2 BACKGROUND

2.1 The Grasslands of North America

2.1.1 The North American Grassland Biome

The grassland biome dominates the interior of the North American continent, extending west-east from the Western Cordillera to the eastern deciduous forest, and north-south from central Saskatchewan to Mexico (Bragg, 1995) (Figure 2.1). This biome contains the widest diversity of grassland types on earth (Kephart et al., 1993), and is home to grasses, grass-like plants (sedges and rushes), forbs and woody plants (Risser, 1985). Indeed, far more species of these latter taxa are actually present, but grasses constitute most of the biomass.

The North American grasslands occur across a large climatic range. Grassland systems are found in semiarid to subhumid regions, where mean annual precipitation (MAP) ranges from 250mm to 1000mm, respectively (Risser, 1985; Brown, 1989; Bragg, 1995). Drier areas generally support deserts whereas wetter areas generally support forests (Kephart et al., 1993). Grassland mean annual temperatures (MAT) typically range from –7°C to 30°C (Whittaker, 1975). These climatic variations exist as a west-to-east gradient of increasing MAP and a north-to-south gradient of increasing MAT. While this precipitation gradient is a product of the rainshadow effect of the entire Western Cordillera, the temperature gradient is controlled by latitude. The interaction of these two factors, prevailing soil conditions and management histories largely determine the distribution of various grassland types across North America (Bragg, 1995).

While, historically, the North American grasslands have been subdivided in various ways, most classifications distinguish at least six types. Each grassland contains its own diversity, a consequence of non-uniform conditions across its range (Bragg, 1995). The largest unbroken grassland formation stretches from the Appalachians to the Rocky Mountains. This expanse is covered by tallgrass, mixed and shortgrass prairie. The physical boundary between these types is rarely, if ever, distinct. Instead, these grasslands grade from one type to another, arranging themselves along moisture, temperature, and

Figure 2.1. The Grasslands of North America (adapted from Center for Great Plains Studies (2001)).

soil gradients (Bragg, 1995). The tallgrass prairie, which occupies the eastern part of the Great Plains, receives more rainfall (as much as 1000mm per annum) than the mixed and shortgrass prairies to the west (500mm per annum and 300mm per annum, respectively). This grassland type is dominated by big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*) and Switchgrass (*Panicum virgatum*) (Risser, 1985). The shortgrass prairie occupies the driest part of the Great Plains. Here, blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*) and western wheatgrass (*Pascopyrum smithii*) are the dominant species (Kephart et al., 1993). Between these two moisture extremes lies the mixed grass prairie. This grassland type contains a mix of species from both the tallgrass and shortgrass prairies, as well as species of the genera *Stipa* and *Pascopyrum* (Risser, 1985; Kephart et al., 1993). While the mixed grass prairie is usually identified as a separate biome (e.g. Coupland and Rowe, 1969), it is considered by some to be only a broad transitional zone between the tall and shortgrass types (Bragg, 1995). However, these three prairie types are not absolutely restricted to separate geographic zones. In an area generally identified as mixed grass prairie, tallgrass communities may exist in low-lying moist spots, while shortgrass communities may develop along dry, rocky outcrops. In such instances it is available soil moisture, rather than rainfall and evaporation, that is the controlling factor on species distribution (Brown, 1989). Nonetheless, in spite of this intermingling, these types are still distinct enough to be mapped as three separate zones (Brown, 1989).

The other grassland communities (not shown) are separated as much by geography as by vegetation (Brown, 1989). The desert grassland is found on the edges of the southwestern deserts, and is dominated by grama grasses as well as woody species such as mesquite (*Prosopis sp.*) and creosote bush (*Larrea tridentata*) (Risser, 1985). The California grasslands are found in the Central Valley of California, and are dominated by species of *Bromus* and *Avena*. The Palouse prairie is found on the volcanic soil of the Columbia Plateau (Brown, 1989), and is dominated by bluebunch wheatgrass (*Agropyron spicatum*) and sagebrush (*Artemisia sp.*) (Risser, 1985). Additional subdivisions (e.g. alpine meadow, coastal prairie, fescue prairie) have been distinguished in various other classifications (e.g. Singh et al., 1983).

2.1.2 The Northern Mixed Grass Prairie

The northern mixed grass prairie occupies the northern portion of the Great Plains grasslands. This biome extends northwards from the northern boundary of the short-grass steppe to the southern border of the fescue prairie, and eastwards from the foothills of the Rocky Mountains to the western border of the tallgrass prairie (Figure 2.2) (Lauenroth et al., 1994). The parent material of the soils of the region are chiefly of glacial origin, although areas exist where pre-glacial material is exposed by erosive processes. While alkali-solonetzic soils occur where underlying shales modify thin glacial deposits, brown and dark brown chernozemic soils occupy most of the region (Coupland, 1992).

The climate of the region is characterized by great annual extremes in temperature (ranging from –7 °C to 17 °C in the southwest and from –14 °C to 24 °C in the northeast) and comparatively low mean annual precipitation (300mm to 450mm) (Bryson and Hare, 1974). Low precipitation, high summer temperatures and dry winds (largely prevailing from the west) frequently make soil moisture the limiting factor for plant growth (Coupland, 1992). The mean climate, however, is not the shaping feature in this region. Rather, it is these aforementioned extremes in temperature and precipitation that create hardy, drought and frost tolerant communities (Peat, 1997).

The mature vegetation communities in the Canadian portion of the northern mixed grass prairie take a variety of forms. In mesic regions, the *Stipa-Agropyron* type is dominant. However, as moisture availability decreases, communities grade from this type to *Stipa-Bouteloua-Agropyron* then to a *Stipa-Bouteloua* type (Coupland, 1961). In all types *Carex* spp. and *Koeleria cristatum* are also common. With the exception of *Bouteloua gracilis*, all of the dominant grasses in the Canadian portion of the northern mixed grass prairie fix carbon through the C3 photosynthetic pathway (Peat, 1997).

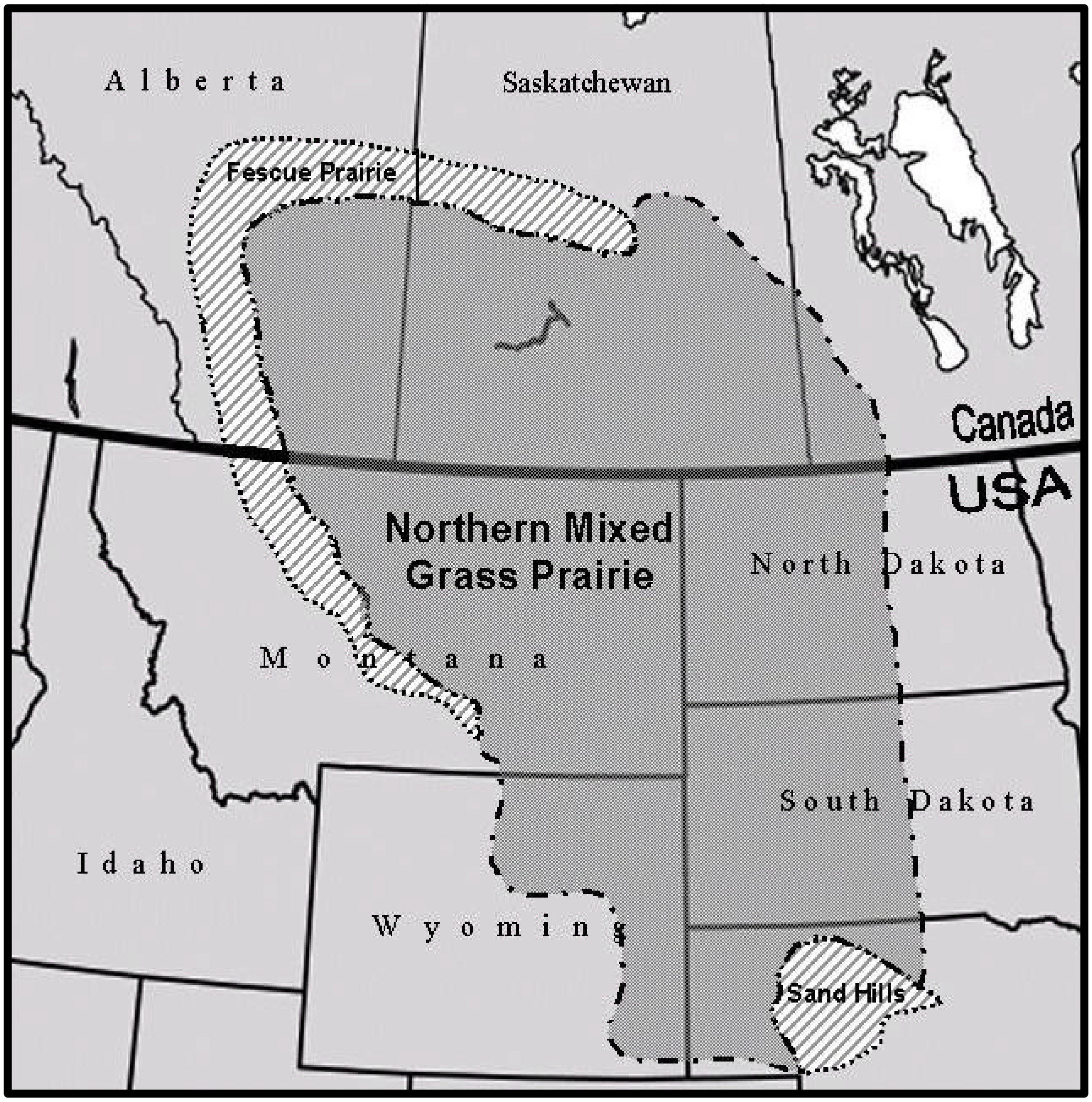

Figure 2.2. The northern mixed grass prairie (modified from Coupland (1992)).

2.1.3 The Study Region: Grasslands National Park, Saskatchewan, Canada

2.1.3.1 Location

Grasslands National Park (GNP) (49° 15’ N, 107° 0’ W) was established in 1988 to preserve a representative portion of the Canadian mixed grass prairie ecosystem (Figure 2.3). The park is divided into two distinct “blocks” (*west* and *east* blocks). At present, these blocks are held privately and by Parks Canada as a patchwork of lands. Once under the control of Parks Canada, these blocks will provide a total protected area of approximately 900 km^2. As of 1999, Parks Canada had already acquired 61% of the lands in the proposed west block and 49% of lands in the proposed east block.

2.1.3.2 Climate

Since the retreat of the glaciers 10,000 years ago, semi-arid grassland conditions (long, cold and dry winters and short, hot and dry summers) have prevailed in the GNP region (Loveridge and Potyondi, 1983). As a result, an overall lack of moisture is the dominant climatic feature of the area. These dry conditions are the result of low precipitation rates and a poor retention of what falls. Total annual precipitation averages 325mm (± 70mm; expressed as one standard deviation around this estimate as calculated from 30-year climate records). These precipitation rates are amongst the lowest and most variable in the prairies. Approximately one third of this total (110mm) falls as snow in the winter, while the remainder (215mm) falls as rain throughout the rest of the year, mostly during heavy (but infrequent) summer thunderstorms (150mm) (Environment Canada, 1998). Mean daily temperature ranges from 15 °C below zero in January to 20 °C in July. The growing season in the park is short, averaging 170 days between killing frosts, and low moisture availability often reduces its effective length (Loveridge and Potyondi, 1983). Prevailing winds are from the southwest and reach their greatest speeds during the summer when water loss can be critical. These winds, in conjunction with high temperatures and bright sunshine, can reduce both ground moisture and surface water levels significantly. However, because the average daily bright sunshine is high during the growing season (2400 hours annually (Environment Canada, 1998)), growth rates can be high when sufficient moisture is available.

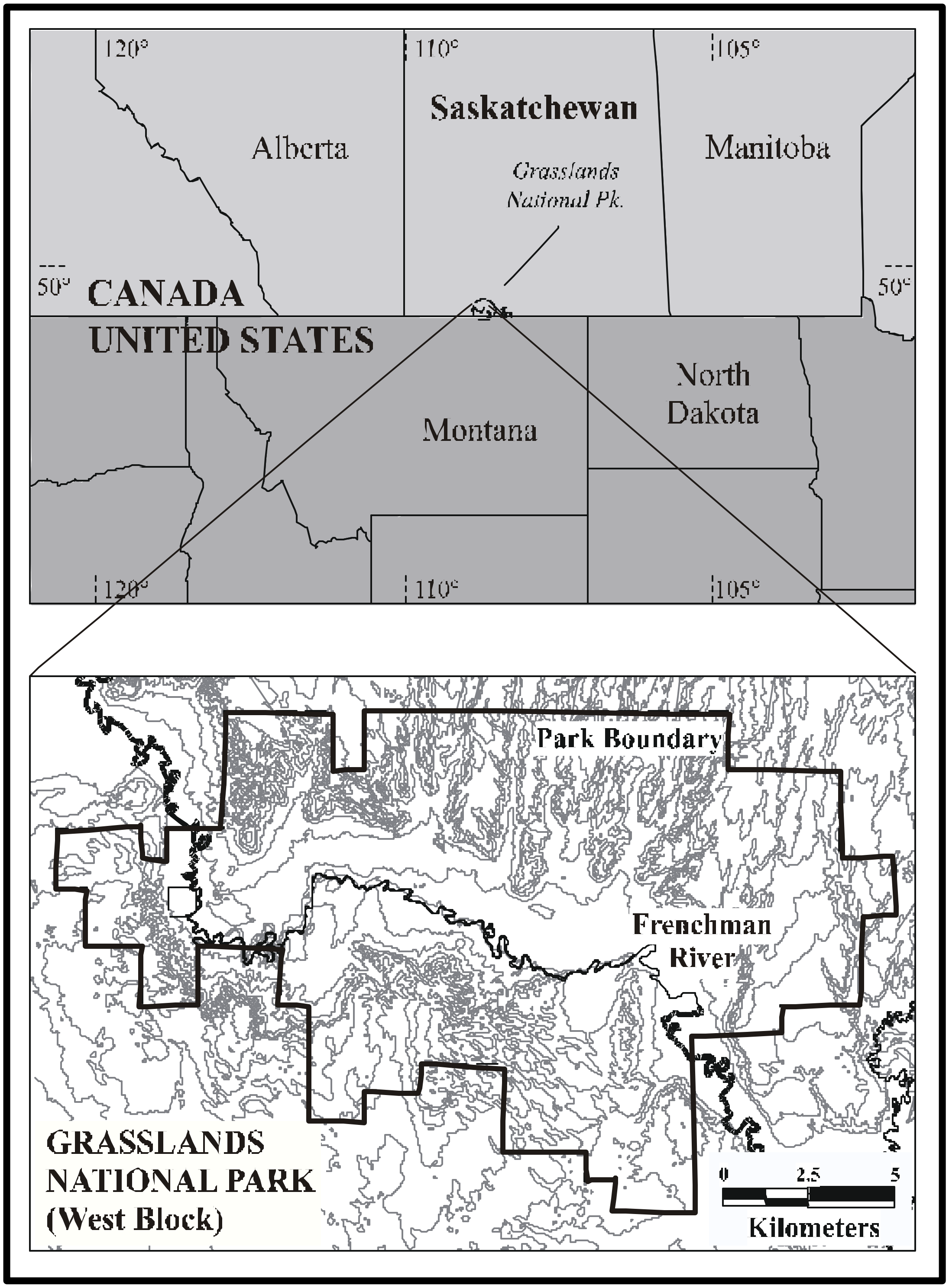

Figure 2.3. Location of Grasslands National Park (Saskatchewan, Canada), and surrounding region.

2.1.3.3 Soils

The Saskatchewan Institute of Pedology completed a detailed soil survey of the GNP region in 1991. The resulting report (Saskatchewan Institute of Pedology, 1992) identified 38 soil associations, within which a total of 115 soil series were described and mapped (Michalsky and Ellis, 1994). These series fall into four main soil orders, namely chernozems, solonetzes, regosols and gleysols. Of these, the most common soils are chernozemic brown soils. Chernozens are typical of grassland communities, and are characterized by a mull, dark, organic-rich surface horizon that reflects the build up of organic debris from grass and herb roots over long periods of time (Rowe, 1980). Although less-common, solonetzes, regosols and gleysols are also found within the GNP region. Solonetzic soils form where salts prevail. These soils are formed in response to the drought and high evaporation associated with grassland systems that tend to concentrate salts at the soil surface (Rowe, 1980). Regosols are poorly developed and have weak profiles that are indicative of surface disturbance (e.g. continuous erosion) or parent materials (e.g. high salt concentrations) that restrict the development of surface horizons (Michalsky and Ellis, 1994). Gleysols have a limited distribution, and are formed where drainage is impeded (Brady, 1990). Most of the area is underlain by Bearpaw Shales, which are exposed by the entrenchment of the Frenchman River valley in the west block of the park (Saskatchewan Institute of Pedology, 1992).

2.1.3.4 Natural vegetation

The presence of rolling uplands, badlands, riparian areas, coulées, and the Frenchman River valley create a diverse landscape which results in a vegetation mosaic that is more complex than most mixed grass prairie regions (Leonard and Dobson, 1991). This mosaic is created by the soil types present and by the amount and distribution of available moisture.

In 1993 a vegetation inventory and classification was conducted on lands for which GNP laid title (Michalsky and Ellis, 1994). This survey identified 7 major vegetation types within the GNP area (Upland, Sloped and Valley grasslands and Disturbed, Eroded, Shrub and Treed communities). Of these, the Upland grassland type is the most common, comprising approximately 35% of the total park area. This vegetation type is characterized by “a dominant cover of grasses or sedges, with shrub cover being low or absent" and occurs primarily on elevations above 900m, has slopes of less than 5%, and is undisturbed (Michalsky and Ellis, 1994). A mixed C3/C4 Upland type forms a large portion of the Upland grassland type (Peat, 1997). C3 grasses (e.g. *Stipa comata*, *Koeleria cristata*, *Pascopyrum spp*.) dominate this association, although a C4 grass (*Bouteloua gracilis*) co-exists in many places. Sage, mosses, lichens and cacti make up a significant part of the plant community in drier locations. These various plant functional types are considered in greater detail in section 2.2.

2.1.3.5 Management and Disturbance History

The land use history of the GNP region is well documented. While climatic instability has limited agricultural development in the region, parts of GNP have been seeded to non-native species or used for annual crops and then abandoned (Michalsky and Ellis, 1994). Over the past century, much of what is now GNP was used as rangeland for the grazing of domesticated animals, although this practice was eliminated in 1980 when the Government of Canada started to purchase land parcels. Because there are no bison left in the region, grazing is restricted to that done by deer, antelope, small animals and insects (Mitchell and Csillag, 2001). The issue of grazing is a controversial one because it is uncertain as to whether grazing is required to maintain northern mixed grass prairie (Axelrod, 1985).

In this study, we located three sampling sites within separate areas of mixed C3/C4 upland grassland vegetation at GNP. These locations were selected because they were undisturbed in recent history (ungrazed for 15 years, possibly longer). All three sampling sites showed no visible signs of human disturbance (i.e. they exhibited surface heterogeneity in the soil profile; showed no evidence of mounds, latrines, trampling, pathways, plowing; and contained very few individuals of plant species normally associated with disturbance events (e.g. invaders such as *Poa Pratensis* (Kentucky blue grass) and *Taraxicum officinale* (Common Dandelion)). Further evidence of minimal disturbance was (a) the fine-scale mixing of plant species present at all three sample sites (Csillag et al., 2002), and (b) the presence of similar species compositions to that of the managed PFRA (Prairie Farm Rehabilitation Administration) pasture lying along the northern border of GNP.

2.2 Grassland Plant Functional Types

2.2.1 What are plant functional types and why should we seek them?

In recent years, ecologists have placed increasing emphasis on the use of non-phylogenetic classifications of organisms when describing the structure and functioning of ecosystems (Gitay and Noble, 1997). The idea that plants can be grouped according to "function" is not a new one (Keddy, 1990). Early classification schemes (e.g. Von Humboldt (1806) and Kerner (1863)), grouped plants according to various morphological and physiognomic attributes such as growth form, height, leaf type and seasonality (Westoby and Leishman, 1997). Since then, plant ecologists have developed a variety of non-phylogenetic classification schemes through which species may be grouped. Such classification schemes include, but are not limited to, resource use, productivity, response to disturbance, reproductive strategy, stress tolerance, physiological types and phenology (see Bahr, 1971; Cummins, 1974; Botkin, 1975; Paine, 1980; Yodzis, 1982; Verner, 1984; Szaro, 1986; Friedel et al., 1988; Grime et al., 1988; Swaine and Whitmore, 1988; Noble, 1989; Keddy, 1992; Walker, 1992). The resultant groupings are generally referred to as *plant functional types*; that is, groups of plant species that are classified according to various aspects of ecosystem function and/or adaptive responses to environmental variables, rather than traditional classifications based on phylogeny (Hobbs, 1992).

Until recently, it was widely believed that the ability of a system to buffer against and recover from disturbance events, and capture and transfer environmental resources, depended solely on the magnitude of its species pool (Mooney et al., 1995; Johnson et al., 1996). Subsequent ecological research at the plot level, however, suggests that it may not be species diversity *per se*, but functional diversity within the species pool, which best explains variations in ecosystem properties such as plant biomass and productivity (Tilman et al., 1997). These results do not suggest that species diversity is unimportant; it is clear that species diversity constrains functional diversity to an extent. Rather, they indicate that measures of functional diversity may be better indicators of ecosystem "health" than the traditionally used measures of species richness.

2.2.2 Plant Functional types of the North American Grasslands

2.2.2.1 Classifications based on photosynthetic pathway

One approach to defining grassland functional types differentiates plants on the basis of their physiology. Many such classifications group plants according to their photosynthetic type; that is, the mechanism through which plants fix carbon into carbohydrate during photosynthesis (see Lauenroth et al., 1997; Scholes et al., 1997). Plants of the North American grasslands fix carbon via three photosynthetic pathways, namely C3, C4 and CAM. Of these, the C3 and C4 pathways contribute most to the overall floral diversity and net primary production of the biome. As a result, many studies of the North American grasslands have tended to focus on these two types (e.g. Tieszen, 1994; Goodin and Henebry, 1997; Tieszen et al., 1997; Epstein et al., 1997, 1998).

Since the discovery in the 1960s of alternative photosynthetic pathways in plants and the associated ecological and evolutionary interest shown in the different mechanisms of CO_2 fixation, the physiological differences between C3 and C4 types has become increasingly well understood (Ehleringer et al., 1991; Knapp, 1993). It is known that the C4 pathway evolved from C3 ancestors and is present in at least 17 families of the plant kingdom (Ehleringer et al., 1999). Although the C3 photosynthetic pathway has been suggested as the phylogenetic precursor to the C4 pathway, it has been widely reported that approximately two dozen species are intermediates between C3 and C4 types (Monson et al., 1984; Teese, 1995). These intermediates can be ordered to show the general sequence of evolutionary stages from the C3 to C4 state.

Most ecophysiological studies of C3 and C4 plants support the generalization that C4 types display certain advantages over C3 types as a result of their differing physiology. Physiologically, C3 and C4 lifeforms are distinguished by differences in the photosynthetic pathway through which atmospheric carbon is fixed into carbohydrate (Goodin and Henebry, 1997). In both groups, net CO_2 assimilation occurs in the chloroplast through the reductive pentose phosphate (RPP) pathway, or Calvin cycle. In C3 plants, CO_2 assimilation takes place in a single cell type (mesophyll cells). There, the enzyme Rubisco catalyses the reaction between atmospheric CO_2 and the plant substrate RuBP to produce a three-carbon molecule, after which C3 plants are named. These molecules are then further metabolized to the major end product of photosynthesis (Ehleringer et al., 1991). However, under conditions of elevated temperature and sunlight, Rubisco is also able to catalyze a reaction that leads to the fixation of O_2, and results in the release of CO_2 at a net cost to the plant. This process is called *photorespiration*, and can reduce potential carbon uptake of C3 plant forms by as much as 30% in warmer environments (Monson et al., 1984; Pearcy and Ehleringer, 1984; Bowman and Turner, 1993; Tieszen, 1994; Teese, 1995).

Plants with the C4 pathway of photosynthesis have evolved a mechanism for overcoming photorespiration. This mechanism utilizes two distinctive photosynthetic cell types (mesophyll and bundle sheath cells) (Monson et al., 1984). In the C4 pathway, CO_2 is shuttled from the atmosphere to the bundle sheath cells, where CO_2 is concentrated and fixed through Rubisco (Pearcy and Ehleringer, 1984; Monson et al., 1984). While Rubisco is unable to distinguish between CO_2 and O_2 over the active site in the C3 mechanism, the C4 mechanism provides a CO_2 concentrating system that allows Rubisco to function relatively unimpeded by O_2 (Tieszen, 1994). This is achieved by the use of an enzyme, PEP carboxylase, which is insensitive to O_2, and carboxylates atmospheric CO_2 to produce a four-carbon molecule, after which C4 plants are named. As a result, an ecological benefit of having the C4 pathway is greater potential carbon gain, growth and competitive ability under environmental conditions favorable to photorespiration (e.g. high temperatures and light) (Bowman and Turner, 1993; Tieszen, 1994). Furthermore, because of their high affinity for CO_2 of the initial carboxylation, C4 species are able to maintain lower stomatal conductances to water vapor, and thus maintain lower transpiration rates, than those of C3 species (Knapp, 1993). However, Tieszen et al (1994) note that the increased water use efficiency of C4 grasses does not always translate into higher regional values of production for C4 plants. Rather, the competitive advantage of C4 plants under resource limitations may lead to site specific rates of production that are lower than those resource rich sites dominated by C3 plants (Barnes et al., 1983). A limitation to C4 photosynthesis is that it requires more energy to fix CO_2 than C3 species. Thus, such species are not adapted to low light conditions (Tieszen, 1970; Tieszen, 1994) and are not found in treed or understory environments. Consequently, warm, dry and open environments are typically most favorable for efficient C4 photosynthesis, whereas C3 grasses occupy cooler, more shaded locations (Tieszen, 1970).

Between 1975 and 1985, the global latitudinal and altitudinal distribution of C4 photosynthesis was mapped, largely as a result of detailed surveys of C4 species representation in regional grass, sedge and dicot floras in North and South America, Asia, Europe and Africa (see Sage et al., 1999 for a review). These studies showed that grasslands vary in composition from systems in which 100% of the grasses are C4, such as lowland tropical environments, to lower temperature systems at higher altitudes or latitudes where no C4 species are present (Tieszen et al., 1979; Tieszen et al., 1997). Numerous studies (see the review of Ehleringer and Monson, 1993) have since confirmed this dominant control by temperature for North America, as first shown by Teeri and Stowe (1976). Teeri and Stowe's (1976) floristic analysis showed that C4 grass abundance is highest in southern Texas where C4 species comprise between 68% and 82% of all grasses, and lowest in central Canada where no C4 species were observed (Figure 2.4).

2.2.2.2 Classifications based on water partitioning strategy

A second approach to defining grassland functional types differentiates plants on the basis of their water partitioning strategy. In environments, such as grasslands, where water availability is an important control on ecosystem structure, it has been suggested that the spatial and/or temporal partitioning of soil moisture by plants allows for the coexistence of different life-forms (e.g. Noy-Meir, 1973; Walter, 1979). According to this model, water partitioning occurs because succulents, grasses, forbs and shrubs each typically exhibit different rooting depths, and thus, draw water from separate stores in the soil profile. Shallow-rooted succulents utilize the shortest-term sources of water from the uppermost soil layers. Grasses, whose roots are generally longer than those of succulents, utilize longer-term sources of water from deeper soil depths. Forbs, whose root structures are generally longer than those of grasses, and shrubs, whose roots are generally longer than those of forbs, tend to access the longest-term stores of water from even deeper in the soil profile (Soriano and Sala, 1983; Weltzin and McPherson, 1997; Dodd et al., 1998). These differing water acquisition strategies are supported by various studies carried out in the Patagonian steppe (Sala et al., 1989; Golluscio and Sala, 1993; Schulze et al., 1996; Sala et al., 1997), African savannas (Knoop and Walker, 1985; Le Roux and Bariac, 1998),.

Figure 2.4. The percent C4 species in the grass floras of North America (modified from Teeri and Stowe (1976)).

temperate savannas (Weltzin and McPherson, 1997) and chaparral (Poole and Miller, 1975; Davis and Mooney, 1986), and the North American short-grass prairie (Lauenroth et al., 1997; Dodd and Lauenroth, 1997; Dodd et al., 1998)

2.2.2.3 A functional group classification for Grasslands National Park

Based on the above classifications, it is possible to develop two conceptual models of plant functional types for Grasslands National Park. These are (a) a model based on photosynthetic type, and (b) a model based on water partitioning strategy. The first model simply classifies the species of Grasslands National Park based on photosynthetic pathway (i.e. C3, C4 or CAM). The second approach modifies the water partitioning models outlined in the previous section in two important ways. First, the most abundance species in Grasslands National Park is *Selaginella densa* (Dense Club Moss), a commonly occurring species of upland grassland regions (McCanny, 2000). This carpet-like plant is able to utilize the shortest-term sources of water from the uppermost soil layer because of its very shallow rooting system and complex architecture. Such water partitioning strategies allow *Selaginella densa* to be considered a separate functional type in its own right (Kertész, pers. comm). Second, the temporal displacements in productivity between C3 and C4 species also reflect temporal displacements in water acquisition between these two types (while C3 species green up in early spring and are most active under the cooler conditions of spring and fall, C4 species green up later in the growing season, and are more active under the hotter and drier summer months (Kemp and Williams, 1980; Ode and Tieszen, 1980). This, conceptually, allows for the further subdivision of grass, shrub and forb types into their respective C3 and C4 components. Both the above models are utilized as measures of diversity in subsequent chapters of this thesis.