1 INTRODUCTION AND OBJECTIVES

1.1 Grassland ecosystems and their importance

Definitions for grasslands vary. Some studies classify grasslands by vegetation type, while others characterize them by climate, soils or human use (White et al., 2000). Floristically, grasslands are plant associations containing few trees and are characterized by a cover of mixed herbaceous vegetation that is dominated by grasses (family *Poaceae*) (Risser, 1985). This mixed vegetation layer usually includes a significant proportion of species from the legume (*Leguminosae*), composite (*Compositae*) and sedge (*Cyperaceae*) families, and sometimes includes shrubs and sparse trees (Kephart et al., 1993). Water availability (or more specifically, a lack thereof) is the principal climatic determinant affecting the development of grassland regions. In general, natural grasslands occur in climates that are too arid to support a fully developed forest, but not so adverse as to inhibit the development of a closed perennial herbaceous layer. Natural and anthropogenic disturbances, such as fire and grazing, also play an important role in maintaining these landscapes.

Permanent grasslands cover approximately 26% of the earth's total land surface (Ikeda et al., 1999). These regions are both economically and ecologically significant. The economic importance of grasslands is primarily a result of their strong links to global food production. Grasslands with suitable climates and fertile soils are almost always quickly converted into croplands (Barrett and Curtis, 1982; Brown, 1989; Lauver and Whistler, 1993). These regions contain much of the grain growing capacity of the world (Parton et al., 1996). Where conditions are too arid for crop production, grasslands are often major rangelands – the natural pastures for grazing animals from which a considerable portion of the world draws its protein foods (Coupland, 1979; Henebry, 1993). Although rangelands are often perceived to be of less economic value than cropland (Girard, 1982), they are nonetheless one of the earth's most valuable resources. Grassland ecosystems are also ecologically important, exemplified in part by the major role they play in regulating the global carbon cycle. This is largely a consequence of their immense land areas, large carbon stores below ground and uncertain CO_2 fluxes (Tieszen et al., 1997). It is estimated that grassland systems contain as much as 30% of the earth's total carbon stocks (Ojima et al., 1996; Parton et al., 1996), and that their annual contribution to global net primary production (NPP) may be as much as 16% of that of the terrestrial biosphere (19 x 10^9 tons C $year^{-1}$) (Whittaker and Likens, 1973).

1.2 Grassland ecosystem function, composition and environmental change

Grassland ecosystem function – i.e. the ability to capture and transfer environmental resources – is known to be responsive to even small fluctuations in environmental conditions (Yang et al., 1998). Short- and long-term changes in grassland productivity can be brought about by a variety of environmental disturbances whose causes are natural (e.g. precipitation and temperature variability), anthropogenic (e.g. land use change, nutrient enrichment, irrigation and the introduction of exotic plant species) or some combination of both (e.g. fire and grazing) (Goodin and Henebry, 1997). While some disturbances (e.g. drought) can directly modify seasonal patterns of grassland productivity by reducing the photosynthetic capabilities of existing species, others (e.g. grazing, fire, fertilization) often do so indirectly by bringing about changes in community composition (i.e. the number, type and relative abundances of plant forms present). For example, in the grasslands of North America, particular sequences and combinations of disturbances are known to produce particular species compositions, especially in terms of the relative abundance of C3 and C4 photosynthetic types (Goodin and Henebry, 1997). Various studies have shown that increased winter precipitation (Karl et al., 1991), rapid nitrogen addition (Seastedt et al., 1991) and overgrazing (Valentine, 1990) typically favor the growth of C3 species, while increased temperature (Owensby et al., 1993) and fire frequency (Anderson, 1990) favor C4 production. However, the impacts of many simultaneous disturbances are complex; disturbances rarely, if ever, occur independently (Coppedge, et al., 1998; Sage et al., 1999), and the presence of many confounding variables makes the isolation of cause and effect difficult. As a result, although it is predicted that large-scale changes in some or all of these factors may combine to dramatically affect grassland biogeochemistry and their carbon stocks, the combined effects of these disturbances on the overall functioning of grassland systems are complex and are not well understood. If this prairie ecosystem is to be properly managed, measurement techniques for detecting changes in productivity and composition must be developed, and the potential effects of changing composition on productivity must be further investigated within- and across-community scales.

The effects of changing plant community composition on the functioning of grassland systems are equally unclear. Of particular interest to ecologists is the degree to which ecosystem function is dependent on the magnitude of its species pool (i.e. species richness), the relative abundances of species present (i.e. species evenness), the number of functional groups present (i.e. functional richness) and the relative abundance of functional groups present (i.e. functional evenness). A review of observational (e.g. Kutiel and Danin, 1987; Cuevas et al., 1991), experimental (e.g. Naeem et al., 1994; Naeem et al., 1995; Hooper and Vitousek, 1997; Tilman et al., 1997a; Symstad et al., 1998) and theoretical (e.g. Tilman et al., 1997b) studies generally reveal a strong dependence of ecosystem function (or, more accurately, its various measured surrogates) on plant diversity. While the form of this dependence varies from study to study, there is sufficient evidence to indicate that it is generally asymptotic, where ecosystem function initially increases in tandem with diversity until a threshold is reached above which function remains constant (Schläpfer et al., 1999; Hughes and Petchey, 2001). However, there is, as yet, no consensus as to the level(s) of diversity at which the ecosystem function response curve asymptotes for various grassland ecosystems, or the effects of species additions and deletions to overall ecosystem functioning.

1.3 Remote sensing as a tool for monitoring grassland function and composition

The above natural and anthropogenic pressures and the uncertainty surrounding the influence of community composition on grassland ecosystem function create a unique challenge for the management of these lands. Because grasslands generally cover large geographical extents and are mostly found in isolated locations, the use of traditional assessment techniques in these regions is often time-consuming and costly (Asrar et al., 1986). Thus, other monitoring approaches must be ultilized. One possible approach is the use of satellite remote sensing systems. Through the unique combination of extensive spatial, spectral and frequent temporal data collection, remote sensing has the potential to provide both scientists and managers with a powerful monitoring tool at regional to local scales (Goodin and Henebry, 1997). The remote sensing approach has great potential to provide quantitative information on the amount, condition, and type of vegetation, provided that the effects of physical and physiological processes on spectral characteristics of grassland canopies are fully understood (Asrar et al., 1986).

The increasing availability of remotely-sensed data at various spatial and spectral resolutions offers the possibility of overcoming the present limitations of traditional methods of large-scale resource assessment (Tucker, 1980), as well as the ability to monitor the biophysical characteristics of ecosystems at various landscape scales (Tieszen et al., 1997). Remote sensing has already contributed considerably to the inventory and mapping of resources, the quantification of environmental characteristics, the description of matter and energy flow within ecosystems, and the evaluation of spatial change (Quattrochi and Pelletier, 1991). This has been particularly well demonstrated by those who have focused their attentions on grasslands.

Spectral observations over large tracts of grassland have typically been acquired using National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) data (e.g. Burke et al., 1991; Tucker et al., 1991; Paruelo and Lauenroth, 1995; Goetz, 1997; Tieszen et al., 1997). While these spatial resolutions (1-4km) provide valuable information about climatic and aggregate anthropogenic forcings on vegetation dynamics (Henebry, 1993), they are often at a coarser spatial resolution than some applications require. Medium spatial resolution satellite observations have been derived from Landsat Multi-Spectral Scanned (MSS) (e.g. Pickup et al., 1993; Mino et al., 1998) and Landsat Thematic Mapper (TM) sensors (e.g. Henebry, 1993; Henebry and Su, 1993; Mino et al., 1998; Todd et al., 1998) at resolutions of 50m and 30m, respectively. At even finer resolutions, information has been provided by airborne (e.g. Walthall and Middleton, 1992) and ground-based observations (e.g. Tucker, 1979; Girard, 1982; Asrar et al., 1986; Weiser et al., 1986; Turner et al., 1992; Pickup et al., 1993; Goodin and Henebry, 1997; Goodin and Henebry, 1998), whose spatial resolutions are determined by sensor height and field of view (FOV), respectively.

One of the greatest challenges in the remote sensing of grasslands has been the reliable estimation of biophysical variables relating to grassland function – such as aboveground biomass and net primary productivity – and their spatial variability from multi-resolution and multi-spectral observations. Remote sensing offers the possibility of measuring such variables on the premise that green vegetation has its own distribution of reflected, emitted and absorbed radiation. However, factors other than the presence and amount of green vegetation (e.g. senescent vegetation, soil, shadow) often combine to form composite spectra (see Ross, 1981; Goel, 1988; Myeni et al., 1989; Curran et al., 1992; Fourty et al., 1996; Asner, 1998; Asner et al., 1998). Spectral mixing frequently makes the discrimination of green vegetation difficult, and has prompted the development of numerous spectral vegetation indices (VIs). VIs combine two or more spectral bands in order to enhance the vegetative signal, while minimizing background effects. Many of these VIs have been found to be well correlated with surrogates of ecosystem function, including vegetation cover (Hurcom and Harrison, 1998; Purevdorj et al., 1998), aboveground biomass (Boutton and Tieszen, 1983; Weiser et al., 1986; Davidson and Csillag, 2001), green leaf area, (Asrar et al., 1986; Weiser et al., 1986; Baret and Guyot, 1991), photosynthetically active radiation (PAR) (Hatfield et al., 1984; Weiser et al., 1986; Baret and Guyot, 1991) and productivity (Box et al., 1989; Running et al., 1989).

While many investigators have successfully correlated remote sensing data with various indicators of ecosystem function, surprisingly few studies have attempted to use remote sensing data to directly monitor grassland community composition, or elucidate possible relationships between community composition and function. To date, the role of remote sensing in biodiversity assessment has typically been limited to "traditional" uses such as land cover mapping, and has thus been qualitative, rather than quantitative, in nature. However, Stoms and Estes (1993) suggest that the actual value of remote sensing in biodiversity research lies in its potential for use in quantitative analyses. Particularly, they emphasize the importance of further investigating what ecological information is contained within multi-temporal remote sensing products. Such headway has been made in various attempts to link grassland composition to function. Nevertheless, although quantitative in nature, most of these studies have been carried out across large extents (e.g. continental to regional scales) using coarse-resolution spectral data (e.g. AVHRR, 1-5km) and basic functional classifications (e.g. C3 and C4 species) as indicators of composition (e.g. Tieszen et al., 1997).

Of particular interest are questions concerning the possible relationship between spatio-temporal variations in plant community function – expressed in terms of spectrally-derived estimates of productivity – and community composition. For example: Through what sampling approach(es) are spatio-temporal variations in community productivity most accurately (and efficiently) characterized? Are the timing and amount of peak seasonal biomass correlated with the relative proportion of C3 and C4 species present? What are the relationships between total seasonal productivity and measures of plant diversity, such as species and functional group richness and evenness? Are relationships uncovered at finer sampling resolutions similar to those found using coarse resolution satellite date? Addressing such questions using spectral observations may not only shed light onto the relationship between grassland function and composition at a variety of ecological scales, but also provide a valuable insight into the potential use of remote sensing for the quick and nondestructive monitoring of plant community composition.

1.4 Problem Statements and Objectives

To investigate the above issues, three methodological concerns must be addressed. First, remotely-sensed data collection and traditional ecological research normally operate at incongruous spatial resolutions. While satellite remote sensing observations are usually taken at spatial resolutions ranging from 10m (SPOT-P) to 4km (AVHRR), biological research has enjoyed most of its success in the study of plot level (<1m) phenomena (Sellers et al., 1990). This disparity is one of the most important limiting factors in the reliable estimation of grassland ecosystem parameters from remotely-sensed data (Csillag et al., 1996), and must be narrowed significantly. Second, many studies fail to consider the effects of scale (sample resolution) on the relationship between spectral reflectance and their variables of interest, and in doing so, ultimately choose a scale of observation that is potentially inappropriate for the task at hand. Relationships often vary with scale, and the ways in which pattern and process vary across scales are not always well understood. The correlation between the state of an environmental variable and plant community composition may appear to be significant at some scales, but not at others (Lobo et al., 1998). In order to identify the most suitable scales of measurement, or to “scale-up” plot level relationships to the scales needed for regional studies, changes in the relationship between spectral data and biophysical parameters must be explicitly investigated across a range of spatial scales. Third, to address these previous two concerns, a field sampling strategy must be devised that allows plot-level measurements and relationships to be characterized across the spatial resolutions of interest. However, the relative merits of various sampling schemes (e.g. nested sampling, geostatistics), particularly across highly patchy landscapes, have yet to be adequately evaluated. Furthermore, guidelines for the collection of ground reference data – that is, the criteria to which sampling strategies should conform in order to best characterize spatio-temporal landscape characteristics – do not exist. Such sampling issues must also be addressed.

The general objective of this thesis is to explore the use of field and remote sensing data for monitoring community function and composition within C3-dominated grassland. More specifically, by addressing the above sampling issues directly, I aim to investigate the various links between composition and remotely-sensed estimates of productivity at plot (0.5m) to satellite (30m - 1km) resolutions. This general objective can be broken down into a set of secondary questions. Question (1) pertains directly to the sampling/scaling issues faced by such a study, questions (2), and (3) pertain to the scale-dependency of empirically-derived relationships between composition and function, while questions (4) and (5) pertain to the broader applicability of such a study:

(1) Given a limited (fixed) sample budget, which sampling approach allows for the most accurate characterization of spatial structure and scaling of plot-level (0.5m) field measurements to coarser resolutions?

(2) What is the relationship between two-date spectral estimates of productivity and the areal coverage of C4 species? Are derived relationships scale (resolution) dependent?

(3) What is the relationship between multi-date spectral estimates of productivity and more complex estimates of plant diversity, such as species and functional group richness and evenness? Are derived relationships scale (resolution) dependent?

(4) How do the above relationships change when the extent of the study is expanded *across* community types and where satellite data are used to quantify community function?

(5) What implications do the above results have for the potential use of satellite remote sensing in grassland biodiversity assessment?

1.5 Organization of dissertation

This dissertation has been set out in a way that highlights a progression of scientific inquiry from the general motivations for the study (chapters 1 and 2) to sample design (chapter 3), the relationship between simple measures of composition and two-date remote sensing data (chapter 4), the relationship between complex measures of composition and multi-date remote sensing data (chapter 5), an expansion of these investigations to larger extents and coarser sampling resolutions (chapter 6) and, finally, the broader implications of the study (chapter 7).

The ensuing chapters are organized as follows. Chapter 2 provides a description of the general environmental characteristics of the study site used in this work (Grasslands National Park, Saskatchewan, Canada). Chapter 3 outlines the nested sampling scheme used to scale plot-level measurements up to coarser resolutions. For publication purposes, this chapter is presented as an exploration into the ability of two sampling approaches – nested sampling and geostatistics – for describing the spatial structure of patchy grassland landscapes. Chapter 4 explores the relationship between various spectral vegetation indices and aboveground live biomass and, based on these results and those of chapter 3, describes and implements a sampling approach for investigating the scale-dependency of the relationship between a two-date remotely-sensed productivity measure and C4 species cover. Chapter 5 extends this study, but explores the scale-dependency of the relationship between multi-date remotely-sensed productivity measures and species and functional richness and evenness. Chapter 6 expands the concepts and conclusions derived from chapter 4 to the entire Grasslands National Park region, using coarse-resolution satellite data (e.g. Landsat-TM, AVHRR) and Parks Canada vegetation survey information. Chapter 7 presents a set of conclusions, and the implications of the results for monitoring grassland biodiversity using ground-, airborne- and satellite-based platforms.

Chapters 3, 4, 5 and 6 have been written as “stand-alone” publishable units (see citations on title page of each chapter). Because of this, and because of the links in subject matter between successive chapters, it is unavoidable that an element of repetition exists among the background sections of each of these four chapters. However, where the removal of such material does not significantly detract from the overall flow of the chapter (e.g. field site description), common elements have been moved to chapter 2 (Background). While each of chapters 3, 4, 5 and 6 have been written as co-authored papers with my advisor, Dr. Ferenc Csillag, data collection, data processing, data analyses and writing were done by myself.