Estimation of Grass Photosynthesis Rates in Mixed-Grass Prairie Using Field and Remote Sensing Approaches

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By

Selena Compton Black

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ABSTRACT

With the increase in atmospheric CO_2 concentrations, and the resulting potential for climate change, there has been increasing research devoted to understanding the factors that determine the magnitude of CO_2 fluxes and the feedback of ecosystem fluxes on climate. This thesis is an effort to investigate the feasibility of using alternate methods to measure and estimate the CO_2 exchange rates in the northern mixed grass prairie. Specifically, the objectives are to evaluate the capability of using ground-level hyperspectral, and satellite-level multispectral data in the estimation of mid-season leaf CO_2 exchange rates as measured with a chamber, in and around Grasslands National Park (GNP), Saskatchewan. Data for the first manuscript was collected during June of 2004 (the approximate period for peak greenness for the study area). Spectral reflectance and CO_2 exchange measurements were collected from 13 sites in and around GNP. Linear regression showed that the Photochemical Reflectance Index (PRI) calculated from hyperspectral ground-level data explained 46% of the variance seen in the CO_2 exchange rates. This indicates that the PRI, which has traditionally been used only in laboratory conditions to predict CO_2 exchange, can also be applied at the canopy level in grassland field conditions.

The focus of the second manuscript is to establish if the relationship found between ground-level hyperspectral data and leaf CO_2 exchange is applicable to satellite-level derived vegetation indices. During June of 2005, biophysical and CO_2 exchange measurements were collected from 24 sites in and around GNP. A SPOT satellite image was obtained from June 22, midway through the field data collection. Cubic regression showed that Normalized Difference Vegetation Index (NDVI) explained 46% of the variance observed in the CO_2 exchange rates. To our knowledge, this is the first time that a direct correlation between satellite images and leaf CO_2 fluxes has been shown within the grassland biome.

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CHAPTER 1 – INTRODUCTION

1.1 Research Background

1.1.1 Global Change & Grasslands

Increasing greenhouse gas concentrations and the potential effects that this has with respect to climate change have made global carbon balance an increasingly important political and scientific topic. The Intergovernmental Panel on Climate Change (IPCC) has predicted that with continued CO_2 and other greenhouse gas emissions, there will be an average global rise in temperature of 1.4 ºC to 5.4 ºC between 1990 and 2010 (IPCC 2001). International agreements to reduce greenhouse gas concentrations, such as the Kyoto Protocol, have identified the development of carbon sinks as a strategy for individual countries to meet their obligations.

Research suggests that the terrestrial ecosystem will act as a carbon sink, as vegetation will thrive in conditions of increased atmospheric CO_2. Lloyd (1999) reviewed a number of studies that examined the relationship between atmospheric CO_2 concentrations and plant growth. In almost all cases, the studies reported increased growth in response to increases in CO_2 concentrations. This has been further supported by research conducted in laboratory conditions. In a compilation of literature sources, Poorter (1993) reviewed the growth responses of 156 different plant species. When the atmospheric CO_2 concentration doubled, it was found that the average growth stimulation of these plants was approximately 37%. It can be concluded that since plants respond to higher levels of atmospheric CO_2 by producing more biomass, vegetation will likely contribute to the management of increasing atmospheric CO_2.

While much attention has focused on the carbon sink capabilities of tropical and boreal forests, grasslands need to be considered in global estimates of carbon sinks. Grasslands are one of the most widespread vegetation types worldwide, covering 15 million km^2 in the tropics, and an additional 9 million km^2 in temperate regions; together, these locations constitute nearly 20% of the world's land surface (Lieth 1978). Although many researchers have concluded that grassland ecosystems are carbon sinks (e.g., Owensby et al. 1993; Scurlock and Hall 1998; Leadley et al. 1999; Flanagan et al. 2002; Li et al. 2004), there is still some debate as recent research has concluded that grasslands may further contribute to atmospheric CO_2 levels being a carbon source (Zhang et al. 2005).

Unfortunately, grasslands have been an understudied ecosystem. Hall and Scurlock (1991) concluded that natural grasslands in particular are an ecosystem that urgently need more research in order to determine the response of this "undervalued ecosystem type to possible climatic changes". More recently, the same authors stated that the potential effects of climate change on grasslands have received much less attention than the potential effects on other ecosystems, such as forests (Hall et al. 2000). However, it becomes apparent that the focus has shifted somewhat to establishing the role of grasslands in the global carbon balance, as evidenced by the quantity of very recently published research in this area (i.e. Flanagan et al. 2002; Wylie et al. 2003; Hunt et al. 2004; Gilmanov et al. 2005; Sims et al. 2005; Zhang et al. 2005; Owensby et al. 2006, Risch and Frank 2006).

Given that grasslands comprise the majority of the grazing capacity of the world (Burke et al. 1989), a further reason to investigate grassland ecosystem productivity is due to its economic importance as a rangeland resource. Degradation and desertification of grasslands are becoming increasingly common problems as a result of intense agricultural activities (Archer 2004; Li and Ji 2002). To ensure that this natural resource remains viable, an understanding of the components contributing to its productivity, as well as a feasible method of measuring productivity, is required.

The importance of gaining a solid understanding of grassland ecosystem fluxes is twofold. First, if we record the characteristics of the ecosystem as it currently exists, it can be monitored for change related to global warming that may occur in the future. Second, an understanding of the factors that determine the magnitude of fluxes and the feedback of ecosystems fluxes on climate can have implications for future grassland and rangeland management policies.

1.1.2 Photosynthesis and CO_2 Flux

Photosynthesis is a key process to understanding grassland ecosystem carbon dioxide flux. Photosynthesis is the process whereby plants synthesize organic compounds using inorganic raw materials in the presence of light energy. This process can be described by the following chemical equation:

$$6\ CO_2 + 12\ H_2O \xrightarrow{\text{light energy}} C_6H_{12}O_6 + 6\ O_2 + 6\ H_2O$$

Essentially, plants use the CO_2 available in the atmosphere and light energy to produce the products described above ($C_6H_{12}O_6$, a carbohydrate, O_2, oxygen and H_2O, water) which in turn will be used in the synthesis of various carbon-based compounds, such as proteins, fatty acids and enzymes. This process is referred to as terrestrial carbon sequestration, as the carbon is removed from the atmosphere and assimilated into the vegetation and soil. It is for this reason that many scientists are concerned with the rate at which plants extract CO_2 from the atmosphere.

CO_2 flux, which is also described as CO_2 exchange rate, refers to a measurement of the balance between the CO_2 sequestered from the atmosphere through plant photosynthesis and CO_2 returned to the atmosphere through plant and soil respiration. There are several variables which influence the rates of photosynthesis. These are temperature and water stresses, quality and quantity of photosynthetically active radiation (PAR), and air humidity (Hall and Rao 1999). Quantifying the photosynthetic process has proven to be a challenging task, given the numerous contributing biological and environmental factors.

Two major methods of measuring the CO_2 flux have been established. First, tower-based systems (such as Euroflux, Fluxnet Canada, Ameriflux) are used primarily as they offer secure, continuous, and long-term measurements of ecosystem scale carbon fluxes across a large spatial area, varying from 400 m^2 to 1500 m^2 (Baldocchi et al. 1988; Dugas 1993; Dugas et al. 1997). Throughout the 1990's and continuing into the new millennium, CO_2 flux studies have been focused on the establishment and expansion of flux tower networks and developing the required methodology. However, the main drawback of these systems is the high cost of installing and maintaining the towers.

Infrared gas analysis (IRGA) chambers are the second method used to measure fluxes. These semi-permanent chambers vary in volume from those that measure the gas exchange for individual leaves ($\approx 10^{-5}$ m^3) to those that measure exchange for an entire soil/plant canopy ($<10^3$ m^3). Unfortunately, this method is also associated with problems: chamber measurements are usually non-continuous and may alter the temperature, radiation, and wind conditions inside the chamber relative to that outside (Denmead 1984; Monteith 1990; Leuning and Foster 1990). This may result in non-representative measurements. In spite of these limitations, chambers are more portable and less expensive than flux towers, and are useful for making replicated measurements in small plots. This thesis will investigate the application of one of the smaller and more portable methods of flux measurement, the leaf chamber, in the estimation of mid-season northern mixed grassland CO_2 exchange rates.

1.1.3 Remote Sensing Systems

Remote sensing is defined as the collection of information about an object with a sensor that is not in contact with that object (Harrison and Jupp 1989). The sensors, either mounted to a satellite, aircraft, or *in situ*, record electromagnetic energy that is reflected, emitted, or backscattered in specific bands or frequencies, by surface objects. When collecting spectral reflectance data, there are two general categories of spectral resolution used: multispectral and hyperspectral. Multispectral remote sensing systems record energy in multiple bands (specific wavelength intervals) of the electromagnetic spectrum. A hyperspectral remote sensing instrument has the ability to record data in hundreds, or even thousands of spectral bands.

Because remote sensing instruments have the ability to record information beyond the visible portion of the spectrum (0.3 - 0.7 μm), it becomes possible to assess the reflectance characteristics of a given object beyond the range of human vision. For example, by recording the near infrared wavelength region, researchers can gain important information regarding both chlorophyll and water content of surface vegetation (Jensen 2000).

There are many methods of processing spectral data in order to isolate essential information about the surface characteristics. These processing methods not only highlight desired information, but can also help reduce the influence of background noise. Within the grasslands, the mixture of soil, mosses and lichens, shadows, and green vegetation in the individual pixels can make remote sensing a challenge because the image is recording information about more than just the surface vegetation (Perry and Lautenschlager 1984; Huete 1988; Todd et al. 1998). To address this problem (in grasslands and other contexts), vegetation indices were produced to minimize the effects of atmospheric haze, soil background, and senescent materials (Jensen 2005). Extensive research has been dedicated to form a link between various vegetation indices, which are derived from the spectral reflectance data collected by satellites, to various surface characteristics.

Remote sensing tools provide a method for investigating the spatial patterns of biophysical properties in a manner less cumbersome than traditional modeling approaches, which require more extensive parameterization (Rahman et al. 2001; Ustin et al. 2004). Spectral data are useful as they have the ability to measure biophysical parameters at both local and regional geographic scales. They enable large area, non-destructive, and real-time acquisition of terrestrial conditions in a more cost effective manner than traditional in situ measurements (Inoue 2003).

1.1.3.1 Biophysical Measurements with Hyperspectral Remote Sensing

Hyperspectral remote sensing systems have proven useful in evaluating the biophysical characteristics of grass species within the field of view of the sensor. Studies have investigated the use of hyperspectral data in the prediction the photosynthesis rates and other photosynthetic parameters, such as light-use efficiency of various species (Gamon et al. 1992; Gamon et al. 1997; Rahman et al. 2001; Evian et al. 2004; Guo and Trotter 2004; Ustin et al. 2004). A linear relationship exists between the Photochemical Reflectance Index (PRI) and photochemical efficiency (Gamon et al. 1992; Gamon et al. 1997; Evian et al. 2004; Guo and Trotter 2004). This relationship was found to be strong when several species were grouped together (Gamon et al. 1997; Guo and Trotter 2004) indicating that this relationship can be generalized across species. Although the results are encouraging, all of these studies were conducted within laboratory conditions and the relationship between reflectance and photosynthesis may not be as robust in field conditions with confounding factors such as background or atmospheric effects.

A study conducted in the boreal forest by Rahman et al. (2001) developed a method of combining optical indices from remotely sensed hyperspectral images with flux data from towers covering different vegetation types to create spatially continuous maps of gross CO_2 exchange. The authors found that they could successfully model the measured fluxes using Normalized Difference Vegetation Index (NDVI) in combination with PRI (Rahman et al. 2001). However, this study was conducted within the boreal forest, and the results may not be extracted to a different type of biome such as the grasslands.

To our knowledge, there has been no research to date situated within a grasslands landscape that investigates the relationship between hyperspectral remote sensing data and photosynthetic parameters. Although this relationship is well-established in the laboratory, it is unknown if it can be extended to field conditions. Therefore, one of the objectives of this thesis is to compare several different methods of spectral analysis in the prediction of leaf CO_2 exchange rates measured in the northern mixed grass prairie.

1.1.3.2 Biophysical Measurements with Multispectral Satellite Images

Multispectral sensors have been used extensively to estimate biophysical characteristics including photosynthetic parameters such as CO_2 exchange in arid grassland ecosystems (Wylie et al. 2003; Hunt et al. 2004; Gilmanov et al. 2005; Sims et al. 2005). Several of these studies utilized either broad or intermediate resolution satellite images (AVHRR, MODIS and SPOT) to predict average daily CO_2 exchange rates (averages were calculated from measurements ranging from 8-14 days) (Wylie et al. 2003; Gilmanov et al. 2005; Sims et al. 2005). In general, the researchers concluded that NDVI, or f_{APAR} (fraction of incident absorbed photosynthetically active radiation, a measurement derived in part from NDVI) were predictive of measured CO_2 exchange rates. To our knowledge, there has been no research to date that incorporates satellite remote sensing data in the estimation of leaf chamber CO_2 exchange rates in a grasslands environment.

Photosynthesis is a complex process with a number of environmental factors contributing to the overall variation seen in plant photosynthetic functioning (Hall and Rao 1999). With so few studies in this area of research, it is difficult to make predictions about the ability of multispectral remote sensing products to estimate leaf CO_2 exchange. With this in consideration, perhaps it would be more reflective of overall grassland productivity to consider not only leaf CO_2 exchange rates, but also other measurements of productivity such as leaf area index and biomass as contributing variables. It can be concluded that there is a need for more research in this area, as the potential for remote sensing products to effectively determine biophysical parameters is known, but its relationship with CO_2 exchange and productivity has not yet been established. Therefore, one of the primary objectives of this thesis is to determine the application of broad band vegetation indices, in combination with other indicators of ecosystem productivity (Plant Area Index (PAI) and dried grass biomass) to explain the variation found in leaf CO_2 exchange rates.

1.2 Research Objectives

The Kyoto protocol named the identification and development of carbon sinks as one of the strategies to assist countries around the world in meeting their obligations to reduce global greenhouse gas concentrations. In laboratory conditions, plants respond to higher levels of atmospheric CO_2 by producing more biomass, and it is believed that vegetation will contribute to the management of this problem by acting as a carbon sink for anthropogenic CO_2 (Poorter 1993; Lloyd 1999). While the majority of previous research has focused on the carbon sink capabilities of the tropical and boreal forests, grasslands need to be considered in global estimates of carbon sink as they are one of the most widespread vegetation types worldwide, covering approximately one-fifth of the Earth's ground surface (Lieth 1978). Many researchers focusing on the carbon flux within grassland ecosystems have concluded that these ecosystems are a carbon sink, and will contribute to mitigation of CO_2 concentrations (e.g., Owensby et al. 1993; Scurlock and Hall 1998; Leadley et al. 1999; Flanagan et al. 2002; Li et al. 2004). However, determining the mitigation capability of the grasslands requires a better understanding of ecosystem fluxes, factors that determine the magnitude of fluxes, the potential for mitigation, and the feedback of ecosystem fluxes on climate. An understanding of the factors affecting productivity can have implications for grassland and rangeland management policies. Further, by gaining an understanding of grassland productivity as it currently exists, it can be monitored for change related to global warming that may occur in the future.

The current research is an effort to investigate the feasibility of using different methods to measure the CO_2 exchange rates in the northern mixed grass prairie. Specifically, where flux towers are traditionally used for estimations of ecosystem exchange, we have explored the use of a leaf chamber, as it is more portable and inexpensive. As well, we have selected remote sensing tools to measure surface vegetation characteristics across a large spatial area as a convenient alternative to traditional modeling approaches, which require more extensive parameterization.

The purpose of this study is to evaluate the capability of using both ground-level hyperspectral, and satellite-level multispectral data in the estimation of leaf CO_2 exchange rates in the northern mixed grass prairie at mid-point in the growing season. The specific objectives of this thesis are identified as:

1) Compare several hyperspectral remote sensing measurements in the prediction of mid-season leaf CO_2 exchange rates measured in the northern mixed grass prairie.
2) Determine the application of SPOT multispectral imagery in combination with other indicators of productivity including PAI and dried grass biomass, to explain the variation found in mid-season leaf CO_2 exchange rates in the northern mixed grass prairie.

1.3 Thesis Structure

There are four chapters in this thesis. Chapter 1 is the Introduction where a general review of pertinent literature is presented, as well as the research objectives, and the thesis structure. The literature review gives an overview of grasslands and their role in global greenhouse gas mitigation, and emphasizes the need for further research in this area. The two main approaches to measuring CO_2 fluxes (flux towers and chambers) are compared and contrasted. The literature review also introduces the two main types of remote sensing tools: hyperspectral and multispectral, and briefly discusses the role of remote sensing tools in grassland biophysical studies. There is also a description of previous research where both hyperspectral and multispectral remote sensing data have been used in the estimation of grassland CO_2 exchange research.

Chapter 2 is the first of two manuscripts; it addresses the first research objective. In this manuscript, there is also an introduction to grasslands, their role in greenhouse gas mitigation, and why more research in this area is required. However, this manuscript provides a more detailed review of the literature regarding hyperspectral reflectance data as it has been used previously in the estimation of leaf CO_2 exchange. Using ground level hyperspectral data, we compare several derived spectral reflectance variables to determine which parameter is best for the prediction of mid-season leaf CO_2 exchange rates measured in the northern mixed grass prairie.

Chapter 3 is the second manuscript; it addresses the second research objective. Similar to the first manuscript, this paper explores remote sensing tools and their ability to estimate leaf CO_2 exchange; however this paper differs in that it is multispectral data obtained from the SPOT satellite rather than hyperspectral data. As well, the ability of biophysical measurements to estimate of leaf CO_2 exchange was also examined. In this paper, a more detailed review of the literature regarding multispectral reflectance data as it has been previously used in the estimation of ecosystem CO_2 exchange is provided.

Finally, in Chapter 4, the results and conclusions of each manuscript are summarized, and the two manuscripts are integrated together. As well, the limitations of the present research are discussed, and recommendations for future work relating to this thesis are given.

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CHAPTER 2 - ESTIMATION OF GRASSLAND CO_2 EXCHANGE RATES USING HYPERSPECTRAL REMOTE SENSING TECHNIQUES

2.1 Abstract

Although the link between CO_2 exchange and spectral reflectance is well-established in laboratory conditions, limited research has been conducted in the field. To determine the applications of remote sensing in the estimation of the northern mixed grasslands as a carbon sink, the primary objective of this study is to evaluate several narrow band vegetation indices and band depth analysis in the prediction of CO_2 exchange rates in a northern mixed grass prairie ecosystem. Spectral reflectance and CO_2 exchange measurements were collected from 13 sites located in Grasslands National Park, Saskatchewan, Canada. Pearson's correlation found a significant relationship between the CO_2 exchange rates and the Photochemical Reflectance Index (PRI). Linear regression showed that PRI explained 46% of the variance seen in the CO_2 exchange rates. This indicates that the PRI, which has traditionally been used only in laboratory conditions to predict CO_2 exchange, can also be applied at the canopy level in grassland field conditions.

Keywords: hyperspectral data, PRI, carbon dioxide exchange, grassland

2.2 Introduction

Increasing atmospheric CO_2 concentrations and the potential for climate change have made global carbon balance an important scientific and political topic. Studies have shown that most plant species respond to an increase in ambient CO_2 levels with an increase in growth (Poorter 1993). However, the magnitude of increase is dependant on the photosynthetic pathway; C_3 species showed a larger increase in biomass than C_4 species (41% and 22% respectively) (Poorter 1993). There is much evidence that the photosynthetic process in grassland ecosystems contributes to the lowering of anthropogenic CO_2 emissions by securing the atmospheric carbon dioxide into plant biomass (Hall and Scurlock 1991; Owensby et al. 1993; Leadley et al. 1999; Li et al. 2004). In contrast, other recent research has found that grasslands may contribute to atmospheric CO_2 levels (Zhang et al. 2005).

Remote sensing tools are useful in large-scale ecosystem studies as they allow large area, non-destructive, and real-time acquisition of biophysical conditions in a more cost-effective manner than traditional *in situ* measurements (Inoue 2003). Remote sensing techniques, based on measuring the reflected radiation from plant canopies, have the potential to evaluate the biochemical characteristics of many plants within the field of view of the sensor. For example, several studies have been dedicated to the estimation of plant pigment content (Broge and Leblanc 2000; Daughtry et al. 2000; Broge and Mortensen 2002; Sims and Gamon 2002; Ustin et al. 2004), plant biomass

(Mutanga and Skidmore 2004 a, b), and leaf area index (Asner et al. 2000; Rahman and Gamon 2004; Ustin et al. 2004). Remote sensing tools provide a method for investigating spatial patterns of biophysical properties in a manner less cumbersome than traditional modeling approaches, which require extensive parameterization (Rahman et al. 2001; Ustin et al. 2004).

Studies have investigated the use of hyperspectral data in the prediction of photosynthesis rates and other photosynthetic parameters, such as light-use efficiency (Gamon et al. 1992; Gamon et al. 1997; Rahman et al. 2001; Evian at al. 2004; Guo and Trotter 2004; Ustin et al. 2004). A linear relationship exists between Photochemical Reflectance Index (PRI) and photochemical efficiency (Gamon et al. 1992; Gamon et al. 1997; Evian et al. 2004; Guo and Trotter 2004). This relationship was found to be strong when several species were grouped together (Gamon et al. 1997; Guo and Trotter 2004) indicating that this relationship can be generalized across species. Although the results are encouraging, all of these studies were conducted in laboratory conditions and the relationship between reflectance and photosynthesis may not be as robust in field conditions due to confounding factors such as background or atmospheric effects.

Rahman et al. (2001) developed a method of combining optical indices from remotely sensed hyperspectral images with flux data from towers covering different vegetation types to create spatially continuous maps of gross CO_2 exchange. The authors found that they could successfully model the measured fluxes using Normalized Difference Vegetation Index (NDVI) in combination with PRI (Rahman et al. 2001). However, since this study was conducted in the boreal forest, the results may not be extracted to a different type of biome such as grasslands.

To date, little work has focused on the relationship between hyperspectral remote sensing data and photosynthetic parameters in grassland environments. Although this relationship is well-established in the laboratory, it is not known if it can be extended to field conditions. The main objective of this study is to compare several visible-NIR narrow band vegetation indices, as well as band depth analysis in the prediction of CO_2 exchange rates measured in the northern mixed grass prairie.

2.3 Methods

2.3.1 Site and Data

The study area was located in the West Block of Grasslands National Park (GNP) and surrounding pastures, in southwest Saskatchewan, Canada (N 49º12', W 107º24'). This area falls within the Great Plains, which are characterized by semi-arid climate, flat landscape and large areas dominated by grass species (Coupland 1993). Grasslands National Park is further located within the mixed grass prairie, one type of biome found within the Great Plains. This region is a transitional zone between tall grass and short grass prairie (Bragg 1995). Average temperatures range from -12.4 ºC in January to 18.3 ºC in July, and average precipitation is approximately 350 mm per year (Environment Canada 2000). In the study year (2004) the total precipitation was higher than normal at 411 mm (refer to Table 2.1 for a description of monthly precipitation). The soils in the study area are brown Chernozemic clay loam soils (Saskatchewan Soil Survey 1992). The dominant native grass species found in the study site are June grass (*Koeleria gracilis*), needle-and-thread grass (*Stipa comata*), blue grama (*Bouteloua gracilis*), and western wheat grass (*Agropyron smithii*).

Table 2.1 Monthly and total precipitation (in mm) of study year (2004) compared with long-term average (1971-2000) (Environment Canada 2000).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
2004	36.4	11.9	13.0	2.8	132.4	47.2	61.2	51.2	22.8	11.0	5.8	15.6	411.3
Avg.	15.9	10.2	17.9	23.4	51.7	65.3	54.0	33.8	27.6	17.4	15.1	15.5	347.7

During June of 2004 13 randomly selected sites were visited (see Figure 2.1). At each of these sites, field sampling was conducted along two 100 m transects that ran perpendicular in north-south and west-east directions, intersecting in the centre to form a cross. Quadrats were located at 20 m intervals along each transect, resulting in a total of 10 quadrats per site. Each quadrat measures 20 × 50 cm. The 20 m sampling resolution interval is supported by previous research conducted in the northern mixed grass prairie indicating that a sampling interval of 10 to 50 m is most suitable for this environment (Davidson and Csillag 2001). Photosynthetic exchange rates, spectral reflectance, cover, PAI, and biomass data were collected from each quadrat.

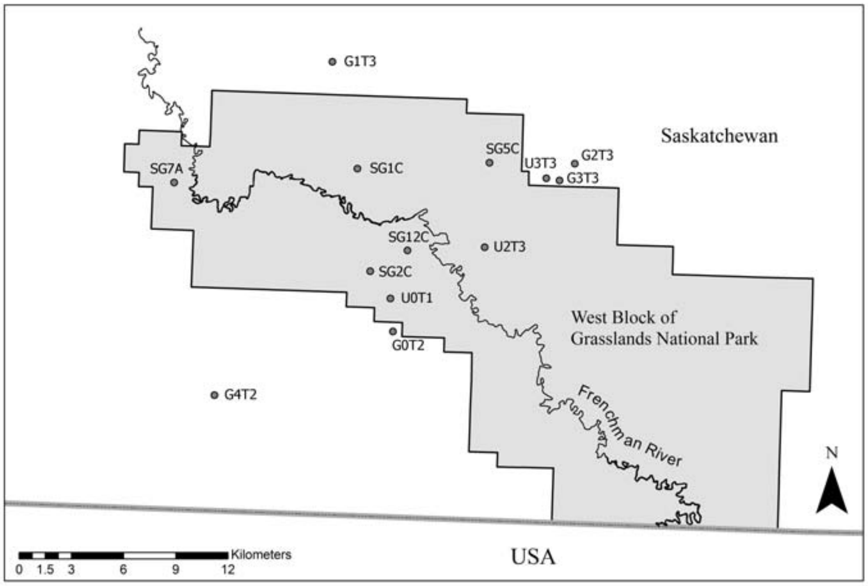

Figure 2.1 Distribution of sites (indicated with dot) within the West Block of Grasslands National Park and surrounding pastures, Saskatchewan, Canada.

Leaf CO_2 exchange rates were sampled along these transects using an LC*pro* (ADC BioScientific Ltd., Hoddesdon, UK). Using an 'open system' configuration (where fresh air is continuously passed through the plant leaf chamber), the chamber conditions were controlled for humidity and temperature to prevent condensation from forming, while incoming CO_2 and photosynthetically active radiation (PAR) levels were maintained at ambient conditions. Gas exchange measurements were made on approximately 3 plant leaves located within the same quadrat used for the reflectance measurements. The photosynthesis data were then amalgamated into mean values for each site (n = 36). This was done in order to reduce variance, and to obtain a measurement for each site that represents the average conditions.

Hyperspectral reflectance measurements were collected at a 5 m interval along each transect using an ASD Fieldspec FR spectroradiometer (ASD, Boulder, USA). However, only the spectral measurements that correspond to the plots for CO_2 exchange measurements were used in this study. The spectroradiometer was fitted with a fiber optic tube having a 25º field of view and was held at a distance of 1 m from the ground, which corresponds to a field of view of approximately 1500 cm^2. The field spectroradiometer collected reflectance data between 350 and 2500 nm. All hyperspectral data were collected under clear skies within two hours of solar noon. In order to reduce atmospheric condition changes, the spectroradiometer was calibrated using a white Spectralon reference panel (Labsphere, USA) at approximately 10 minute intervals. The hyperspectral data were then amalgamated into mean values for each site in order to reduce the variance (n = 12).

Canopy cover was estimated at both canopy and ground level. Canopy level cover was recorded by species. Lichen, moss, litter, bare soil, and rock were recorded at ground level. To standardize the data, only the cover that could be observed from overhead was recorded, so the sum of canopy level cover was less than 100%. The remaining gap was assigned to lichen, moss, litter, and bare ground according to the proportion they contributed to the total ground level cover. Therefore the sum cover of grass, forbs, shrubs, litter, moss, lichens, bare ground and rock is equal to 100%. Plant biomass was harvested after the other measurements were completed. Clipped fresh biomass was sorted into four groups: grass, forbs, shrubs, and dead material, and then dried in an oven at 60 ºC for 48 hours. A description of these measured variables can be found in Table 2.2.

Table 2.2 Maximum, minimum, mean and standard deviation values for measured and calculated variables (n = 13).

Variables	Maximum	Minimum	Mean	Standard Deviation
Grass (%)	39.29	21.95	28.71	4.73
Forbs (%)	10.19	2.48	6.19	2.39
Shrubs (%)	3.62	0.00	0.74	1.04
Standing Dead (%)	38.81	6.57	19.47	9.77
Litter (%)	19.45	5.38	10.68	4.43
Moss (%)	39.68	6.28	26.05	9.53
Lichen (%)	10.59	1.22	4.84	2.98
Rock (%)	2.56	0.00	0.58	0.74
Bare Ground (%)	2.21	0.02	0.51	0.74
Dried Grass Biomass (g/m^2)	95.38	32.88	56.02	18.58
Dried Forb Biomass (g/m^2)	66.38	8.38	24.95	17.95
Dried Shrub Biomass (g/m^2)	4.50	0.00	0.86	1.39
Dried Dead Biomass (g/m^2)	258.50	50.13	112.05	69.12
Total Dried Biomass (g/m^2)	364.75	116.50	193.88	83.18
CO_2 Exchange Rates (µmol/m^2/s)	51.45	22.76	33.88	8.47
PRI	-0.052	-0.064	-0.056	0.004
MCARI	0.029	0.018	0.022	0.004
SAVI	0.351	0.205	0.245	0.043
OSAVI	0.448	0.278	0.326	0.053
CAA	116.1	101.8	106.5	3.79
BDMax	0.60	0.39	0.46	0.07

2.3.2 Spectral Transformations

Two types of transformations were completed on the reflectance data collected with the spectroradiometer: 1) narrow band vegetation indices and, 2) band depth parameters calculated for spectral data ranging between 550 and 750 nm.

2.3.2.1 Narrow Band Vegetation Indices Spectral vegetation indices are ratios of two or more bands or slopes derived from the reflectance of the green vegetation. These vegetation indices act to minimize variation due to noise, while maximizing sensitivity to the variable of interest. The vegetation indices were selected due to their applicability to this study; they either 1) measured leaf pigments related to photosynthesis, or 2) adjusted for dead materials and soil background effects in the field of view. The narrow band vegetation indices calculated for this study include the Photochemical Reflectance Index (PRI) (Gamon et al. 1992), the modified Chlorophyll Absorption in Reflectance Index (MCARI) (Kim 1994), the Soil-adjusted Vegetation Index (SAVI) (Huete 1988), and finally the Optimized SAVI (OSAVI) (Rondeaux et al. 1996).

The PRI is a normalized difference index using two narrow reflectance bands located at 531 nm and 570 nm (as seen in equation (1)), and was developed to detect changes in the xanthophyll pigment. Through a process called de-epoxidation, which occurs when available light energy exceeds the capacity of photosynthetic reactions, the xanthophyll cycle pigments provide a means to dissipate excess light energy through the production of heat, thus protecting the photosynthetic apparatus.

$$PRI = \frac{(R_{531} - R_{570})}{(R_{531} + R_{570})} \tag{1}$$

The MCARI is a modification of the Chlorophyll Absorption in Reflectance Index, which in turn was developed by Kim (1994) to minimize the effects of non-photosynthetic materials within the field of view. This index relates the depth of the chlorophyll absorption region located at 670 nm with reflectance values found at 550 nm and 700 nm (as seen in equation (2)).

$$MCARI = (R_{700} - R_{670}) - 0.2(R_{700} - R_{550}) \times \left({}^{R_{700}}\!/_{R_{670}} \right) \tag{2}$$

The SAVI and OSAVI were developed to reduce the influence of soil on canopy reflectance, especially in locations where the leaf area index is very low. These two vegetation indices are essentially identical to one another as both compare the depth of the chlorophyll absorption region located at 670 nm with reflectance values found at 801 nm. They only differ in the value assigned to the constant L, 0.5 for the SAVI, which is replaced by 0.16 in the OSAVI (as seen in equations (3) and (4)).

$$SAVI = (1 + L) \times \frac{(R_{801} - R_{670})}{(R_{801} + R_{670} + L)} \tag{3}$$

$$OSAVI = (1 + 0.16) \times \frac{(R_{801} - R_{670})}{(R_{801} + R_{670} + .016)} \tag{4}$$

2.3.2.2 Band Depth Parameter Calculations The band depth analysis was completed on continuum-removed spectra located between 550 and 750 nm (refer to Figure 2.2), the red absorption pit (Mutanga and Skidmore 2004 b). To our knowledge, continuum removal has not yet been used for the estimation of photosynthesis rates, but this area of the spectrum has been strongly related to chlorophyll a and b absorption regions (Thomas and Gausman 1977). Because chlorophyll pigments act to absorb and transfer light energy to the photosynthetic apparatus, they may provide useful information concerning the physiological state of the leaves (Guo and Trotter 2004). It follows that there may be a link between this region of the spectral curve and the measured leaf CO_2 exchange rates.

For this analysis, the continuum-removed spectrum is obtained using the methods followed by Mutanga and Skidmore (2004 a). The initial step is to calculate the equation of a line between the continuum end points of the reflectance data. The continuum line is a series of straight-line segments that connect local spectral maxima. For the present study, this corresponds to the spectral maxima on either side of the chlorophyll absorption region. Subsequently, the continuum-removed reflectance $R'_{(\lambda i)}$ is obtained by dividing the reflectance value $R_{(\lambda i)}$ for each waveband ($_i$) in the absorption feature by the reflectance level of the continuum line $R_{c(\lambda i)}$ at the corresponding wavelength (see equation (5)).

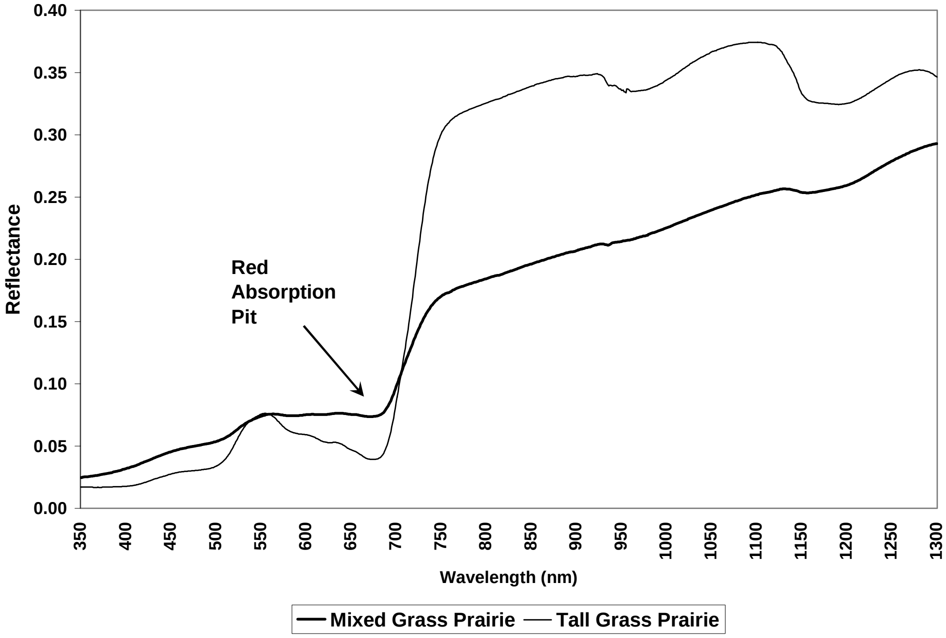

Figure 2.2 Mean spectral curves for typical northern mixed grass prairie and tall grass prairie. The red absorption pit (located at 550 – 750 nm) is also indicated. Spectral data for tall grass prairie were collected by Guo (unpublished data) at Douglas County, Kansas, in June of 2000.

$$R'_{(\lambda i)} = \frac{R_{(\lambda i)}}{R_{c(\lambda i)}} \tag{5}$$

Continuum-removed absorption features can be compared to one another by first scaling them to the same depth at the band center, thus allowing a comparison of the shapes of absorption features. Band depth (BD) is calculated by subtracting the continuum-removed reflectance $R'_{(\lambda i)}$ from 1 (see equation (6)).

$$BD_{(\lambda i)} = 1 - R'_{(\lambda i)} \tag{6}$$

The band depth maximum (BDMax), is simply the maximum band depth value attained for each continuum-removed spectrum.

From the continuum removed spectra, the chlorophyll absorption area (CAA) can also be calculated by multiplying the depth (BD) by the width ($\Delta\lambda$) of each channel, and then summing the products (see equation (7)).

$$CAA = \sum \left(BD_{(\lambda i)} \times \Delta\lambda \right) \tag{7}$$

2.3.3 Data Analysis

There were several CO_2 exchange measurements with extremely high values that were likely caused by machine abnormality or environmental conditions. Using the method described by Stevens (1996), outliers located three standard deviations above and below the mean were identified and then removed from the photosynthesis dataset. The Kolmogorov-Smirnov goodness of fit test and the Shapiro-Wilk test both indicated that the data were normally distributed.

The statistical analysis included Pearson correlation analysis, linear regression, and stepwise multiple regression using a commercial software package (Statistical Product and Service Solutions 11.0, SPSS Inc., Chicago, Illinois). A significance of $p = 0.05$ was used for all analyses. Pearson's correlation analysis was used to identify the strength of the relationships between CO_2 exchange and the following spectral variables: PRI, MCARI, SAVI, OSAVI, BDMax, and CAA based on site averaged data. Using the variable with the highest correlation with CO_2 exchange, linear regression was completed in order to determine the coefficient of determination between the two variables. Finally, stepwise multiple regression was conducted to determine if any other reflectance variables could account for any unique variance in CO_2 exchange rates.

2.4 Results

2.4.1 Biophysical Properties of the Study Area

The mixed grass prairie has unique biophysical properties with large amounts of dead materials (Table 2.2). Percentage cover indicates that on average, the largest proportion of ground cover consists of grass (28.7%), followed by moss (26.1%), and then standing dead material (19.5%). When the biomass was dried and weighed, dead material contributed 55% of the total biomass on average, ranging from 32% to 72% among the 13 sites. Dead materials consistently made up the largest fraction among the four biomass categories: grass, forbs, shrubs and dead materials across all of the sites.

2.4.2 Spectral Characteristics of Mixed Grass Prairie

The typical spectral curve of the northern mixed grasslands differs from the typical spectral curve of healthy, green vegetation such as that found in tall grass prairie (refer to Figure 2.2). When looking at the spectral curve of northern mixed grasslands vegetation, there is less distinction between the green and red absorption regions, located at 550 nm and 650 nm respectively. As well, the near-infrared region has lower reflectance values compared to the typical tall grass prairie vegetation. Overall, the spectral curve of the grasslands vegetation appears flattened, with less variation.

2.4.3 CO_2 Exchange Rates and Spectral Properties

Pearson's correlation analysis of the CO_2 exchange rates and spectral variables revealed that PRI was the only variable that has a significant relationship with the measured CO_2 exchange rates ($r = 0.678$, $p = 0.05$) (refer to Table 2.3).

Table 2.3 Correlation between CO_2 exchange and spectral variables for sites (n=13).

	PRI	MCARI	SAVI	OSAVI	CAA	BDMax
CO_2 Exchange	.678*	.042	0.155	.121	.247	.063

*Correlation is significant at the 0.05 level (2-tailed)

Upon further investigation into the relationship between the CO_2 exchange and PRI, it was found that the linear regression r^2 value was 0.46

(*p*=0.011) (refer to Figure 2.3). A stepwise multiple regression revealed that no other measured variables contributed to explaining the variance observed in the CO_2 exchange.

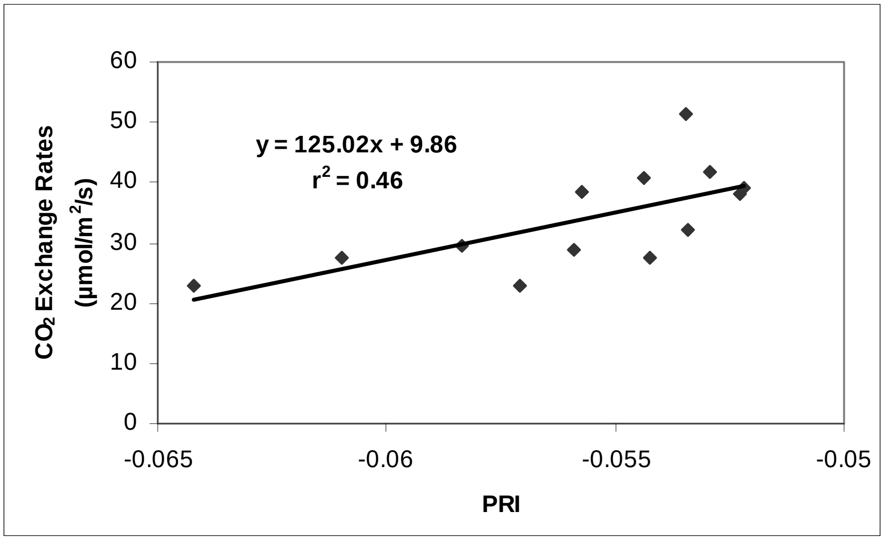

Figure 2.3 Graph of data points and linear regression line for sites (n=13).

2.5 Discussion

2.5.1 CO_2 Exchange and PRI

The present study found PRI to be the best vegetation index for the prediction of CO_2 exchange rates for our research area in the northern mixed grass prairie. Having established this, the relationship between PRI and CO_2 exchange rates was slightly lower than anticipated (explaining 46% of the variance), while R^2 in previous laboratory experiments explained as much as 54% of the variance (Gamon et al. 1997). However, the current research was conducted in field conditions where there are background effects from soil, litter and dead materials, which are negligible in laboratory conditions. Furthermore, previous research has focused on the relationship between CO_2 and PRI with only one species within the field of view, while the northern mixed grasslands can have a number of different species within each quadrat. These additional confounding factors under field conditions would be expected to result in a weaker relationship between PRI and CO_2 exchange than those found under laboratory conditions.

The finding that PRI is the best spectral measurement to represent photosynthesis is consistent with previous research (Gamon et al. 1992; Gamon et al. 1997; Evian et al. 2004; Guo and Trotter 2004). The success of this index is likely because it is specifically related to the reflectance of the xanthophyll pigments (located at 531 nm), and this region is a useful optical indicator of changing photosynthetic activity (Rahman et al. 2001).

2.5.2 Shortcomings with Other Spectral Transformations

There are several reasons as to why the other spectral transformation variables (MCARI, SAVI, OSAVI, CAA, and BDMax) did not have satisfactory results. Although the MCARI was developed to measure the depth of the chlorophyll absorption region while minimizing the effects of non-photosynthetic materials, it is sensitive to soil reflectance properties; as a result, it can be difficult to interpret for low leaf area index (LAI) values (Daughtry et al. 2000). The LAI values collected for this study were generally found to be below 1.5 (Guo et al. 2005). Another reason for the poor results is because vegetation indices that are insensitive to background reflectance, such as the SAVI and OSAVI, are also relatively insensitive to leaf chlorophyll concentration (Daughtry et al. 2000). Consequently, it is difficult to remove soil background effects, yet enhance the reflectance of the photosynthetic apparatus of the plants. Further to these difficulties are problems associated with utilizing the chlorophyll absorption region. For example, relatively low chlorophyll contents are sufficient to saturate the absorption region in the 660-680 nm region, thus reducing the sensitivity to high chlorophyll contents for the spectral indices which are based in this region (Sims and Gamon 2002). Although the chlorophyll contents of species found in the research area are unknown, it is possible that they are high enough to cause saturation.

While PRI is specifically related to the reflectance characteristics of the xanthophyll pigment, the other spectral transformation variables are associated with the general chlorophyll absorption region. While chlorophylls are necessary for photosynthesis, absorbing and transferring light energy to the photosynthetic apparatus, perhaps the xanthophylls more closely reflect the photosynthetic activity of the plant. This is because they contribute not only to energy transfer but also to the dissipation of excess light energy, which better represents the physiological state of the leaves.

2.6 Conclusions and Future Directions

The primary conclusion of this study is that PRI is the best vegetation index for the prediction of mid-season CO_2 exchange rates for our study area located in the northern mixed grass prairie landscape. This indicates that the PRI, which has traditionally been used in laboratory conditions to predict CO_2 exchange, can also be applied at the canopy level in grassland field conditions. To our knowledge, this is the first time that a direct correlation between hyperspectral indices and landscape-level CO_2 fluxes has been shown within the grassland biome. This research is a step towards the development of a simpler alternative to the more complex models used to estimate terrestrial biophysical properties (e.g. SiB2 [Sellers et al. 1996]), which typically require far more parameterization. Research in the future should establish the relationship between CO_2 exchange rates and hyperspectral data at the landscape level through the incorporation of satellite images.

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CHAPTER 3 - PREDICTION OF LEAF CO_2 EXCHANGE RATES USING A SPOT IMAGE

3.1 Abstract

With increasing atmospheric CO_2 concentrations, researchers are looking for alternative methods to quantify the terrestrial carbon sink. Although the link between CO_2 exchange and spectral reflectance has been established with flux net towers, limited research has been conducted using a leaf chamber. We have found that narrow band vegetation indices derived from hyperspectral remote sensing data can be used to predict leaf CO_2 exchange rates. However, this relationship was developed using ground level hyperspectral data, and it is unknown whether this relationship is applicable to satellite derived vegetation indices. In an effort to determine the applications of satellite remote sensing in the estimation of carbon exchange measured with a leaf chamber, the primary objective of this study is to evaluate several broad band vegetation indices derived from a SPOT image in the prediction of leaf CO_2 exchange rates in a northern mixed-grass prairie ecosystem. Biophysical measurements and CO_2 exchange rates were collected from 24 sites located in and around Grasslands National Park, Saskatchewan, Canada. Cubic regression showed that both Normalized Difference Vegetation Index and Soil Adjusted Vegetation Index could explain 46% of the variance observed in the CO_2 exchange rates.

Key Words: Leaf CO_2 exchange, mixed-grass prairie, vegetation index

3.2 Introduction

International agreements, particularly the Kyoto Protocol have made increasing atmospheric CO_2 concentrations and global carbon balance an important political and scientific topic. While much attention has focused on the carbon sink capabilities of tropical and boreal forests, grasslands need to be considered in global estimates of carbon sinks. Grasslands are one of the most widespread vegetation types worldwide, covering 15 million km^2 in the tropics and a further 9 million km^2 in temperate regions; together, these locations constitute nearly one-fifth of the world's land surface (Lieth 1978). There is much evidence that the photosynthetic process in grassland ecosystems contribute to the lowering of anthropogenic CO_2 emissions by securing the atmospheric carbon dioxide into plant biomass (Hall and Scurlock 1991; Owensby et al. 1993; Leadley et al. 1999; Li et al. 2004). Yet there is still some debate as more recent research has concluded that grasslands may contribute to atmospheric CO_2 levels as they are a carbon source (Zhang et al. 2005).

Determining the mitigation capacity of grasslands on atmospheric CO_2 requires a better understanding of ecosystem fluxes, factors that determine the magnitude of fluxes, and the feedback of ecosystems fluxes on climate. Two major methods of measuring the CO_2 flux have been established. First, tower-based systems (such as Euroflux, Fluxnet Canada, Ameriflux) are used primarily as they offer secure, continuous, and long-term measurements of ecosystem scale carbon fluxes (Baldocchi et al. 1988; Dugas 1993; Dugas et al. 1997). Throughout the 1990s and continuing into the new millennium, CO_2 flux studies have been focused on the establishment and expansion of flux tower networks and developing the required methodology. However, the main drawback of these systems is the high cost of installing and maintaining the towers.

Infra-red gas analysis chambers are also used to measure fluxes. Chambers vary in volume from those that measure the gas exchange for individual leaves ($\approx 10^{-5}$ m^3) to those that measure it for an entire soil/plant canopy ($<10^3$ m^3). Unfortunately, this method is also associated with problems: chamber measurements are usually non-continuous and may alter the temperature, radiation, and wind conditions inside the chamber relative to that outside (Denmead 1984; Monteith 1990; Leuning and Foster 1990). This may result in non-representative measurements. In spite of their limitations, chambers are more portable and less expensive than flux towers, and are also useful for making replicated measurements in small plots.

Remote sensing tools are useful in large-scale ecosystem studies as they allow large area, non-destructive, and real-time acquisition of biophysical conditions in a more cost effective manner than traditional *in situ* measurements (Inoue 2003). Remote sensing techniques, based on measuring the reflected radiation from plant canopies, have potential to evaluate the biochemical characteristics of many plants within the field of view of the sensor. For example, a number of studies incorporating satellite data have been dedicated to the estimation of plant biomass (Friedl et al. 1994; Todd et al. 1998; Wylie et al. 2002), leaf area index (Friedl et al. 1994; Qi et al. 2000; Broge and Leblanc 2000; Wylie et al. 2002), and plant pigment content (Broge and Leblanc 2000; Broge and Mortensen 2002). Remote sensing tools provide a method for investigating spatial patterns of biophysical properties in a manner less cumbersome than traditional modeling approaches, which require more extensive parameterization (Rahman et al. 2001; Ustin et al. 2004).

Broad band remote sensing data has previously been used to estimate different measurements of productivity, including CO_2 exchange and gross primary productivity (GPP) in the grasslands region (Wylie et al. 2003; Hunt et al. 2004; Wylie et al. 2004; Gilmanov et al. 2005; Sims et al. 2005). Several of these studies utilized either broad or intermediate resolution satellite images (AVHRR, MODIS and SPOT) to predict average daily CO_2 exchange rates (averages were calculated from measurements ranging from 8-14 days) (Wylie et al. 2003; Gilmanov et al. 2005; Sims et al. 2005). In general, the researchers concluded that NDVI, or f_{APAR} (fraction of incident absorbed photosynthetically active radiation, a measurement derived in part from NDVI) were predictive of measured CO_2 exchange rates. However, flux towers were used to measure the CO_2 exchange rates in each of the above studies.

Hunt et al. (2004) came to similar conclusions as the flux net studies discussed above; they found f_{APAR} to be useful in estimating net ecosystem exchange of CO_2. However, their methods differed slightly as they collected the net ecosystem exchange data from an aircraft. More pertinent to the current study, Hunt et al. (2004) took a secondary measurement of net ecosystem exchange using a 1 m^2 semi-permanent ecosystem chamber to compare the AVHRR spectral measurements, and found that f_{APAR} explained 44% of the variance observed in the net ecosystem exchange measurements.

Gamon et al. (1995) employed a leaf chamber to measure midday leaf CO_2 uptake in two types of California canopies: semi-deciduous shrubs, and evergreens. The researchers calculated broad band vegetation indices from ground level hyperspectral data to simulate satellite data. Only a weak relationship was found between the NDVI measurements and leaf CO_2 exchange in the semi-deciduous shrub environment (Gamon et al. 1995). Since the canopies of California semi-deciduous shrubs and the northern mixed prairie are very different from one another, it is unlikely that the previous findings are applicable for our landscape. To our knowledge, there have been no studies to date that incorporate satellite level remote sensing data and grassland CO_2 exchange as measured with a leaf chamber.

With little research in this area, it is difficult to make predictions about the ability of multispectral satellite images to estimate leaf CO_2 exchange rates. However, the relationship between Photochemical Reflectance Index (PRI) derived from ground level hyperspectral spectral data and leaf CO_2 exchange rates has been established in the northern mixed grass prairie, with results that are comparable to similar studies conducted in laboratory conditions (Black and Guo, In Press). It is possible that this relationship may be extended to satellite level, yet it may be more reflective of overall grassland productivity to consider not only leaf CO_2 exchange rates, but also other measurements of productivity such as leaf area index and biomass as contributing variables. It can be concluded that there is a need for more research in this area, as the potential for multispectral remote sensing products to effectively determine biophysical parameters is known, but the relationship with leaf CO_2 exchange has not yet been established.

This research explores the utility of using a multispectal SPOT image and biophysical measurements in the prediction of mid-season CO_2 exchange rates as measured by a small leaf chamber, the LC*pro*. The primary objective of this study is to determine the application of broadband vegetation indices, in combination with other indicators of productivity: Plant Area Index (PAI) and dried grass biomass, to explain the variation found in leaf CO_2 exchange rates.

In addition, a secondary objective of this research was to investigate leaf CO_2 exchange rates across different management schemes (grazed and ungrazed) as well as different topographies (sloped and upland). While the impacts of topography upon photosynthesis are fairly well established, previous research regarding the impacts of grazing has not been consistent. Grazing has been correlated to a decrease in CO_2 exchange (Frank 2004; Hafercamp and MacNeil 2004), as well as an increase (Owensby et al. 2006). Yet other studies have concluded that grazing, even heavy grazing has no effect on CO_2 exchange (LeCain et al. 2002; Risch et al. 2006). The portability of the leaf chamber allows us to measure the photosynthesis across these different environments, and compare them to one another.

3.3 Methods

3.3.1 Site and Data

The study area was located in the West Block of Grasslands National Park (GNP) and surrounding pastures, in southwest Saskatchewan, Canada (N 49º12’, W 107º24’). This area falls within the Great Plains, which are characterized by semiarid climate, flat landscape and large areas dominated by grass species (Coupland 1993). Grasslands National Park is further located within the mixed grass prairie, one type of biome found within the Great Plains. This biome is a transitional zone between tall grass and short grass prairie (Bragg 1995). The climate in the study area is semi-arid; winters are long, cold and dry, while summers are short, hot and comparatively wet (Environment Canada 2000). Average monthly temperatures range from -12.4 ºC in January to 18.3 ºC in July, and average precipitation is approximately 350 mm per year (Environment Canada 2000). In the study year (2005) the total precipitation was lower than normal at 300 mm. The soils in the study area are brown Chernozemic clay loam soils (Saskatchewan Soil Survey 1992). The dominant native grass species found in the study site are June grass (*Koeleria gracilis*), needle-and-thread grass (*Stipa comata*), blue grama (*Bouteloua gracilis*), and western wheat grass (*Agropyron smithii*).

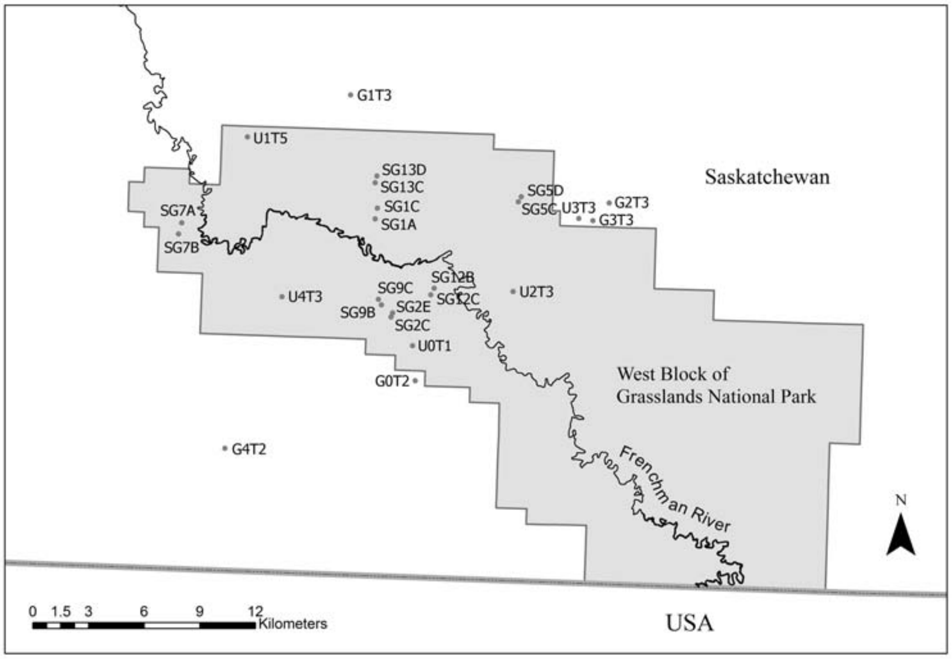


Figure 3.1 Distribution of sites in Grasslands National Park and surrounding pastures.

The data were collected in mid-June 2005, the approximate date for peak greenness in the study area. A total of 24 randomly selected sites were visited, of which 5 were upland grazed, 5 were upland ungrazed, and 14 were sloped ungrazed (see Figure 1). The grazed sites were grazed by cattle herds. The grazing pressure was moderate to heavy, and the range condition would be classified as poor (Abouguendia 1990). Unfortunately, due to the steeply sloping topography in our research area, it is impossible to measure sloped grazed sites for comparison, as they are too steep to be grazed by cattle.

At each of these sites, field sampling was conducted along two 100 m transects that ran perpendicular in north-south and west-east directions, intersecting in the centre to form a cross. Quadrats were located at 20 m intervals along each transect, resulting in a total of 10 quadrats per site. The 20 m sampling resolution interval is supported by previous research conducted in the northern mixed grass prairie indicating that a sampling interval of 10 to 50 m is most suitable for this environment (Davidson and Csillag 2001). Photosynthetic exchange rates, spectral reflectance, cover, PAI, and biomass data were collected from each quadrat.

Leaf CO_2 exchange rates were sampled along these transects using an LC*pro* (ADC BioScientific Ltd., Hoddesdon, UK). Using an ‘open system’ configuration (where fresh air is continuously passed through the plant leaf chamber), the chamber conditions were controlled for humidity and temperature to avoid condensation forming, while incoming CO_2 and photosynthetically active radiation (PAR) levels were maintained at ambient conditions. Gas exchange measurements were made on approximately 3 plant leaves located within the same quadrat used for the biophysical measurements. The photosynthesis data were then amalgamated into mean values for each site. This was completed in order to reduce variance and to obtain a measurement for each site that represents the average conditions.

Plant area index (PAI - projected area of all vegetation parts normalized by the subtending ground area) was measured using the LiCor LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, NE, USA). At each site, PAI is the average of four automatically calculated PAI values; each was the comparison result of one above canopy reading followed by 10 below canopy readings completed within two minutes to avoid atmospheric variation. The 10 below canopy readings were set at 5 m intervals. The sensor was shaded when observations were being taken to reduce the glare effect of direct sunshine.

Canopy cover was estimated at both canopy and ground level. Canopy level cover was recorded by species. Lichen, moss, litter, bare soil, and rock were recorded at ground level. To standardize the data, only the cover that could be observed from overhead was recorded, so the sum of canopy level cover was less than 100%. The remaining gap was assigned to lichen, moss, litter and bare ground according to the proportion they contributed to the total ground level cover. Therefore, the sum cover of grass, forbs, shrubs, litter, moss, lichens, bare ground, and rock is equal to 100%. Biomass was harvested after the other measurements were completed. Clipped fresh biomass was sorted into four groups: grass, forbs, shrubs, and dead material. These samples were dried in an oven for 48 hours at 60 ºC and weighed again. A description of these measured variables can be found in Table 3.2.

A SPOT 4 HRV image with 20 m resolution was acquired for the research area on June 22nd, 2005 (Path 37, Row 26) (false colour composite shown in Figure 3.2). The satellite image was processed for geometric and radiometric corrections using PCI Geomatica V.9.1. An accuracy of 0.3 RMS or better (representing approximately 6 metres or less error on the earth’s surface) was ensured throughout the geometric correction process. Topography distortions were corrected using a Digital Elevation Model (DEM), obtained from Grassland National Park’s GIS database. The improved dark object image subtraction method was employed for atmospheric and radiometric corrections

Chavez (1988). After corrections, the digital number (DN) values were converted to reflectance values. Each of the 24 sites was located on the image using GPS coordinates. For each site location, the central pixel, as well as the pixel directly to the north, south, east, and west, were used to calculate a mean value for each of the bands: red, green, NIR, and SWIR. This pattern was selected as it approximately corresponds to the north-south and west-east transects employed for the biophysical data collection.

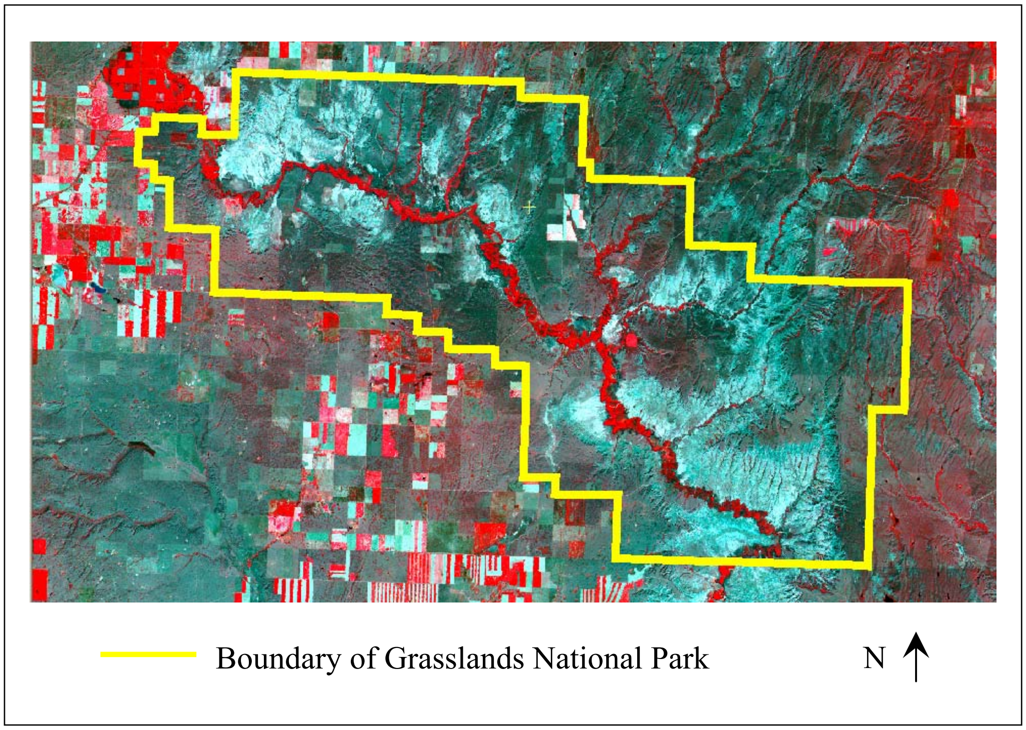


Figure 3.2 False colour composite of study area, acquired June 22nd 2005 (SPOT 4 HRV, Path 37, Row 26). (R: NIR; G: Red; B: Green). Note that this image is not to scale.

3.3.2 Broad Band Vegetation Indices

Spectral vegetation indices (VIs) are ratios of two or more bands or slopes derived from the reflectance of the green vegetation. Numerous VIs have been developed to characterize vegetation canopies. They are formulated to enhance the spectral reflectance of the green portion of the spectrum (associated with vegetation) while minimizing noise caused by variations in soil colour, irradiance conditions, sun angle, amount of senescent materials, and atmospheric conditions.

Table 3.1 Vegetation indices and formulae.

Acronym	Index Name	Formula	Reference
SR	Simple Ratio	$SR = \frac{\rho_{red}}{\rho_{nir}}$	Birth and McVey (1968)
NDVI	Normalized Difference Vegetation Index	$NDVI = \frac{(\rho_{nir} - \rho_{red})}{(\rho_{nir} + \rho_{red})}$	Rouse et al. (1974)
SAVI	Soil Adjusted Vegetation Index	$SAVI = (1 + L) \times \frac{(\rho_{nir} - \rho_{red})}{(\rho_{nir} + \rho_{red} + L)}$	Huete (1988)
ATSAVI	Adjusted Transformed Soil-Adjusted Vegetation Index	$ATSAVI = \frac{a(-a\rho_{red} - b)}{a\rho_{nir} + \rho_{red} - ab + X(1 + a^2)}$	Baret and Guyot (1991)

For the current study, several VIs were calculated from the SPOT image including: Simple Ratio (SR), Normalized Difference Vegetation Index (NDVI), Soil Adjusted Vegetation Index (SAVI), and Adjusted Transformed Soil-Adjusted Vegetation Index (ATSAVI). The VI formulae and references are presented in Table 3.1. NDVI and SR were selected because they have both been used to predict net ecosystem exchange in previous research (Gamon 1995; Wylie et al. 2003; Gilmanov et al. 2005; Sims et al. 2005). SAVI was selected due to its applicability to the research site; it was developed to reduce the influence of soil on canopy reflectance, especially in locations where the leaf area index is very low. ATSAVI was selected because previous research has demonstrated that this index is suitable for our study area (He and Guo In Press).

3.3.3 Data Analysis

Using the method described by Stevens (1996), outliers located three standard deviations above and below the mean were identified and then removed from the photosynthesis dataset. Only one CO_2 exchange measurement with an extremely high value was removed with this method; it was likely caused by machine abnormality or environmental conditions. The Kolmogorov-Smirnov goodness of fit test and the Shapiro-Wilk test both indicated that the data was normally distributed.

The statistical analysis was completed using a commercial software package (Statistical Product and Service Solutions 11.0, SPSS Inc., Chicago Illinois). A significance of $p = 0.05$ was used for all analyses. The statistical analysis included Pearson's correlation analysis, linear and non-linear regression, and MANOVA. Pearson's correlation analysis was used to identify the strength of the relationships between CO_2 exchange and the following spectral and biophysical variables: SR, NDVI, SAVI, ATSAVI, dried grass biomass, and PAI. Linear and non-linear regressions were used to determine the coefficient of determination between CO_2 exchange and the most highly correlated variable as determined by the Pearson's correlation. Stepwise multiple regression was conducted to determine which of the reflectance or biophysical variables could account for any unique variance in the measured CO_2 exchange rates. Finally, MANOVA was used to determine if there were significant differences between the three categories of sites (upland ungrazed, upland grazed, sloped ungrazed) in terms of CO_2 exchange rates, dried grass biomass, and PAI.

3.4 Results

3.4.1 Biophysical Properties of the Study Area

The northern mixed grass prairie has unique biophysical properties with large amounts of dead materials (Table 3.2). Percentage cover indicates that on average, the largest proportion of ground cover consists of moss (27 %), followed by litter (21 %), and then grass (18 %). When the biomass was dried and weighed, dead material contributed 67 % of the total biomass on average, ranging from 28 % to 83 % among the 24 sites. Dead materials consistently made up the largest fraction among the four biomass categories: grass, forbs, shrubs and dead materials across all of the sites.

There is further evidence of this found in the false colour composite of the SPOT image (Figure 3.2). The red areas in the image correspond to higher vegetation quantities, located mainly along the Frenchman River (shrubs) and in agricultural areas outside of park boundaries. However, the bright aqua colour which covers the majority of the park area is associated with lower green vegetation cover (grass).

Table 3.2 Maximum, minimum, mean and standard deviation values for measured and calculated variables.

Variables	Maximum	Minimum	Mean	Standard Deviation
Grass (%)	25.10	13.20	18.31	3.49
Forbs (%)	12.90	1.75	6.47	2.39
Shrubs (%)	7.90	0.00	0.72	1.67
Standing Dead (%)	31.35	7.15	13.49	4.94
Litter (%)	38.05	8.40	20.58	7.50
Moss (%)	44.40	6.61	27.29	11.42
Lichen (%)	21.96	0.24	6.68	5.21
Rock (%)	12.02	0.00	2.73	3.26
Bare Ground (%)	10.67	0.00	2.38	3.12
Dried Grass Biomass (g/m^2)	72.35	17.35	45.24	15.96
Dried Forb Biomass (g/m^2)	29.01	1.07	11.53	6.68
Dried Shrub Biomass (g/m^2)	110.98	0.00	10.13	24.68
Dried Dead Biomass (g/m^2)	292.88	53.45	146.53	68.21
Total Dried Biomass (g/m^2)	373.66	80.93	213.44	80.52
CO_2 Exchange Rates ($\mu mol/m^2/s$)	9.91	4.20	7.18	1.65
SR	0.58	0.44	0.51	0.04
NDVI	0.39	0.27	0.32	0.03
SAVI	0.58	0.40	0.48	0.05
ATSAVI	0.23	0.09	0.15	0.04

3.4.2 Predicting CO_2 Exchange Rates with Spectral and Biophysical Properties

Of all the spectral and biophysical variables, Pearson's correlation analysis found a significant relationship between CO_2 exchange and SR (refer to Table

3.3). Pearson's correlation analysis found no significant relationships between the CO_2 exchange rates and either dried grass biomass or PAI.

Table 3.3 Correlation between CO_2 exchange and spectral and biophysical variables for sites (n=24).

	SR	NDVI	SAVI	ATSAVI	Dried Grass Biomass	PAI
CO_2 Exchange Rates	-0.413*	0.398	0.398	0.375	0.248	-0.020

*Correlation is significant at the 0.05 level (2-tailed)

Upon further investigation into the relationship between the CO_2 exchange and SR, it was found that the linear regression r^2 value was 0.17 ($F_{1,22} = 4.53$, $p = 0.045$) (refer to Figure 3.3). However, it appears that this relationship is better represented with a non-linear model, as r^2 increased to 0.46 with the cubic regression model ($F_{1,21} = 8.81$, $p = 0.002$) (refer to Figure 3.4). A stepwise multiple regression determined that SR in combination with SAVI increased r^2 to 0.46 ($F_{2,21} = 8.84$, $p = 0.02$).

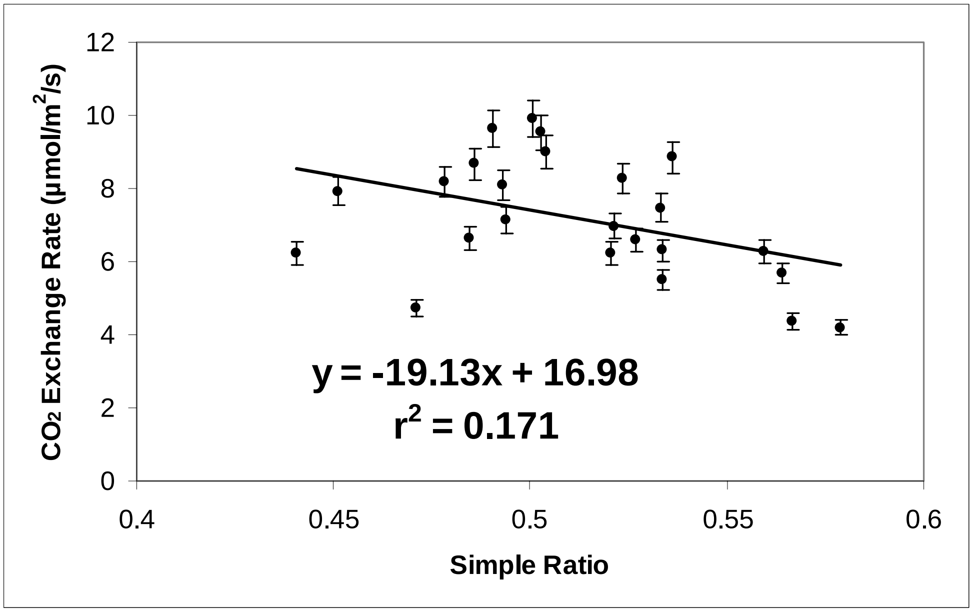


Figure 3.3 Graph of data points and linear regression line for sites (n=24).

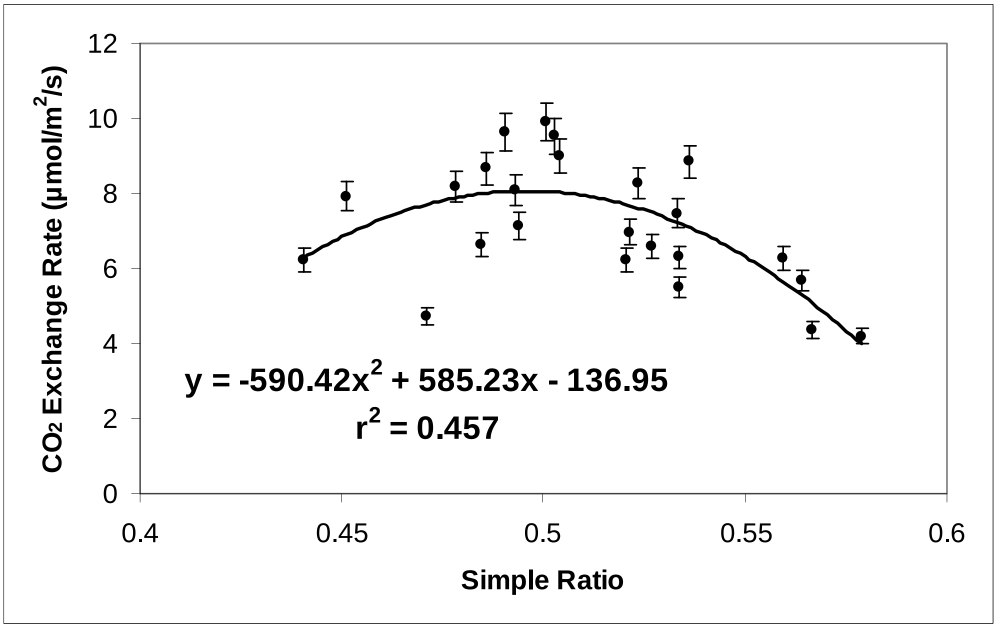


Figure 3.4 Graph of data points and cubic regression line for sites (n=24).

3.4.3 CO_2 Exchange Rates in Different Management Schemes and Topographies

A MANOVA identified significant differences between the site locations with regards to CO_2 exchange rates, ($p = 0.026$). Post-hoc analyses using Tukey's Honestly Significant Difference revealed that the CO_2 exchange rates for sloped ungrazed sites were significantly lower than CO_2 rates for upland grazed sites ($p = 0.033$). However, the CO_2 exchange rates for upland ungrazed sites were not significantly different from upland grazed sites ($p = 0.758$) or sloped ungrazed ($p = 0.179$) (refer to Table 3.4). We can conclude that the difference observed in CO_2 exchange rates is due to a combination of change from both site topography and site management. MANOVA found no significant differences in the means of the different site locations (grazed upland, ungrazed upland, and sloped ungrazed) with regards to PAI (p = 0.165), and dried grass biomass (p = 0.741).

Table 3.4 Mean CO_2 exchange rates for each site, where a and b are significantly different from one another.

Site	n	Mean CO_2 Exchange Rate for Each Site ($\mu m/m^2/s$)	
Sloped Ungrazed	14	6.46^{a}	
Upland Ungrazed	5	7.86^{ab}	7.86^{ab}
Upland Grazed	5		8.52^{b}

3.5 Discussion

3.5.1 Predicting CO_2 Exchange Rates with Linear Regression

The finding that SR was the only vegetation index correlated to leaf CO_2 exchange rates for our research area within the northern mixed grass prairie was unexpected, especially given the consistent results of NDVI with similar research (i.e. Gamon et al. 1995; Wylie et al. 2003; Hunt et al. 2004; Gilmanov et al. 2005; Sims et al. 2005). However, upon investigation it appears that NDVI, SAVI, and ATSAVI have correlation values with CO_2 exchange only slightly lower than the correlation value between SR and CO_2 exchange. Perhaps with a larger sample size, these vegetation indices would also be significant.

The results from the linear regression model were lower than expected; Hunt et al. (2004) found f_{APAR} to explain approximately 64% of the variance observed in the net ecosystem exchange as measured from an aircraft. In the same study, Hunt et al. found that this value dropped to 44% when the net ecosystem exchange was measured with an enclosed ecosystem chamber. Hunt et al. do not explain this loss of variance accounted for. This is the lowest r^2 we found in pertinent research, all studies utilizing a flux net tower were higher, ranging from 0.46 (Gilmanov et al. 2005) to 0.79 (Gamon et al. 1995).

It is possible that a flux tower will allow for a more accurate representation of the ecosystem flux to be captured. Flux towers have the ability to incorporate all sources of respiration, including that of non-photosynthetic plant materials, as well as heterotrophic respiration from animals, fungi and bacteria associated with the decomposition of residue and soil organic matter. Furthermore, flux towers measure the flux across a large spatial area, referred to as the footprint, which can vary in size from 400 m^2 to 1500 m^2 (Baldocchi et al. 1988; Dugas 1993; Dugas et al. 1997). Perhaps this type of measurement, extending across a large geographic area better corresponds to the pixilated data obtained from the satellite images.

With a semi-permanent chamber, as with the one used by Hunt et al. (2004) there may still be an adequate measurement of the net ecosystem exchange, as soil and plant respiration are also captured. However, the leaf chamber employed for the current research does not measure heterotrophic respiration, nor any respiration associated with non-photosynthetic plant materials. Although the leaf chamber measurements were averaged to site level in order to better correspond to the satellite data, they may not give an adequate representation of ecosystem exchange in comparison to a flux tower.

3.5.2 Predicting CO_2 Exchange Rates with Non-Linear Regression

A non-linear regression appears to be a better fit for our data set than a linear model, as SR explained more of the variance seen in CO_2 exchange rates with the cubic model compared to the linear model, $r^2 = 0.456$ and 0.171, respectively. Interestingly, although SR was the only vegetation index that resulted in a significant linear relationship with CO_2 exchange, all of the vegetation indices resulted in significant relationships with CO_2 exchange when employing the cubic model. The r^2 varied from 0.442 with ATSAVI ($p = 0.008$), to 0.457 for both SAVI and NDVI ($p = 0.002$) (refer to Table 3.5). All of these relationships replicate the curve shown in Figure 3.4. As all vegetation indices are generally indicative of biomass quantity and health, it appears that sites with very low and very high biomass levels are associated with lower CO_2 exchange rates. Sites with intermediate quantities of biomass have higher CO_2 exchange rates; there appears to be an optimum biomass window for increased levels of CO_2 exchange.

Table 3.5 Significant relationships between vegetation indices and CO_2 exchange using the cubic model.

Vegetation Index	r^2	p
SR	0.456	0.002
NDVI	0.457	0.002
SAVI	0.457	0.002
ATSAVI	0.442	0.008

In arid climates such as the northern mixed grass prairie, regions with very low biomass are often associated with limited soil moisture availability.

Available soil moisture has also been identified as one of the primary determinants of photosynthetic functioning (Hall and Rao, 1999). It is probable that sites with low vegetation index measurements (corresponding to decreased biomass) also have low soil moisture, and this is likely responsible for the decrease in photosynthesis. At locations with very high biomass quantities however, it is possible that there is increased competition for available resources, and perhaps the plants in this location have decreased photosynthetic functioning as a result. This finding adds support to previous research concluding that an increase in competition corresponds to a decrease in biomass (Bonser and Reader 1995; Fowler 2002; Foster 2002). Unfortunately, for the current research these explanations are speculation, as we do not have measurements for soil moisture or soil nutrient status.

3.5.3 Predicting CO_2 Exchange Rates with Stepwise Multiple Regression

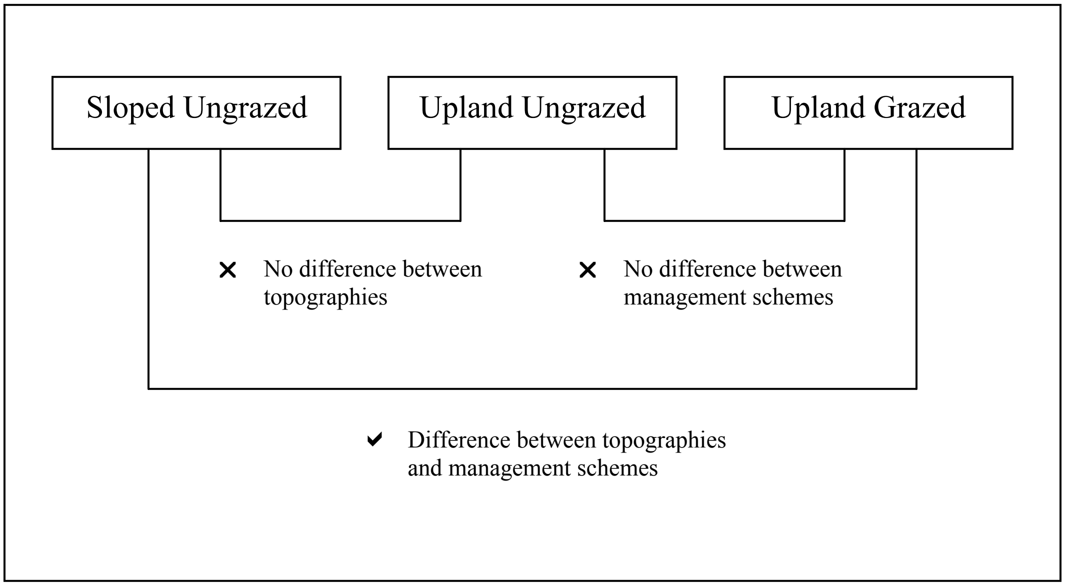
The stepwise multiple regression determined that SR in combination with SAVI explained 46% of the variance observed in the CO_2 exchange rates. This is reasonable, given that SR is indicative of vegetation health (Jensen 2005), while SAVI was developed to reduce the influence of soil on canopy reflectance in locations where the leaf area index is very low (Huete 1988). The combination of these two vegetation indices should act to maximize sensitivity to vegetation, while minimizing sensitivity to soil effects.

The finding that neither PAI, nor dried grass biomass were selected by the stepwise multiple regression to explain the variance observed in the CO_2 exchange rates was unanticipated. A possible explanation is that the measurements acquired for the leaf CO_2 exchange rates were averaged to site level in order to represent the gas exchange for that area, however these measurements represent individuals within the site and not the net exchange for the site as a whole. The pixels from the satellite data, which have been transformed through the vegetation indices, represent the net exchange for each 20 m pixel. Perhaps it would be logical to replace the vegetation index values as the dependant variable, and the PAI, dried grass biomass, and CO_2 exchange measurements as the independent variables. However, our research is focused on predicting CO_2 exchange rates, rather than satellite reflectance data.

3.5.4 Effects of Topography and Land Management

A significant difference in mean CO_2 exchange rates between the sloped ungrazed and upland grazed sites was identified; the exchange rates for sloped ungrazed areas were found to be significantly lower than the upland grazed areas (6.46 $\mu mol/m^2/s$ and 8.52 $\mu mol/m^2/s$ respectively). Because there was no difference in mean CO_2 exchange rates between the upland ungrazed sites and either the upland grazed or sloped ungrazed sites, it can be concluded that a change in both topography and land management is required before a significant difference in CO_2 exchange is observed (displayed visually in Figure 3.5).

Figure 3.5 Significant differences found in CO_2 exchange rates between different topographies and management schemes.



There are a number of different factors which have been found to affect plant productivity including the quality and quantity of incident light (PAR), temperature and water stresses, availability and utilization of mineral nutrients and air humidity (Hall and Rao 1999). Many of these factors have also been found to vary with the changes in topography including air temperature, soil temperature, soil moisture distribution, nutrients, and humidity (Si and Farrell 2004; Rische and Frank 2006). It is likely that the differences in observed CO_2 exchange rates between the upland and sloped sites are due to a change in microclimate, particularly water availability.

Although the current research concludes that upland topographical relief in combination with grazing has a positive effect on mean CO_2 exchange rates, previous research regarding the impacts of grazing on photosynthesis has not been consistent. Grazing has been correlated to a decrease in CO_2 exchange (Frank 2004; Hafercamp and MacNeil 2004), as well as an increase (Owensby et al. 2006). Other studies have concluded that grazing, even heavy grazing has no effect on CO_2 exchange (LeCain et al. 2002; Risch et al. 2006). Since grazing results in the removal of photosynthetic materials, a reduction in gross CO_2 exchange is logical. However, there is a contradicting argument stating that CO_2 exchange efficiency is greatest when grazing utilization is highest (Owensby et al. 2006).

Our research supports the second argument, as we have found that measurements taken from individual leaves in the grazed upland sites indicate higher rates of exchange compared to either of the ungrazed sites. However, because the leaf chamber measures only the exchange from individual leaves, it is impossible to take into account the decrease in photosynthetic materials with this method. Unfortunately, grazed systems are very complex; it is unlikely that the leaf chamber adequately captures the CO_2 exchange occurring in this type of biome in order to relate this data to a satellite image.

MANOVA found no difference in mean PAI and dried grass biomass measurements between the three types of sites, upland ungrazed, upland grazed, and sloped ungrazed. A possible explanation for this can be found within the history of Grasslands National Park. The park was set up in 1984 with the purpose to restore the natural northern mixed grass prairie. Prior to this, the park landscape was heavily modified due to farm and rangeland practices

(Penny 2004). In the 20 years since the creation of the park, it is unlikely that a sufficient time period has passed for the biomass to completely recover from the intensive human modifications. Because of this, it is possible that the grazed sites located outside of the protected park boundaries, and ungrazed areas located within, are too similar to one another.

3.6 Conclusions and Future Directions

The current study has found that the relationship between spectral data and leaf CO_2 exchange is non-linear in nature. Both NDVI and SAVI were identified as the best vegetation indices to estimate mid-season leaf CO_2 exchange rates for our study area located in the northern mixed grass prairie landscape. To our knowledge, this is the first time that a direct correlation between satellite images and leaf CO_2 fluxes has been shown within the grassland biome.

There may be problems inherent with using the leaf chamber, as it allows us to measure only the photosynthesis and respiration taking place through the leaves; we are limited in our ability to estimate the carbon exchange of the entire stand. By employing the leaf chamber, we have excluded the respiration of the non-photosynthetic plant materials as well as heterotrophic respiration. The relative contributions of these respiration sources are important; unfortunately they cannot be measured through this method. This problem is compounded when the leaf exchange data is compared to satellite imagery, where each pixel represents the net ecosystem exchange across a 20 × 20 m area. Recent research has begun to investigate spatial scaling of net primary productivity using sub-pixel information within a boreal forest environment (Simic et al. 2004). This research certainly needs to be continued in other ecosystems, such as the grasslands. Until a valid method to estimate these sources of CO_2 can be established, the application of the small, portable, and more affordable leaf chamber is inadequate.

Our previous research conducted in the mixed grass prairie using a leaf chamber in combination with hyperspectral reflectance has found relationships comparable to those obtained from laboratory conditions (Black and Guo In Press). This is possible because the hyperspectral data allows for the Photochemical Reflectance Index (PRI) to be calculated. This index represents the spectral reflectance of leaf xanthophyll content, a pigment closely associated with the photosynthetic functioning of the plant (Rahman et al. 2001). Unfortunately, the present research employs a SPOT satellite image, and does not allow for PRI to be calculated. More research is required, as it is possible that a hyperspectral satellite image, in combination with the leaf chamber CO_2 exchange measurements may procure better results.

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CHAPTER 4 - SUMMARY AND CONCLUSIONS

4.1 Thesis Conclusions

With the increase in atmospheric CO_2 concentrations, and the resulting potential for climate change, there has been more research devoted to understanding the factors that determine the magnitude of fluxes and the feedback of ecosystem fluxes on climate. The purpose of this thesis is to assess the use of alternate methods to estimate CO_2 flux. First, we chose to use the LC*pro*, a small, portable, and inexpensive leaf chamber to determine if it is a feasible substitute for flux tower systems, which are traditionally used to model ecosystem fluxes. Previous research has illustrated that a relationship exists between hyperspectral reflectance and photosynthetic functioning in laboratory conditions (Gamon et al. 1992; Gamon et al. 1997; Evian at al. 2004; Guo and Trotter 2004; Ustin et al. 2004). Yet this relationship may not be robust in field conditions where there are background effects from soil, litter, and dead materials which are negligible in laboratory conditions.

A study conducted in the boreal forest using a flux net tower and a hyperspectral satellite image indicated that it is possible for this relationship to be transferred to field conditions (Rahman et al. 2001). However, this study used a flux tower, not a leaf chamber and it is unlikely that the results from the boreal forest environment can be transferred to different ecosystems, such as the northern mixed grasslands. To our knowledge, this research is the first to explore the relationship between leaf CO_2 exchange and spectral reflectance in grassland field conditions.

As well, we tested to see if the relationship between leaf CO_2 exchange and spectral reflectance could be extended to satellite-level multispectral data. Research in the past has shown that multispectral satellite-level images can be used to estimate productivity, either CO_2 exchange or gross primary productivity (GPP) as measured with a flux tower in the grasslands region (Wylie et al. 2003; Hunt et al. 2004; Wylie et al. 2004; Gilmanov et al. 2005; Sims et al. 2005). Since this was found to be possible, perhaps satellite level remote sensing tools can be used in combination with the leaf chamber as a convenient alternative to traditional modeling approaches, which require extensive parameterization.

The objective of this thesis was to address the gaps in previous research. Specifically, the goals of this research were to evaluate the capability of using ground-level hyperspectral, and satellite-level multispectral data in the estimation of leaf CO_2 exchange rates in the northern mixed grass prairie at mid-point in the growing season.

4.1.1 Hyperspectral Remote Sensing Tools and Leaf CO_2 Exchange Rates

The primary conclusion from this study is that the Photochemical Reflectance Index (PRI) is the best vegetation index for the prediction of CO_2 exchange rates for our study area located in the northern mixed grass prairie landscape.

Although our research does not demonstrate a relationship as strong as those exhibited in previous studies, our findings are still impressive as a large proportion of the field of view recorded by the spectroradiometer consists of dead materials, mosses, and litter (19%, 26%, and 10% respectively). Previous research has been conducted in laboratory conditions where the reflectance of pure stands of species was recorded; background effects are negligible in these conditions.

The findings of this manuscript are encouraging as it is a step towards the development of a simpler alternative to more complex models used to estimate terrestrial biophysical properties (e.g. SiB2 [Sellers et al. 1996]), which typically require measurements for a number of input parameters. With the findings from this study, research in the future should aim to establish the relationship between CO_2 exchange rates and spectral data at the landscape level through the incorporation of satellite image. With a reliable method of relating CO_2 exchange with satellite data, it would be easier to model CO_2 exchange across a large geographic extent.

4.1.2 Multispectral Remote Sensing Tools and Leaf CO_2 Exchange Rates

This manuscript is a continuation of the findings from the first manuscript. In this study we investigated the use of broad-band satellite-level data in the estimation of leaf CO_2 exchange rates. The results of this research indicated that the relationship between satellite-level spectral data and leaf CO_2

exchange is non-linear in nature. Similar to previous research, Normalized Difference Vegetation Index (NDVI) was identified as the best vegetation index to estimate mid-season leaf CO_2 exchange rates for our study area located in the northern mixed grass prairie landscape. Unfortunately, the results from this study were somewhat lower than previous research employing flux towers.

The second manuscript also investigated differences CO_2 exchange rates across the three different types of sites (grazed upland, ungrazed upland, and ungrazed sloped). A significant difference in mean CO_2 exchange rates between the sloped ungrazed and upland grazed sites was identified; the exchange rates for sloped ungrazed areas were found to be significantly lower than the upland grazed areas (6.46 $\mu mol/m^2/s$ and 8.52 $\mu mol/m^2/s$ respectively). Because there was no difference in mean CO_2 exchange rates between the upland ungrazed sites and either the upland grazed or sloped ungrazed sites, it can be concluded that a change in both topography and land management is required before a significant difference in CO_2 exchange is observed.

4.2 Synthesis of Research Results and Limitations

The two manuscripts presented in this thesis both attempt to predict the same variable (CO_2 exchange rates), through different methods (ground-level hyperspectral and satellite-level multispectral data). However, the results procured from the first study were somewhat more successful than those from the second manuscript, as the r^2 from the linear regression were much higher for the hyperspectral ground-level data in comparison to the multispectral satellite data. There are several possible explanations for this.

First, leaf infrared gas analysis chambers such as the LC*pro*, simply measure the exchange from the individual leaves, and do not capture all sources of respiration including that of non-photosynthetic plant materials, as well as heterotrophic respiration from animals, fungi and bacteria associated with decomposition of residue and soil organic matter. This does not limit the ability of the hyperspectral data to estimate CO_2 exchange. This is because PRI, which we identified as the best vegetation index to predict leaf CO_2 exchange, was developed specifically to detect the xanthophyll content of the leaves, a pigment correlated highly with the photosynthetic functioning of the plant (Gamon et al. 1992). While the leaf chamber does not measure all sources of ecosystem respiration, the PRI is most suitable as it focuses only on the plant xanthophyll content within the field of view.

The second manuscript utilized SPOT data and unfortunately there is no broadband equivalent for the PRI. Although the leaf CO_2 exchange measurements were averaged to site level in order to represent the gas exchange for that area, these measurements represent individuals within the site and not the net exchange for the site as a whole. When compared to the satellite data, where a pixel represents the gross exchange for a ground area of 20 × 20 m, the leaf chamber measurements may not give an adequate representation of ecosystem exchange.

As well, when the hyperspectral data is collected it is at approximately the same time as the CO_2 exchange rates; the two measurements are taken nearly congruently. Plant photosynthetic functioning changes fairly rapidly (Gamon et al. 1997), but the environmental conditions are likely stable enough throughout the hyperspectral data collection time frame that there would be minimal change. The SPOT image was taken at mid-point throughout the field collection, and even though the leaf exchange rates were averaged for each site, perhaps the LC*pro* is too sensitive, and records too much variation throughout the data collection period to be compared to the SPOT data.

Another limitation of this research is that it was conducted throughout a two-week period at mid-point during the growing season, and the results may not be applicable for the rest of the growing season. As well, we only had 24 sites located throughout upland and sloped areas, and it would be useful to collect data from more sites, and also extend the research area throughout the valley areas of Grasslands National Park.

This thesis demonstrates that hyperspectral remote sensing techniques can be used successfully in northern mixed grass prairie, with results comparable to those attained in laboratory studies. While such successful results were not achieved with the multispectral SPOT data and the leaf CO_2 exchange measurements, it would be premature to conclude that satellite images have no role in this area of research. Research in the future should incorporate a hyperspectral satellite image in lieu of the SPOT image, as a hyperspectral image would allow researchers to further explore the function of the PRI, which is identified as the vegetation index most highly related to CO_2 exchange in the first manuscript.

Recently, research has begun to develop approaches for the spatial scaling of boreal forest ecosystem productivity using sub-pixel information (Simic et al. 2004). This research certainly needs to be continued in other ecosystems, such as the grasslands. Particularly with the current research, it would be very useful to be able to scale our leaf measurements to plant, to community, and to stand level. Until a valid method to estimate the CO_2 exchange across a stand can be established, the application of the small, portable, and affordable leaf chamber is inadequate for this application.

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CHAPTER 5 - REFERENCES

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APPENDIX A – FIELD DATA COLLECTION FORMS

A.1 Photosynthesis data collection form

Site:		Date: Conditions:		Collected by:
Series #	Quadrat	Species	Width (mm)	Comments
1				
2				
3				
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39				
40				

A.2 Biophysical data collection form

Date: **Time:** **Recorder:**

2005 Fieldwork Form -- Site

Plot Series:			**Rel. elev.:**			**Lat.:**			**Long.:**		
Quadrat	**Series**										
	Slope										
	Aspect										
Cover-top layer	**Grass**										
	Forb										
	Shrub										
	Standing dead										
Cover-Low layer	**Litter**										
	Moss										
	Lichen										
	Rock										
	Bare ground										
Height	**Litter depth**										
	Average height										
	No. of hits: 0-10										
	10-20										
	20-30										
	30-40										
	40-50										
Cover of grass species	**Needle & thread**										
	Western wheatgrass										
	Slender wheatgrass										
	Northern wheatgrass										
	Blue grama										
	June grass										
	Pasture sage										
	Sage brush										
	Cactus										
	Unidentified grasses										
Soil moisture											
Soil temperature											
Biomass											

Notes (location description, community, etc.

APPENDIX B – 2004 AND 2005 BIOPHYSICAL DATA

B.1 Average measured biophysical data for 2004 sites.

Site Code	CO_2 Exchange (μmol/m^2/s)	Dried Grass Biomass (g/m^2)	Dried Forb Biomass (g/m^2)	Dried Shrub Biomass (g/m^2)	Dried Dead Biomass (g/m^2)	Grass (%)	Forbs (%)	Shrubs (%)	Standing Dead (%)	Litter (%)	Moss (%)	Lichen (%)	Rock (%)	Bare Ground (%)
G0T2	38.28	53.38	8.38	1.88	80.88	25.76	3.81	0.24	22.14	13.43	29.20	4.99	0.28	0.15
G1T3	22.76	48.50	9.00	0.00	59.00	39.29	8.05	0.00	13.48	7.33	30.04	1.81	0.00	0.02
G2T3	27.38	49.25	12.50	0.00	83.00	30.82	6.00	0.00	16.18	5.38	17.99	1.22	0.00	0.03
G3T3	41.72	32.88	43.88	0.00	56.38	21.95	10.19	0.00	11.95	8.28	39.68	7.36	0.11	0.48
G4T2	29.49	39.00	23.00	0.00	66.00	28.95	6.81	0.81	11.52	9.30	36.07	4.27	1.36	0.91
SG12C	40.64	51.63	10.00	4.50	93.13	29.67	2.48	0.76	12.05	19.45	25.77	3.41	1.23	0.42
SG1C	38.61	55.38	43.75	0.00	66.75	30.48	6.62	3.62	6.57	8.43	39.01	2.79	0.41	0.08
SG2C	51.45	90.00	38.00	0.00	218.50	34.52	7.05	1.57	24.76	19.15	6.28	1.89	2.56	2.22
SG5C	27.48	36.63	66.38	2.38	50.13	22.19	10.10	1.62	15.33	13.67	28.87	7.42	0.52	0.28
SG7A	32.04	59.00	22.88	1.63	126.63	25.14	5.95	0.71	18.48	9.45	27.14	10.59	0.64	1.90
U0T1	38.97	52.13	23.00	0.00	96.25	28.05	6.14	0.00	25.00	8.32	22.78	9.32	0.34	0.05
U2T3	22.86	65.13	12.75	0.75	201.50	26.90	3.57	0.24	38.81	8.16	17.64	4.61	0.01	0.05
U3T3	28.73	95.38	10.88	0.00	258.50	29.48	3.76	0.00	36.81	8.48	18.15	3.27	0.03	0.03

B.2 Measured biophysical data for 2005 sites.

Site Code	CO_2 Exchange (μmol/m^2/s)	Dried Grass Biomass (g/m^2)	Dried Forb Biomass (g/m^2)	Dried Shrub Biomass (g/m^2)	Dried Dead Biomass (g/m^2)	Grass (%)	Forbs (%)	Shrubs (%)	Standing Dead (%)	Litter (%)	Moss (%)	Lichen (%)	Rock (%)	Bare Ground (%)
G0T2	7.92	57.86	7.11	0.00	127.13	23.90	4.55	0.00	11.60	27.33	28.26	0.67	0.50	0.65
G1T3	6.97	21.08	10.27	3.13	87.29	19.20	6.85	0.00	14.85	8.40	39.23	3.92	0.00	0.21
G2T3	9.53	48.70	8.44	0.00	114.54	20.15	6.55	0.00	11.50	15.02	41.95	1.99	0.00	0.76
G3T3	8.25	29.28	10.54	2.49	77.71	14.30	8.45	0.00	8.25	10.29	39.38	11.34	0.15	1.81
G4T2	9.91	49.08	13.73	0.93	72.07	17.65	5.15	1.50	9.25	19.35	38.35	2.42	4.55	1.78
SG12B	6.27	32.45	12.18	0.00	107.43	13.20	6.95	0.00	11.40	15.00	44.40	8.89	3.41	0.94
SG12C	6.22	40.25	5.96	8.70	141.18	16.25	4.45	0.00	13.50	23.86	29.91	7.69	3.31	0.00
SG13C	4.20	17.35	24.70	110.98	59.59	13.80	7.30	2.60	7.15	11.97	13.43	21.96	11.55	7.54
SG13D	4.36	19.04	8.43	0.00	53.45	16.25	3.20	0.75	11.50	13.28	30.70	7.22	12.02	5.09
SG1A	6.60	26.53	6.58	6.02	84.88	13.30	8.50	0.10	10.85	14.37	39.62	6.79	3.74	2.15
SG1C	5.67	46.61	11.13	12.06	114.33	16.15	12.90	1.45	9.90	21.71	14.36	7.75	5.12	10.67
SG2C	6.24	62.43	6.92	6.58	248.98	18.40	4.80	1.40	17.00	38.05	6.61	1.85	5.16	6.13
SG2E	4.73	59.04	18.17	0.10	248.36	25.10	10.95	0.00	13.75	20.05	17.61	10.44	1.97	0.00
SG5C	7.15	54.71	29.01	27.93	149.54	17.00	8.50	7.90	10.95	21.77	17.52	7.26	1.69	4.11
SG5D	7.47	45.60	9.43	0.00	145.53	17.30	7.30	0.35	17.25	24.80	12.49	10.51	3.26	2.44
SG7A	6.30	47.44	12.18	55.00	259.03	19.00	5.10	0.00	12.00	26.58	32.13	2.38	1.36	1.46
SG7B	8.17	56.10	23.09	0.00	179.47	18.45	7.00	0.00	14.30	15.62	27.64	13.03	2.31	0.40
SG9B	8.09	67.84	1.07	1.58	292.88	20.65	1.75	0.50	31.35	25.46	7.56	3.33	0.16	9.24
SG9C	8.99	57.72	9.80	0.00	168.70	16.60	6.50	0.80	15.65	21.38	26.98	10.41	2.92	1.32
U0T1	6.64	54.61	17.43	0.00	127.95	17.55	7.25	0.00	11.50	22.03	27.79	12.75	1.13	0.00
U1T5	8.85	29.77	8.99	0.00	189.62	25.00	5.10	0.00	20.25	23.29	24.42	0.24	0.00	0.00
U2T3	5.51	59.15	6.73	2.88	209.36	22.00	5.05	0.00	9.05	33.99	24.13	1.14	0.16	0.06
U3T3	8.67	72.35	3.43	0.00	183.18	22.65	4.45	0.00	15.50	28.93	26.47	1.12	0.00	0.00
U4T3	9.64	30.75	11.41	4.80	74.64	15.60	6.70	0.00	15.50	11.39	44.05	5.30	1.14	0.33

APPENDIX C – 2004 AND 2005 SPECTRAL DATA

C.1 Spectral data for 2004 sites.

Site Code	PRI	MCARI	SAVI	OSAVI	CAA	BDMax
G0T2	-0.052	0.019	0.225	0.300	105.68	0.42
G1T3	-0.064	0.026	0.293	0.400	109.75	0.58
G2T3	-0.054	0.023	0.267	0.354	109.49	0.49
G3T3	-0.053	0.021	0.233	0.306	104.11	0.42
G4T2	-0.058	0.026	0.280	0.366	107.23	0.50
SG12C	-0.054	0.019	0.218	0.295	105.05	0.42
SG1C	-0.056	0.018	0.205	0.283	103.79	0.41
SG2C	-0.053	0.029	0.351	0.448	116.38	0.60
SG5C	-0.061	0.019	0.208	0.279	101.80	0.39
SG7A	-0.053	0.019	0.212	0.291	104.66	0.43
U0T1	-0.052	0.019	0.210	0.282	103.79	0.39
U2T3	-0.057	0.020	0.226	0.293	104.82	0.39
U3T3	-0.056	0.024	0.262	0.344	108.27	0.48

C.2 Spectral data for 2005 sites.

Site Code	SPOT NIR	SPOT Red	SR	NDVI	SAVI	ATSAVI
G0T2	0.201	0.091	0.451	0.378	0.567	0.223
G1T3	0.179	0.093	0.521	0.315	0.472	0.141
G2T3	0.169	0.085	0.503	0.331	0.496	0.152
G3T3	0.175	0.092	0.524	0.313	0.469	0.136
G4T2	0.180	0.090	0.501	0.333	0.499	0.161
SG12B	0.169	0.095	0.559	0.283	0.424	0.098
SG12C	0.172	0.090	0.521	0.315	0.473	0.137
SG13C	0.184	0.107	0.579	0.267	0.400	0.091
SG13D	0.179	0.101	0.567	0.277	0.415	0.098
SG1A	0.165	0.087	0.527	0.310	0.465	0.125
SG1C	0.168	0.095	0.564	0.279	0.418	0.094
SG2C	0.191	0.084	0.440	0.388	0.583	0.230
SG2E	0.171	0.080	0.471	0.360	0.539	0.184
SG5C	0.181	0.090	0.494	0.339	0.508	0.169
SG5D	0.175	0.094	0.533	0.304	0.456	0.127
SG7A	0.172	0.092	0.533	0.304	0.456	0.124
SG7B	0.182	0.087	0.478	0.353	0.529	0.185
SG9B	0.177	0.087	0.493	0.339	0.509	0.167
SG9C	0.173	0.087	0.504	0.330	0.495	0.153
U0T1	0.181	0.088	0.485	0.347	0.521	0.177
U1T5	0.172	0.092	0.536	0.302	0.453	0.122
U2T3	0.162	0.087	0.534	0.304	0.456	0.117
U3T3	0.167	0.081	0.486	0.346	0.519	0.167
U4T3	0.176	0.086	0.490	0.342	0.513	0.168