). In general, the bison space use in drainage bottoms and hillslopes was lower than that in lowlands and uplands. In May – June, lowlands had the highest kernel densities of bison space use. In August – September, the use of uplands increased and became the highest.
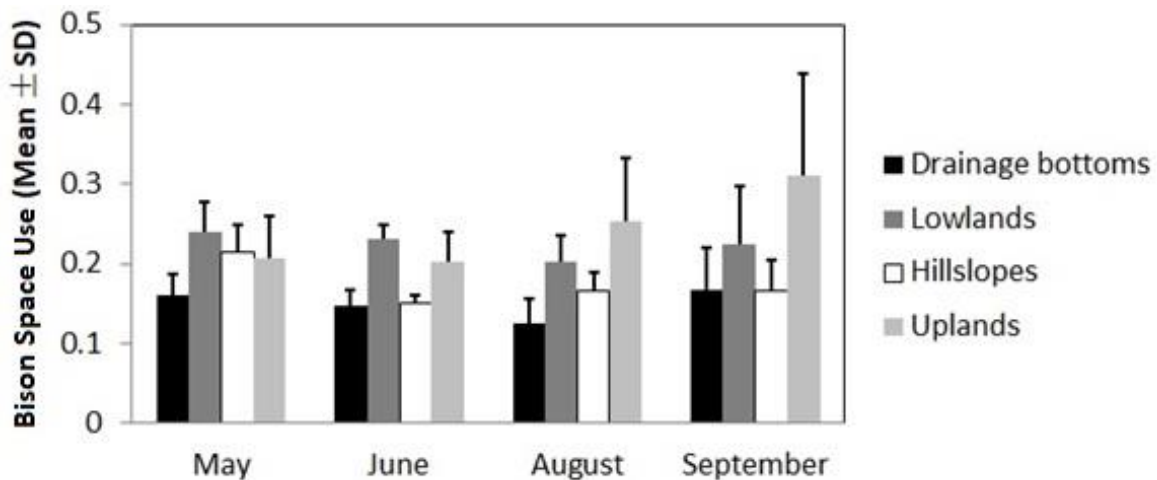
Figure 5.5 Kernel densities of bison space use in different topography positions

Table 5.2 One-way ANOVA for kernel densities of space use by bison in different topography positions.

	May	June	August	September
F	9.523	40.160	17.890	8.676
p-value	<0.001	<0.001	<0.001	<0.001

Table 5.3 Tukey's HSD post-hoc test for bison space use in different topography positions

	Difference	Adjusted p-value
May		
Lowlands - Drainage bottoms	0.079	<0.001
Hillslopes - Drainage bottoms	0.053	0.005
Uplands - Drainage bottoms	0.046	0.019
June		
Lowlands - Drainage bottoms	0.084	<0.001
Uplands - Drainage bottoms	0.055	<0.001
Lowlands - Hillslopes	0.081	<0.001
Uplands - Lowlands	-0.029	0.014
Uplands - Hillslopes	0.052	<0.001
August		
Lowlands - Drainage bottoms	0.075	0.001
Uplands - Drainage bottoms	0.128	<0.001
Uplands - Lowlands	0.053	0.027
Uplands - Hillslopes	0.087	<0.001
September		
Uplands - Drainage bottoms	0.143	<0.001
Uplands - Lowlands	0.087	0.050
Uplands - Hillslopes	0.145	<0.001

5.4.2 RSF and RUF

The relative importance of slope, elevation and canopy vegetation characteristics in habitat selection by bison was compared using the standardized coefficients of RSF and RUF (Table 5.4). Results of RSF were slightly different from that of RUF in the statistical significance and relative importance of habitat selection factors. Otherwise, there was no significant contradiction between the two sets of results. Combining results from the two modeling methods, the slope variable had consistently negative coefficients over seasons, indicating that bison always avoided slope zones. In May – August, the elevation variable tended to have significantly positive coefficients, indicating bison preferences for elevated sites. In September, the coefficient of elevation was negative and statistically significant in the analysis of RSF, whereas it was insignificant in RUF. This indicated a feeding site transfer by bison during the senescent season.

A seasonal pattern across the canopy nitrogen coefficients was that they were positive in May but negative in June – September. During May – August, coefficients of canopy nitrogen were statistically significant in the analysis of RSF, but insignificant in RUF. In September, the variable of canopy nitrogen had significantly negative coefficients. This suggested that bison selected high canopy nitrogen patches in the early growing season; however, they tended to avoid sites with high canopy nitrogen in the later growing season. This contradiction may be explained by the "forage maturation hypothesis" (Fryxell 1991) and the selective forage behavior by bison. In the "grazing lawns", bison may select the young plants in the areas with low-to-moderate vegetation quantity to feed, which are potentially superior to mature, high-biomass vegetation cover in forage quality. Meanwhile, bison typically select graminoids (Plumb and Dodd 1993). Forbs contain many secondary chemicals that deter bison feeding. Bison grazing activities reduce the palatable grass species and allow forbs to flourish. The high canopy nitrogen

sites shown on the remote sensing imagery in the later growing season may be forb communities

and therefore avoided by bison. These results were consistent with findings by Raynor (2015),

which revealed that bison selected low-to-moderate grass covers and avoided high forb covers.

Table 5.4 Comparing the standardized coefficients determined by RSF and RUF. The variables are highlighted in bold as the results of RSF are consistent with that of RUF.

Variable	RSF			RUF			
	Standardized β	Standardized β SE	p-value	Standardized β	Standardized β SE	t	p-value
May							
Slope	**-0.0494**	**0.0209**	**0.018**	**-0.0435**	**0.0133**	**-3.2785**	**0.006**
Elevation	**0.2022**	**0.0153**	**<0.001**	**0.0468**	**0.0218**	**2.1507**	**0.050**
Canopy nitrogen	0.2778	0.0297	<0.001	0.0217	0.0329	1.6588	0.121
Canopy nitrogen SD	0.1378	0.0268	<0.001	0.0117	0.0130	0.9018	0.384
Contagion	-0.0487	0.0228	0.033	0.0064	0.0094	0.6812	0.508
SIDI	-0.15637	0.0378	<0.001	-0.0093	0.0141	-0.6551	0.524
June							
Slope	**-0.3365**	**0.0191**	**<0.001**	**-0.0593**	**0.0059**	**-10.126**	**<0.001**
Elevation	**0.2056**	**0.0145**	**<0.001**	**0.0596**	**0.0093**	**6.4193**	**<0.001**
Canopy nitrogen	-0.0956	0.0175	<0.001	-0.0053	0.0039	-1.3721	0.1933
Canopy nitrogen SD	**-0.1954**	**0.0306**	**<0.001**	**-0.0235**	**0.0070**	**-3.3453**	**0.005**
Contagion	**0.0860**	**0.0212**	**<0.001**	**0.0098**	**0.0026**	**3.8044**	**0.002**
SIDI	**0.2945**	**0.0339**	**<0.001**	**0.0349**	**0.0051**	**6.8772**	**<0.001**
August							
Slope	**-0.3192**	**0.0231**	**<0.001**	**-0.0579**	**0.0126**	**-4.6020**	**<0.001**
Elevation	**0.1355**	**0.0189**	**<0.001**	**0.0417**	**0.0173**	**2.4025**	**0.032**
Canopy nitrogen	-0.1766	0.0235	<0.001	-0.0276	0.0133	-2.0796	0.058
Canopy nitrogen SD	-0.0428	0.0354	0.227	-0.0089	0.0110	-0.8087	0.433
Contagion	0.0661	0.0327	0.043	0.0082	0.0068	1.2014	0.251
SIDI	0.2003	0.0529	<0.001	0.0133	0.0115	1.1626	0.266
September							
Slope	**-0.5637**	**0.03906**	**<0.001**	**-0.1211**	**0.0215**	**-5.6196**	**<0.001**
Elevation	-0.1642	0.03054	<0.001	-0.0033	0.0262	-0.1255	0.902
Canopy nitrogen	**-0.1850**	**0.02951**	**<0.001**	**-0.0564**	**0.0228**	**-2.4722**	**0.029**
Canopy nitrogen SD	0.0085	0.03755	0.822	-0.0021	0.0107	-0.1967	0.847
Contagion	**0.0770**	**0.02678**	**0.004**	**0.0197**	**0.0086**	**2.2949**	**0.041**
SIDI	0.1160	0.04251	0.006	0.0121	0.0134	0.9042	0.384

Effects of canopy vegetation heterogeneity on bison habitat selection were most evident in June. The coefficient of canopy nitrogen standard deviation was significantly negative, whereas the metric of contagion and SIDI had positive coefficients. This indicates that bison prefer sites with low variance in canopy nitrogen, where the patch types are highly aggregated and evenly proportioned. Among the three factors of vegetation heterogeneity, canopy nitrogen standard deviation and SIDI had higher importance than the contagion variable. Additionally, in September, the contagion variable had significantly positive coefficients, suggesting that bison selected highly aggregated patches. In most cases, the magnitudes of slope and elevation coefficients were greater than that of coefficients for canopy nitrogen characteristics. This indicates that topography is potentially a more important factor than vegetation resources in bison habitat selection. In fact, prairie vegetation characteristics themselves are greatly affected by topography (Hartnett et al. 1996).

The slope variable showed a consistent effect on bison habitat selection, and itself can be an important factor influencing distribution of canopy properties. Analyses of RSF and RUF excluding the slope zones (Table 5.5) revealed effects of canopy properties on bison resource selection in more detail, in which influences of topography on vegetation characteristics, and therefore on bison forage were reduced. Results in Table 5.5 verified the seasonal pattern of canopy nitrogen coefficients observed in Table 5.4. The coefficients of canopy nitrogen were positive in May but negative in June – September, and at this time, the canopy nitrogen coefficients were statistically significant in both RSF and RUF. This indicated that bison had evident preference for grass patches with high nitrogen in the early growing season. However, they tended to select the low-to-moderate grass covers with potentially high forage quality to feed and avoided forbs of high biomass in the later growing season.

Table 5.5 Analyses of RSF and RUF excluding the slope zones. The variables are highlighted in bold as the results of RSF are consistent with that of RUF.

| Variable | RSF | | | RUF | | | |
	Standardized β	Standardized β SE	p-value	Standardized β	Standardized β SE	t	p-value
May							
Elevation	0.2188	0.0168	<0.001	0.0218	0.0250	0.8719	0.399
Canopy nitrogen	**0.3202**	**0.0258**	**<0.001**	**0.0546**	**0.0194**	**2.8142**	**0.015**
Canopy nitrogen SD	**0.2448**	**0.0319**	**<0.001**	**0.0400**	**0.0180**	**2.2172**	**0.045**
Contagion	-0.0288	0.0283	0.307	0.0090	0.0113	0.7982	0.439
SIDI	-0.2090	0.0429	<0.001	-0.0396	0.0268	-1.4788	0.163
June							
Elevation	**0.1931**	**0.0132**	**<0.001**	**0.0691**	**0.0109**	**6.3513**	**<0.001**
Canopy nitrogen	**-0.1590**	**0.0193**	**<0.001**	**-0.0126**	**0.0042**	**-3.0011**	**0.010**
Canopy nitrogen SD	**-0.1709**	**0.0332**	**<0.001**	**-0.0142**	**0.0066**	**-2.1594**	**0.050**
Contagion	**0.0773**	**0.0229**	**<0.001**	**0.0134**	**0.0040**	**3.3488**	**0.005**
SIDI	**0.2761**	**0.0401**	**<0.001**	**0.0306**	**0.0054**	**5.6613**	**<0.001**
August							
Elevation	**0.1357**	**0.0179**	**<0.001**	**0.0414**	**0.0156**	**2.6612**	**0.020**
Canopy nitrogen	**-0.2449**	**0.0272**	**<0.001**	**-0.0395**	**0.0159**	**-2.4872**	**0.027**
Canopy nitrogen SD	-0.0806	0.0371	0.030	-0.0293	0.0144	-2.0346	0.063
Contagion	0.0421	0.0372	0.258	0.0091	0.0075	1.2075	0.249
SIDI	0.2008	0.0561	<0.001	0.0247	0.0197	1.2533	0.232
September							
Elevation	0.0289	0.0253	0.252	0.0421	0.0246	1.7090	0.113
Canopy nitrogen	**-0.3218**	**0.0318**	**<0.001**	**-0.0734**	**0.0317**	**-2.3141**	**0.039**
Canopy nitrogen SD	0.0417	0.0414	0.3133	0.0015	0.0129	0.1128	0.912
Contagion	0.1015	0.0332	0.0022	0.0227	0.0112	2.0263	0.066
SIDI	0.1172	0.0459	0.0107	0.0281	0.0244	1.1513	0.272

Again, the influences of vegetation heterogeneity were most evident in June. The relative importance of canopy nitrogen SD, contagion and SIDI was consistent with that analyzed in Table 5.4. The coefficients of canopy nitrogen SD in May were positive and statistically

significant. Effects of elevation were significant only in June and August, which was slightly different from results in Table 5.4.

5.4.3 Bison Grazing Density Influencing Vegetation Heterogeneity

Vegetation heterogeneity at sites with high and low bison space use was shown in Table 5.6. Mean and standard deviation of canopy nitrogen contents were summarized. Metrics that measure vegetation heterogeneity on categorical nitrogen maps included percentage of high-nitrogen patches (%H), IJI for high-nitrogen patches (H-IJI), contagion index and Simpson's diversity. The mean of nitrogen content, %H and H-IJI showed interesting patterns of vegetation characteristics between sites with high and low bison space use across seasons. In the early growing season, shortly after the fire treatments initiated, the areas with high space use by bison had greater canopy nitrogen contents than the zones with low-level bison space use. In addition, zones with high-level bison space use had a greater proportion of high-nitrogen patches, and the high-nitrogen patches were more aggregated. At a later stage of the growing season during June – September, the mean of canopy nitrogen content and proportions of high-nitrogen patches in the areas with high bison space use became lower than that with low bison space use; meanwhile, the interspersion of high-nitrogen patches in the areas with high bison space use became greater than that with low bison space use. This suggested a difference between high and low levels of ungulate grazing density. A high level of herbivory reduced vegetation density and increased vegetation heterogeneity.

Table 5.6 Vegetation heterogeneity at sites with high and low levels of bison space use. Mean and standard deviation of canopy nitrogen are calculated. Vegetation heterogeneity is measured on categorical nitrogen maps using metrics, including percentage of high-nitrogen patches, IJI for high-nitrogen patches, contagion index and Simpson's diversity.

Month	High bison space use					Low bison space use				
	Mean (SD)	%H	H-IJI	Contag	SIDI	Mean (SD)	%H	H-IJI	Contag	SIDI
May	1.62 (0.34)	4.72	11.06	37.12	0.65	1.53 (0.34)	2.91	14.86	36.21	0.65
June	1.80 (0.29)	12.60	48.59	16.27	0.76	1.89 (0.29)	21.10	40.93	18.78	0.76
August	0.78 (0.46)	5.77	35.18	21.61	0.77	1.03 (0.51)	16.64	28.00	19.45	0.79
September	0.59 (0.23)	4.26	26.80	23.80	0.76	0.74 (0.24)	13.85	17.56	23.54	0.76

5.5 Conclusions

In this study, influences from fire, topography and vegetation canopy nitrogen on habitat selection by bison were analyzed and compared. Fire played a predominant role in affecting bison distribution at the watershed level. Space use by bison was found to be more concentrated in watersheds burned in spring of the current year. Bison preference for burned areas was evident over seasons from May – September, which was especially strong during the early growing season in May. At a later stage of growing season from June – September, use of unburned watersheds by bison was increased. This fire-promoted herbivory is caused by a shifting mosaic of vegetation patterns resulting from the fire and grazing interactions across landscape (Fuhlendorf et al. 2009; Fuhlendorf et al. 2010).

Topography is a landscape-level factor that affects bison forage and habitat selection. In general, bison avoid steep slope and prefer elevated sites. Avoidance of steep slope is common in resource selection by large herbivores (Allred et al. 2011; Frank and Groffman 1998; Frank et al. 1994). Drainage bottoms, where woody plants are thriving, are avoided by bison. This is different from forage strategy of cattle, in which woody vegetation is preferred (Allred et al.

2011). In the flat, higher lowlands and uplands (compared to drainage bottoms), space use of lowlands by bison was found to be slightly higher than uplands during May – June, whereas use of uplands was increased at a later stage of growing season from August – September. Topography had higher importance than vegetation in bison habitat selection. Topography itself can be an important driver that controls spatial distribution of vegetation characteristics (Hartnett et al. 1996).

As for vegetation resources, bison preference for patches with high canopy nitrogen was evident in May. However, during June – September, bison even avoided sites with high canopy nitrogen. This contradiction may be explained by the "forage maturation hypothesis" and the selective forage behavior by bison. Bison select palatable grass species and allow forbs to flourish. In the later growing season, bison may select the low-to-moderate grass covers that are nutritionally superior to forb covers of high biomass.

Vegetation heterogeneity (i.e., SD, contagion and SIDI of canopy nitrogen) showed significant effects on bison resource selection in June. Bison tended to select sites with low variance in canopy nitrogen, where the patch types were highly aggregated and equitably proportioned. These findings on bison responses to vegetation resources extended observations reported by Raynor (2015), Wallace et al. (1995), Plumb and Dodd (1993) to a finer spatial scale.

Influence of bison forage on spatial heterogeneity of vegetation cover was examined using FRAGSTATS metrics at class level (i.e., proportion and interspersion of high-nitrogen patches) and landscape level (i.e., contagion and Simpson's diversity). The class-level metrics for high-nitrogen patches revealed evident differences between areas with high and low bison space use across seasons. In May, a greater proportion of high-nitrogen patches with lower interspersion were observed at sites with high bison space use. During June – September, a high

level of herbivory reduced vegetation density and increased the evenness of high-nitrogen distribution. The landscape-level metrics, which measured contagion and diversity across all the five classes of canopy nitrogen from low to high, showed insignificant differences associated bison space use.

In summary, this study investigated interactive processes among fire, vegetation and bison forage in a tallgrass prairie topography. Spatial heterogeneity of vegetation cover and bison locations were acquired precisely using remote sensing and GPS techniques, respectively. The fine spatio-temporal resolution allowed accurate evaluations on dynamics between bison movement and vegetation responses. My study provided insights into applications of remote sensing imagery to spatial analysis of bison forage pattern associated with canopy nitrogen. As spectral methods for other vegetation nutritional elements, such as Mg, P, S, K, and Ca, are validated in the remote sensing imagery, bison selection for vegetation nutritional elements can be assessed more comprehensively. A potential limitation of the use of remote sensing imagery in this study is that it is difficult to detect plant species, whereas plant species can be an important factor in resource selection by large herbivores. Further studies of determining plant species (grasses *vs.* forbs) using spectral analysis will improve the use of remote sensing imagery in grassland science.

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Chapter 6 - Summary

My dissertation research focused on: (1) spectral analysis of grassland vegetation characteristics, and (2) spatial analysis of grassland dynamics and grazer behavior. In spectral analysis at the leaf level, I estimated the foliar pigments and nutritional elements using hyperspectral data. The foliar pigments, chlorophylls and carotenoids, were retrieved by inverting the PROSPECT leaf model. The nutritional elements, Mg, P, S, K and Ca, were empirically modeled by Partial Least Squares (PLS) regression applied to *in-situ* spectral measurements. At the canopy level, I assessed the use of broadband vegetation indices, NDVI and GRVI, in detecting vegetation quality and quantity. The relationships between the vegetation indices and vegetation characteristics were examined in the canopy model, PROSAIL, and validated by a field dataset of tallgrass prairie vegetation. In the spatial analysis, I examined interactions between pyric herbivory and grassland heterogeneity at multiple scales from the remote sensing imagery. At a coarse, watershed scale, I evaluated effects of fire and large herbivores on the spatial distribution of canopy nitrogen. The effects from the two grazer species, bison and cattle, were compared. At a fine, patch scale within watersheds, bison forage pattern was examined associated with canopy nitrogen heterogeneity. Here, I summarize my findings and provide suggestions for follow-on research.

6.1 Spectral Analysis

6.1.1 Leaf Level

In Chapter 2, the hyperspectral analysis of leaf pigments and nutritional elements focused on the region of 470 – 800 nm. A spectral standardization method using a form of normalized difference was developed and proved effective to reduce the significant background impact in measurements of leaf reflectance for grassland species. There are four feature points highlighted,

including the nadirs in the blue and red regions, the green peak and the turning point in the near infrared region. The positions and reflectance values of these feature points have been proven useful for detecting leaf pigments.

In retrieval of leaf pigments, the leaf structure parameter in PROSPECT 5 model showed a significant effect on the spectral response pattern. A proper selection of the range of leaf structure parameter can reduce much of the bias in model validation and improve model prediction accuracy. This study documented that a range of leaf structure parameter from 1.7 – 1.9 is reasonable for tallgrass species. Estimation of nutritional elements required more finely resolved spectral features, and resulted in more complex spectral models than retrieval of leaf pigments. A reasonable selection of the modeling and validation datasets was critical to improving prediction accuracy of the empirical models for leaf nutrients.

It was promising to quantify leaf pigments and nutritional elements using the hyperspectral analysis methods developed in this study. Results of this study were comparable with those reported by Mutanga et al. (2004) and Feret et al. (2008). Further, this study examined relationships between leaf photosynthetic pigments and nutritional elements, providing a comprehensive assessment of leaf nutrition status for grassland species. Results showed that chlorophylls were positively correlated with the element K, and the carotenoids were negatively correlated with Mg and Ca. The ratio of chlorophylls to carotenoids showed positive correlations with P, S and K, consistent with previous studies which concluded that the ratio of chlorophylls to carotenoids can be an important index that reflected plant phenology and nutritional status (Feret et al. 2008; Yang et al. 2010).

6.1.2 Canopy Level

In Chapter 3, the broadband vegetation indices, NDVI and GRVI, were compared in the PROSAIL canopy model. Results showed that NDVI reflected combined information of vegetation quantity (LAI) and leaf quality (leaf chlorophyll concentration), which can be used to quantify plant biochemical characteristics at the canopy level. GRVI performed better than NDVI in estimating LAI in an environment with varying leaf chlorophyll concentrations, suggesting that GRVI can be a more robust and reliable indicator of vegetation quantity than NDVI. GRVI has been widely used in qualitative analyses to track vegetation changes over seasons or canopy differences across ecosystem types (Ishihara et al. 2015; Motohka et al. 2010; Nagai et al. 2014). Its feasibility to quantify vegetation characteristics has not been studied sufficiently. My dissertation has verified the feasibility of GRVI in estimating vegetation quantity. Neither NDVI nor GRVI can be used to estimate leaf chlorophyll concentration as the LAI varies. However, a combination of GRVI and NDVI, proposed as GNVI (green-red normalized vegetation index), showed a great improvement in estimating leaf chlorophyll concentration across varying LAI values. The findings of this study were important for improving the use of broadband vegetation indices from multispectral remote sensors to detect vegetation quality and quantity over a wide spatial extent.

6.2 Spatial Analysis

6.2.1 Watershed Scale

In Chapter 4, the effects of fire and large herbivores (bison and cattle) on canopy nitrogen distribution were examined at a coarse, watershed scale from the remote sensing imagery. It was found that fire improved grassland production and resulted in more uniform canopies with adjacent high-nitrogen patches during the growing season in May – August. Fire interacted with

large herbivores in that large herbivores preferred new, burned grasslands. The high level of herbivory in the burned watersheds reduced the canopy density and increased the interspersion of high-nitrogen patches.

Effects from bison and cattle were compared in the burned watersheds. Generally, at the early growing season in May, bison grazed areas had lower canopy nitrogen and higher interspersion of high-nitrogen patches than cattle grazed sites. During the mid of growing season in June – August, differences between sites grazed by bison and cattle were insignificant except in the uplands. This indicated that bison had more evident influences on vegetation canopies in uplands than cattle did. The variogram analysis showed that the sites with bison had higher sills and variance proportions, indicating that bison created greater grassland heterogeneity than cattle. The differences in canopy nitrogen distribution between sites with bison and cattle across topography positions and seasons may be explained by the differences in the grazing intensity (Afzal and Adams 1992; Augustine and Frank 2001), forage herbivore and habitat selection (Allred et al. 2011) between the two grazer species. My study extended the previous research of effects from fire (Collins and Wallace 1990; Loucks 1970) and large herbivores (Allred et al. 2011; Augustine and Frank 2001) on grassland heterogeneity across topography (Abrams and Hulbert 1987). It can be a baseline study for further modeling grassland dynamics involving interplay between vegetation variability, nutrition cycling and ungulate grazing behavior.

6.2.2 Fine Scale within Watersheds

In Chapter 5, I investigated the bison forage pattern associated with canopy nitrogen distribution within watersheds. Results indicated that vegetation resources influenced bison forage pattern and habitat selection at a finer scale than fire and topography. Bison preference for high canopy nitrogen patches was evident and statistically significant in May. It was interesting

that bison showed avoidance of sites with high canopy nitrogen in June – September. This contradiction may be explained by the "forage maturation hypothesis" and the selective forage behavior by bison. In the "grazing lawns", bison tended to select the low-to-moderate grass covers with potentially high vegetation quality to feed and avoid forbs of high-biomass. The high canopy nitrogen sites shown on the remote sensing imagery in the later growing season may be high forb covers, and therefore avoided by bison.

Evident effects of vegetation heterogeneity on bison habitat selection were present in June. Bison tended to select canopies with low variance in nitrogen values, where the canopy nitrogen patch types were highly aggregated with equitable proportion distribution. These findings extended observations of bison forage responses to vegetation resources reported by Raynor (2015), Wallace et al. (1995), Plumb and Dodd (1993) to a finer spatial scale within watersheds.

6.3 Limitations and Further Directions

My study provided insight into remote sensing applications to analyses of grassland dynamics at multiple scales. A limitation of the use of remote sensing is that the fineness of the analysis scale is determined by the spatial resolution of the remote sensor. On the remote sensing imagery, vegetation characteristics are generalized within the spatial resolution, where the heterogeneity is not detectable. This makes the field measurements important and indispensable to the finer-scale (< the remote sensing spatial resolution) analysis.

Another challenge in my study is that the plant species, grasses *vs.* forbs, are not detectable from the remotely sensed nitrogen maps. However, plant species can be an important factor that affects forage selection by large herbivores. Further studies of differentiating forbs

from grass species in a tallgrass prairie canopy using spectral analysis may improve the use of remote sensing imagery in grassland science.

In the analysis of bison forage strategy and habitat selection, canopy nitrogen was the only vegetation characteristic taken into account. Further studies that incorporate other nutrients (Mg, P, S, K, and Ca) and canopy properties (plant species and vegetation quantity) in analysis are necessary for a more comprehensive assessment of bison response to spatial distributions of vegetation resources. As the bison forage hierarchy and pyric herbivory effects on canopy property distributions are fully understood, a dynamic model of bison movement and grassland heterogeneity can be simulated. This can provide valuable implications to grassland conservation and management.

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