SEASONAL AND INTER-ANNUAL VARIATION IN CARBON DIOXIDE EXCHANGE AND CARBON BALANCE IN A MIXED GRASSLAND

by

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Bachelor of Science (Distinction)
Environmental Science
The University of Lethbridge
May 23, 1998

A Thesis submitted to the Council on Graduate
Studies of the University of Lethbridge in Partial
Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

The University of Lethbridge
Lethbridge, Alberta
December, 2000

Abstract

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Eddy covariance measurements were carried out to document the seasonal and inter-annual variation in CO_2 flux in a mixed prairie grassland. There was very different net ecosystem carbon exchange between the two years of study. In 1998 the maximum net carbon exchange was 4.95 g C m^{-2} d^{-1}, compared to 2.50 g C m^{-2} d^{-1} in 1999. The most important environmental control on CO_2 uptake was volumetric soil moisture content through its affect on leaf area index. There was evidence of stomatal limitation of CO_2 uptake, during periods of atmospheric drought. The total seasonal net ecosystem carbon gain for 1998 was 190.0 g C m^{-2}, compared with 46.8 g C m^{-2} in 1999. This grassland is a large carbon sink in a growing season of above normal precipitation. In a year of normal summer precipitation, this grassland is a small carbon sink, replacing slightly more carbon than is lost through winter respiration.

ACKNOWLEDGMENTS

The author wishes to thank my supervisor, Professor Lawrence Flanagan for his tireless and sometimes frustrated efforts to get me to do my best. It was Professor Flanagan's inspired teaching of ecosystem physiology that got me this far and he was most helpful in its completion. This experience was interesting and became quite enjoyable when I worked, had discussions with, or just hung out with my comrade in arms, Linda Wever.

I would also like to thank the members of the Thesis Supervision Committee for the time and good advice they have supplied to me. Professor Stewart Rood was very supportive and supplied the use of his land for the research effort. Professor Jim Byrne had thoughtful questions and a cheerful attitude. Dr. Ben Ellert was very helpful in getting samples analyzed and provided interesting points to ponder. Thank you to the University of Calgary for providing the space and lab time to process my samples and to Dr. Bernard Mayer for instructing an informative graduate course. There are a number of nameless tradesmen and rental shop employees who had an important part in this effort. Thank you all.

I gratefully acknowledge The Natural Sciences and Engineering Research Council of Canada for providing the funding that allowed for my graduate studies.

A big and never-ending thank you goes to my long-suffering family without whose support I would not have survived. If I have inspired my boys to reach for their dreams then it will have all been worth it.

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List of Abbreviations and Symbols

A = assimilation of CO_2 (GP expressed as μmol m^{-2} s^{-1})

a = isotopic fractionation due to diffusion of CO_2 in air (4.4‰)

ABG = aboveground biomass (g m^{-2})

b = isotopic fractionation caused by rubisco (27‰)

C_a = ambient CO_2 concentration (μmol mol^{-1})

C_i = intercellular CO_2 concentration (μmol mol^{-1})

c_p = specific heat of dry air (J g^{-1} K^{-1})

$\mathit{c_p}$ = specific heat of dry air (J mol^{-1} C^{-1})

E = water flux (g m^{-2} s^{-1})

e = ambient air vapour pressure (Pa)

*e** = saturated air vapour pressure (Pa)

F= net ecosystem flux (μmol m^{-2} s^{-1})

F_{st} = flux storage term (μmol m^{-2} s^{-1})

G = soil heat flux (W m^{-2})

GP = gross photosynthesis (μmol m^{-2} s^{-1})

g = total conductance (mol m^{-2} s^{-1})

g = acceleration due to gravity (10 m s^{-2})

g_a = total aerodynamic conductance (m s^{-1})

g_b = excess aerodynamic conductance for heat and water vapour transfer to crops (m s^{-1})

g_c = canopy conductance (mol m^{-2} s^{-1})

g_e = eddy diffusive aerodynamic conductance between the canopy surface and the measurement height (m s^{-1})
H = sensible heat flux (W m^{-2})
h = air column height (m)
k = von Karman constant (0.4)
LAI = leaf area index (m^2 m^{-2})
M_s = soil moisture (%)
NEE = net ecosystem exchange (µmol m^{-2} s^{-1})
NDVI = normalized difference vegetation index
PAR_o = incident photosynthetically active radiation (µmol m^{-2} s^{-1})
R = respiration (µmol m^{-2} s^{-1})
R_d = day respiration (µmol m^{-2} s^{-1})
r_a = aerodynamic resistance (s m^{-1}) = $1/g_a$
rh = relative humidity (unitless)
Rn = Net radiation (W m^{-2})
S = sensible heat flux (W m^{-2})
T = air temperature (°C)
T_s = 4 cm soil temperature (°C)
u = wind speed (m s^{-1})
u_* = friction velocity (m s^{-1})
VPD = vapour pressure deficit (kPa)
w' = vertical wind velocity fluctuation (m s^{-1})
z = measurement height (m)

z_h = roughness length for heat (m)

z_m = roughness length for momentum (m)

z_v = roughness length for vapour (m)

$\Delta = \delta^{13}C_{air} - \delta^{13}C_{leaf}$ (‰) ($\delta^{13}C_{air}$ = -7.8‰)

$\Delta[CO_2]$ = change in CO_2 concentration (μmol mol^{-1})

Δt = change in time (s)

γ = psychometric constant (Pa K^{-1})

λ = latent heat of vapourization (J g^{-1})

ρ_a = density of dry air (mol m^{-3})

ρ_a = density of dry air (kg m^{-3})

χ'= concentration fluctuation (μmol mol^{-1})

ζ = atmospheric stability (unitless)

Ψ_M = diabatic correction factor for momentum (unitless)

Ψ_H = diabatic correction factor for heat (unitless)

1. Introduction

Human activities are increasing the CO_2 concentration of the atmosphere (Keeling *et al.* 1995) and this will impact our lives but there remains some controversy as to how it will impact us. Will the impacts be positive, with such things as increased crop growth and improved water use efficiency, or negative with disrupted weather cycles and increased respiratory losses of CO_2, which would further add to the carbon in the atmosphere (Baldocchi 1997).

There are three rapid exchange or "mobile" reservoirs for carbon storage along with the geological reservoir that exchanges carbon very slowly. The three rapid exchange reservoirs are the atmosphere, the surface ocean, and the terrestrial biosphere (Tans and White 1998). There are large fluxes moving to and from the atmosphere constantly but the ocean and terrestrial biosphere are in near equilibrium with it. Since the industrial revolution there have been increasing CO_2 emissions from fossil fuel burning which are larger than the net exchange between the atmosphere and the oceans or the atmosphere and the terrestrial biosphere, this causes the increase in atmospheric CO_2 concentration (Tans and White 1998). There are estimates that fossil fuel emissions have added 6.2 gigatons (Gt) of carbon per year to the atmosphere between 1991-1997 (Battle *et al.* 2000). During that same period the atmospheric CO_2 concentration increased by only 2.8 Gt of carbon per year, with the balance (3.4 Gt/yr) taken up by the oceans and the terrestrial biosphere. A global carbon budget, for the period 1991-94, suggested that 60% of the fossil fuel emissions were removed from the atmosphere by photosynthesis in the northern terrestrial biosphere and the oceans (Battle *et al.* 2000). This net uptake of carbon was split approximately evenly between the terrestrial and ocean sinks (R Keeling *et al.* 1996). However, the partitioning of the fossil fuel carbon between the oceans and the terrestrial biosphere is not completely understood (Battle *et al.* 2000). It appears that the terrestrial biosphere has a significant role in the global carbon budget, although it is a highly variable reservoir for carbon storage (Battle *et al.* 2000, Schimel *et al.* 2000, Houghton *et al.* 1999).

If the terrestrial biosphere is a sink for the fossil fuel carbon dioxide, then where and how is that sequestration occurring? Fossil fuel emissions are released predominantly in the Northern Hemisphere and as a consequence there is a higher concentration of CO_2 in the atmosphere of the Northern Hemisphere. However, the observed concentration gradient between the northern and southern hemisphere is smaller than expected (based on fossil fuel emissions statistics), so this implies a net carbon sink for fossil fuel emissions in the Northern Hemisphere (Fung *et al.* 1997). Fan *et al.* (1998) used measurements of an east-west gradient of CO_2 concentration to calculate that the North American continent was the strongest carbon sink in the Northern Hemisphere. Recent studies with atmospheric $^{13}C/^{12}C$ ratios and oxygen concentration have also concluded that the Northern hemisphere sink was caused primarily by terrestrial biosphere uptake (R Keeling *et al.* 1996, Ciais *et al.* 1995). It is necessary to understand not only where the missing carbon is going but also the mechanism of uptake. Understanding the mechanisms will allow better prediction of how much carbon can be sequestered, how long it will remain "bound" and if the process might reverse and release some or all of this carbon back into the atmosphere in the near future.

Another general problem of the global carbon budget is the substantial inter-annual variation in the growth rate or increase in atmospheric CO_2 concentration (Keeling *et al.* 1995). The increase in CO_2 concentration can vary from 0.5 to 3 parts per million (ppm) per year (Tans and White 1998). Why is there such a large inter-annual variability in atmospheric CO_2 growth rate? Many researchers think it is due to variability in the uptake of CO_2 by the terrestrial biosphere and oceans. Recent studies by Battle *et al.* (2000), that used atmospheric measurements of O_2/N_2 ratios and carbon isotope analyses, concluded that terrestrial carbon storage seems more variable than oceanic storage. The variability must be driven by climate fluctuations, but terrestrial ecosystem response to environmental variation is complex. For example a study in a deciduous forest in North America showed a range of annual net CO_2 uptake from 1.4 to 2.8 tons C ha^{-1} (140 to 280 g C m^{-2}) over a 5-year period (Goulden *et al.* 1996). Similarly a 120-year-old boreal forest had a range of annual net carbon uptake from -0.7 to 0.1 tons C ha^{-1} (-70 to 10 g C m^{-2}) from 1994 to 1997 (Goulden *et al.* 1998). The negative values indicate a net loss of CO_2 to the atmosphere. A major objective of current carbon cycle research is to better understand and document what controls year to year variation in CO_2 exchange in terrestrial ecosystems (Canadell *et al.* 2000).

The mechanisms most responsible for terrestrial net carbon sequestration and the contribution of the various ecosystems are in debate (Lloyd 1999). Some of the suggested mechanisms for the sequestration of carbon in terrestrial ecosystems are CO_2 fertilization of photosynthesis, nitrogen deposition, and climatic factors (Sala *et al.* 2000). For example, elevated atmospheric CO_2 concentration should allow for an increase in CO_2 uptake by ecosystems. An increase in the atmospheric CO_2 concentration would allow for higher leaf intercellular CO_2 concentration. This would give a higher supply of CO_2 for the photosynthetic process and less photorespiratory loss in C_3 plants (Lambers *et al* 1998). However, the short-term response is generally greater than the long-term response to increased CO_2 because of acclimatization by the plants, but an increase of CO_2 assimilation would be expected even over the long term (Lambers *et al* 1998). A modeling experiment, which estimated the terrestrial carbon sink in the continental United States, indicated that the bulk of the increase in net carbon storage per unit area was the result of CO_2 fertilization. The rate of uptake varied with and was modulated by climate (Schimel *et al.* 2000). This showed that where climatic conditions became more favourable to plant growth, the increased supply of CO_2 had a positive affect on CO_2 uptake.

Nitrogen produced by industrial processes and fossil fuel combustion, and later added to terrestrial ecosystems as wet and dry deposition, can affect CO_2 uptake, but the magnitude and direction of the influence is still unclear (Nadelhoffer *et al.* 1999). Ecosystem models tend to support the conclusion that nitrogen deposition will increase the degree of carbon sequestration that an ecosystem can achieve (Norby 1998) because the two most frequent controls over net primary production are water and nitrogen availability (Burke *et al.*

1997). However, there are additional factors that can alter the interaction of nitrogen deposition and carbon sequestration. Some of these factors include; nitrogen saturation, interaction between N input and CO_2 concentration, and changes in community composition (Norby 1998). Low levels of nitrogen deposition along with a doubling of CO_2 concentration caused an increase of plant dry mass in *Sphagnum* moss, however higher levels of nitrogen in combination with CO_2 did not show a significant production increase because of nitrogen saturation (Van Der Hiegden *et al.* 2000). In a study of a grassland subjected to various levels of nitrogen deposition, it was noted that there were changes in species composition and a loss of diversity. Along with the changes in composition and diversity, there was a change to low carbon sequestration rates and an increase in nitrogen losses with higher levels of N deposition (Wedin and Tilman 1996). Recent ^{15}N-tracer studies have shown that elevated nitrogen deposition is unlikely to be a major contributor to the CO_2 sink (Nadelhoffer *et al.* 1999) because soil rather than trees was the primary sink for nitrogen inputs to temperate forests. Nitrogen inputs to soil can be subject to loss as inorganic nitrogen or nitrate leaching. These additional factors further confound the expected interaction of nitrogen deposition and increased CO_2 concentration. Studies of the effects of nitrogen deposition on carbon sequestration will need to account for these factors when making predictions of ecosystem carbon sequestration.

Several workers have looked at climate change effects on ecosystem carbon sequestration and the results of these studies indicate that there could be a variety of responses to increased temperature (Sellers *et al.* 1996). Studies of mid-latitude deciduous forests showed increased rates of annual CO_2 uptake in association with positive temperature anomalies and a lengthening of the growing season (Goulden *et al.* 1996, C Keeling *et al.* 1996). However, in a boreal conifer forest there was a different response to temperature. High temperatures had more of an effect on increasing soil respiration than on increasing carbon uptake (Goulden *et al.* 1998). This variability in response to increased air temperature will lead to quite different carbon budgets for different ecosystems and there is a need for further investigation.

Soil water availability will have an effect on net CO_2 uptake and this has only recently started to be addressed for different ecosystems (Baldocchi 1997b, Miranda *et al.* 1997, Grace *et al.* 1998). Recent studies suggested that the cause of increased soil water content in a grassland subjected to increased nitrogen deposition, was because of decreased losses through evapotranspiration (Lutze and Gifford 1998, Owensby *et al.* 1999). A decrease in evapotranspiration may have other effects not readily apparent or as beneficial as increased soil water. In a coupled biosphere-atmosphere model study it was indicated that there would be a drop in evapotranspiration and an increase in air temperature due to increased CO_2 concentration (Sellers *et al.* 1996). The increase in soil moisture would be a benefit for ecosystems that normally operate in water deficit. However, that benefit may not be realized if surface air temperatures rise too far above the optimum for photosynthesis. The CO_2 assimilation of ecosystems under these possibly conflicting responses is not well understood.

The International Convention on Climate Change and the more recent Kyoto Protocol have attempted to address the issue of human-caused CO_2 emissions through the establishment of emission reduction targets for the world's developed countries. Canada agreed to an emission target of 6% below its 1990 emissions for the period spanning 2008 to 2012 (Environment Canada 1999). A major research challenge presented by Canada's commitment is to understand how our biosphere will respond to climate change. Recent models suggest that some regions of Canada will experience more dramatic climate change than others (NOAA 1999). It is necessary to investigate the function of landscapes or ecosystems composed of many individuals or groups of organisms so that we can understand the development of current conditions, in order to predict changes in carbon sequestration (Wofsy and Hollinger 1997). Houghton (1997) estimated that the global temperature would increase by 2.5°C in a century, if there was no change in the rise of CO_2 emissions. Such an increase may have serious environmental, social and economic consequences.

It is now feasible to make continuous measurements of whole ecosystem CO_2 exchange using the eddy covariance technique (Baldocchi *et al.* 1988). Eddy covariance sampling imposes a minimum of influence from the investigative apparatus, and can be automated to collect data continuously so that any temporal patterns can be observed and a record of ecosystem reaction to all environmental conditions can be developed (Aubinet *et al.* 2000). Some eddy covariance studies have estimated an annual carbon balance based on a short and intensive sampling period with assumptions of CO_2 flux made for the unsampled periods (Valentini *et al.* 1995. Clarke *et al.* 1999). However, for complete understanding of ecosystem carbon budgets, measurements made over an entire annual cycle would be required, especially in northern latitudes where winter respiratory losses are not well understood (van Bochove *et al.* 2000).

There were 4 specific questions addressed in this study. How does ecosystem CO_2 exchange vary among seasons and between years in a northern grassland ecosystem? What environmental factors most control CO_2 uptake and loss and how do the controls work? What is the annual carbon budget for the grassland, and is the ecosystem a net source or sink for carbon? How does the annual carbon budget, calculated from the eddy covariance measurements, compare to estimates from plant biomass harvests?

2. Materials and Methods

2.1 Study Site Description

2.1.1 GENERAL SITE CHARACTERISTICS

The Rood Grassland study site was located at 49.43° North latitude; 112.56° west longitude (NE-05-09-22-W4 Canada Land Survey) approximately 1.5 km west of Lethbridge city limits. The site was 951 m above mean sea level. In the Lethbridge area monthly mean minimum air temperature ranges from -1.1 to 10.5°C, and the mean maximum ranges from 12.2 to 25.6°C for the period April to September, with the mean July air temperature of 18.1°C. The range of soil temperature at the 5 cm depth was 6.7 to 20.5°C for the April to September period. The mean annual precipitation was 401.5 mm (AAFC 2000). The study site was a 64 hectare (160 acre) square block of grassland. The majority of the study site has not been cultivated since settlement (personal communication with the land owner). A narrow strip of land on the eastern edge of the site was cultivated in the 1930's but has been recolonized by the dominant grass and forb species. There are two vehicle trails evident in an air photo, taken in May of 1961 (Fig. 1), running from northeast to southwest. The longest of these trails was not evident in ground surveys and the shorter trail, while evident on the ground, does not greatly impact the study site. The site was a mixed grass prairie (Coupland 1960) characterized as having low temperatures, relatively low precipitation, a single peak in precipitation during the early summer, and severe to moderate drought conditions following the peak precipitation (Lauenroth 1979).

2.1.2 SOIL CHARACTERISTICS

The soil was classified as Orthic Dark Brown Chernozem (Canadian System of Soil Classification 1987) soil of clay loam to clay texture. The soil texture and nutrient analysis were determined from a composite soil sample sent to the Norwest Labs [Lethbridge AB.]. The composite sample consisted of 24 separate samples taken from a grid pattern surrounding the eddy covariance instrument hut. The grid cells were 30 X 30 m squares with the soil sample taken in the centre of the cell. The soil plugs were inspected and horizon depth recorded, the horizons were then separated and placed in a bulking container for later sub-sampling. The composite horizon samples were sub-sampled and a 0.5 kg sub-sample for each horizon was transported to the soil testing lab on the day of sampling.

The textural analysis indicated that the A horizon contained 28.8% sand, 40% silt and 31.2% clay content placing it in the Clay Loam textural category (Canadian System of Soil Classification 1987). The B horizon contained 27.4% sand, 29.6% silt and 40% clay placing it in the Clay category of the textural triangle. Organic matter content of the surface horizon or top 10 cm was 5.2%. Nutrient status as of May 26, 1998 is reported in Table 1.

Four soil pits were dug, 40 cm deep, within 100 m of the eddy covariance instrument hut. The horizons observed in the pits concurred with the horizons of the soil cores. Individual triangular slices, 8 cm on a side and 2 cm deep, were removed from the wall of the pit to a depth of 30 cm for a total of 15 samples from each pit. These samples were latter analyzed for Carbon and Nitrogen concentration.

2.1.3 PLANT SPECIES COMPOSITION AND ABUNDANCE

The Rood Grassland was a mixed grass prairie composed of mid-grasses and short-grasses with lesser amounts of forbs. The site was dominated by the *Agropyron* sp. (Rydb., Hook & Scribn.) grasses and the biennial forb *Tragopogon dubius* (Scop.) [Goats Beard] for both 1998 and 1999 (cf. section 3.2). The other grasses and forbs occur in bunches or thinly scattered throughout the grassland.

In order to determine the abundance of individual species at the study site, a point frame survey was done on July 5, 1998 and for 1999 there were three surveys done; June 20, July 20, and August 20. A survey consisted of 20 placements of a 1 meter wide frame with a pin positioned every 10 cm along the frame. The pin was lowered into the vegetation and a pin "hit" was recorded every time the pin touched a plant. The species and number of "hits" were tabulated along with the bare ground "hits". A point frame placement scheme was established, using random numbers as coordinates (Smith 1990).

2.2 Plant Biomass and Leaf Area Index Sampling

The total above ground biomass samples in 1998 were gathered from mid May to mid September. The sampling sites were located using a stratified random method and the clippings were done using a 0.2 m X 0.5 m rectangular frame. The plots were clipped to remove all plant material above the soil surface, the plant material was placed in a large resealable plastic bag and transported to a refrigerator for latter processing. The clipped samples were separated into living plant material and non-living material. Six replicate clippings were harvested each sample day. The leaf area for each species was determined using a LI-3100 Area Meter [LI-COR, Lincoln NE]. The samples were dried in an oven at 60°C for at least 24 hrs and then weighed on a Mettler PJ400 [Greifensee, Switzerland] scale. The samples were then ground to a fine powder using liquid nitrogen and a mortar and pestle. In 1999 the live aboveground biomass was collected from a grid of sampling plots established in proximity to the eddy covariance instrument hut. The sample plots were chosen using a random number generator. The living plant material was further separated into species of interest. Six replicate clippings were harvested each sample day and processed in the same manner as described above.

2.2.1 CARBON AND NITROGEN ANALYSIS

The plant bulk biomass and species biomass samples were analyzed for N and C content using an elemental analyzer (NC2500, CE Instruments, ThermoQuest Italia, Milan, Italy). The ground samples were weighed to approximately 2 mg with three to six replicates for each sample date. A calibration curve was established using graduated weights of a laboratory standard plant material with a known N content of 1.229% and C content of 45.344%. There were 10 unknown plant samples run followed by two laboratory standards run as unknowns per group. An analysis of variance was performed to compare the differences between the sample dates to the differences within a sample date.

2.2.2 CARBON ISOTOPE ANALYSIS

The plant bulk biomass carbon isotope composition (^{13}C) was determined using an Optima gas isotope ratio mass spectrometer (Micromass, Ltd., Manchester, UK) which receives input from a CN analyzer (Carlo Erba NA-1500 Series 2, CE Instruments, Milan Italy) via a continuous flow arrangement. Automated continuous flow gas isotope ratio mass spectrometry advances have been described by Brand (1996). The interface of the CN analyzer to the mass spectrometer (MS) was accomplished using the IsochomEA system and software (Micromass, Ltd., Manchester, UK). The ^{13}C content is measured as a ratio of ^{12}C and data was expressed relative to carbon dioxide obtained from an international standard (PDB) as shown below.

$$\delta^{13}C\text{‰} = \left[\frac{\left(\frac{^{13}C}{^{12}C_{\text{sample}}} \right)}{\left(\frac{^{13}C}{^{12}C_{\text{standard}}} \right)} - 1 \right] \times 1000 \qquad \text{eq. 1}$$

2.3 Meteorological Measurements

Net radiation was measured with a net radiometer (REBS Q*7.1, Radiation Energy Balance System, Seattle, WA), photosynthetically active photon flux density was measured with a quantum sensor (LI 190SA, LI-COR, Lincoln, NE) both of these sensors were mounted on a 3 m tower approximately 2 m south of eddy covariance tower. Soil heat flux density was measured by averaging data from two heat flux plates (HFT-3.1, REBS, Seattle WA.) buried at 0.02 m below the soil surface, placed within 2 m of the flux tower. Soil temperatures were measured with thermocouples placed at 0.02, 0.04, 0.08, 0.16 m below the soil surface within 1 m of flux tower. Air temperatures were measured with fine wire aspirated thermocouples (ASPTC, Campbell Scientific, Logan, UT) mounted at 1 m and 5 m on the flux tower. A model 207 temperature and relative humidity probe (Campbell Scientific, Logan, UT) was mounted at 2 m on the flux tower and protected by a gill radiation shield. The meteorological and soil data were logged on a digital data logger (CR10X, Campbell Sci. Logan, UT) sampled at one second intervals and half-hour averages were calculated to coincide with the flux measurements. Precipitation was measured with a tipping bucket rain gauge (TE525, Campbell Sci., Logan, UT) with a total every 15 minutes when rain occurred then logged to the same data logger.

Soil moisture content was measured by harvesting a known volume of soil with a soil corer to the 10 cm depth for 1998 and to 15 cm depth for 1999. The soil samples were transported to the lab and weighed immediately then dried for 24 hrs at 105°C, the samples were then re-weighed and a percent water volume calculated (Gardner 1986).

2.4 Ecosystem CO_2 Flux Measurements

Net ecosystem CO_2 flux was measured using the eddy covariance technique (Baldocchi *et al.* 1988). The eddy covariance system measures the net flux of CO_2 across the interface between the atmosphere and the biosphere. Over a plant canopy packets of air may move in any direction, upward pulses carry substances away from the canopy, and downward pulses carry substances into the canopy. This turbulent transport can be measured because the pulses or packets of air carry with them the properties from their original layer to their new layer (Campbell and Norman 1998). In a photosynthesizing canopy the turbulent transport must, over time, replenish the disappearing CO_2. The CO_2 concentration of the downward moving air packets will be higher than that of the upward moving packets or there will be more packets of air moving downward. This means that the net flux of a substance will be equal to the covariance of the fluctuation of vertical wind velocity and the fluctuation of the concentration of that substance (Field *et al.* 1989). Fluxes of momentum, water vapor, CO_2, and sensible heat flux were computed using the University of Edinburgh EdiSol software (Moncrieff *et al.* 1997). A vertical eddy flux can be estimated as:

$$F = -\rho_a \overline{w'\chi'} \qquad \text{eq. 2}$$

where F= net flux (μmol m^{-2} s^{-1})
ρ_a= density of dry air (mol m^{-3})
w'= vertical wind velocity fluctuation (m s^{-1})
χ'= concentration fluctuation (μmol mol^{-1})

This flux is directed downward when $F<0$ and is directed upward when F is positive (Baldocchi *et al.*1988). The vertical wind velocity fluctuation (w') was the difference between the instantaneous vertical wind velocity and the mean vertical wind velocity. The mean vertical wind velocity was calculated from the vertical wind velocities measured over the previous 300 seconds. The concentration fluctuation was calculated in the same way. The fluctuation (or variance from the mean) of the vertical wind velocity and variance from the mean of concentration were then multiplied for each instantaneous measurement taken. The covariances were binned and the covariance best correlated with the fluctuations in vertical wind velocity are used to determine the time lag. At the end of the averaging period (30 minutes), the average of the correlated instantaneous covariances was used to calculate the half-hourly flux.

A bias error can occur when CO_2 is stored in the air column below the eddy flux sensor location. This can be particularly important during periods of low wind speeds, or temperature inversion (Ruimy *et al.* 1995). The storage term was calculated as the time rate of the change in the CO_2 concentration (Baldocchi *et al.* 1997) for the height of the air column:

$$F_{st} = \frac{\rho_a h \Delta[CO_2]}{\Delta t} \qquad \text{eq. 3}$$

where F_{st} = storage term (μmol m^{-2} s^{-1})
ρ_a = molar density of air (mol m^{-3})
h = air column height (m)
$\Delta[CO_2]$ = change in CO_2 concentration (μmol mol^{-1})
Δt = change in time (s)

The sum of the air column storage term (F_{st}) and the measured ecosystem CO_2 flux (F) equals the net ecosystem exchange (NEE). A negative value of NEE represents a loss of CO_2 from the atmosphere and a gain by the biosphere, this was in keeping with the meteorological convention. Other researchers (Baldocchi 1997b, Miranda *et al.* 1997) have used a CO_2 profile measurement system, this can facilitate a more rigorous measure of storage flux. This site, however, was relatively windy with low productivity and low stature vegetation. The air column was often well mixed and a profile measurement system proved unnecessary for estimates of storage flux.

The three-dimensional sonic anemometer (3-D Ultrasonic Anemometer, Solent 1012, Gill Instruments Ltd., Lymington, England) was placed on a 1 meter boom attached to a 6 meter tall tower. The boom was oriented to place the instrument into the predominant wind direction, which was west for every month of the year (Canadian Climate Normals for Lethbridge CDA). The study site was relatively flat (slopes approximately 2%), extending for 600-700 meters in direction of the prevailing wind. There was >600 m of fetch for the 6 meters instrument height, which gave ample distance for any necessary readjustment of the internal boundary layer in the direction of the prevailing wind (Businger 1986).

A Capex V2X 12 VDC (Charles Austen Pumps Ltd., Surrey, England) diaphragm pump was used to collect air from the sonic anemometer. The pump was placed down stream of the CO_2 analyzer drawing air through 15 meters of tubing (3 mm id Bev-A-Line IV). This provided flow rates ranging from 7-8 L/min, resulting in a pressure drop of 15-16 kPa from ambient air pressure. A fast response CO_2/water vapour infra-red gas analyzer (LI 6262, LI-COR, Lincoln, NE) was calibrated weekly for CO_2 concentration using a prepared air mix (Praxair, Lethbridge, AB) calibration standard, tested and corrected against an NOAA/CMDL standard. There was <5% drift of the IRGA between CO_2 calibrations. The IRGA was calibrated for water vapour every 2 weeks, during the growing season, with a dew point generator (LI-610, LI-COR, Lincoln, NE.). There was little drift (<5%) of the IRGA between water vapour calibrations. The data were digitized, processed and stored on a laptop computer.

2.5 Flux Data Analysis and Gap Filling Strategies

The CO_2 flux measurements can provide insight into the ecosystem physiological response. To understand ecosystem function, it is useful to calculate photosynthetic light-use efficiency and the response of other physiological processes such as total ecosystem respiration and canopy conductance to variation in environmental conditions (light, temperature, humidity). The relationships seen in this ecosystem can then be compared to responses from other ecosystems.

To estimate the rate of gross photosynthetic uptake of carbon, the total ecosystem respiration rate was subtracted from the daytime NEE flux previously determined. The loss of CO_2 from the ecosystem as represented by a positive C flux, was defined as the total ecosystem respiration. The eddy covariance system measures the net flux of the system and therefore includes both additions and withdrawals occurring in that system (Ruimy *et al.* 1995). However, at night the measured fluxes must represent the ecosystem respiration, as there was no photosynthetic uptake occurring. Studies have shown that total soil respiration is strongly controlled by variation in soil temperature and soil moisture (Rochette and Flanagan 1997, Sigh and Gupta 1977, Valentini *et al.* 1995, Miranda *et al.* 1997, Baldocchi *et al.* 1997, Colello *et al.* 1998). In this study the total daytime ecosystem respiration rate was calculated using a relationship established between the nighttime NEE values and soil moisture/soil temperature (eq. 3). The nighttime NEE fluxes were sorted according to photosynthetically active radiation ($PAR<1 \mu mol\ m^{-2}\ s^{-1}$) and friction velocity ($U^*>0.4\ m\ s^{-1}$) to give dark respiration measurements in low light and high turbulence, to ensure well mixed conditions. Using a statistical software package (Super-ANOVA), a multiple linear regression was calculated with dark respiration as the dependent variable and volumetric soil moisture and soil temperature at 4 cm as the independent variables. The respiration model was improved by elimination of high CO_2 flux occurring after rain events (Luo *et al.* 1996). Ecosystem respiration was calculated as:

$$R = aT_s + bM_s - y \qquad \text{eq. 4}$$

where R = respiration (μmol m^{-2} s^{-1})
T_s = 4 cm soil temperature (^{o}C)
M_s = soil moisture (%)
y = intercept (μmol m^{-2} s^{-1})

The values for the coefficients 'a' and 'b' were 0.13 and 0.092 in 1998; and 0.067 and 0.037 in 1999. The y intercepts were 2.45 in 1998 and 0.947 in 1999. The calculated R-squared values using 4 cm soil temperature and percent soil moisture are r^2=0.71 for 1998 and r^2=0.31 for 1999 with a P=0.0001 for both years.

The photosynthetic efficiency was taken as the initial slope of the linear relationship between NEE and incident PAR (mol CO_2/mol photons). For comparison to previously published data, daily-integrated total NEE and PAR were calculated (Valentini *et al.* 1995).

To investigate the influence of sky conditions on the NEE to PAR response curve, a method of determining clear, cloudy and overcast periods was devised based on suggestions in the Gap Filling Strategies Appendix of the Ameriflux web site. Potential PAR was calculated for each half hour period using equations that were dependant on the latitude, Julian day and time of day. A ratio of measured PAR to potential PAR can be used as an indicator of sky conditions. The thresholds for different categories of sky conditions were arbitrarily set at >0.6 for clear conditions, between 0.6 and 0.3 for cloudy conditions and <0.3 for overcast conditions. The 1999 data set was sorted into 2°C temperature classes in order to focus the investigation and limit confounding temperature influences.

The use of models in ecosystem carbon budgets requires the input of information based on an understanding of the physiological response of the ecosystem to environmental conditions. Models that correlate stomatal or canopy conductance to environmental variables such as humidity and CO_2 concentration provide insight into conditions that affect CO_2 uptake. The Ball-Berry model is an empirical model of conductance (Collatz et al 1991), that has been used by several authors (Valentini *et al.* 1995, Baldocchi and Myers 1998) to describe experimental data. The Ball-Berry model of conductance was calculated using gross photosynthetic rate, relative humidity and CO_2 concentration. This model is appealing for several reasons not the least of which is the few and relatively easy to collect parameters involved.

$$g_c = m\frac{A(rh)}{C_a} + g_o \qquad \text{eq. 5}$$

where g_c = canopy conductance (mol m^{-2} s^{-1})
A = assimilation of CO_2 (GP as µmol m^{-2} s^{-1})
rh = relative humidity (unitless)
C_a = CO_2 concentration (µmol mol^{-1})
m = slope of the relationship (g_c/[Arh/ C_a])
g_0 = y intercept (mol m^{-2} s^{-1})

The canopy conductance calculated from the eddy covariance data was plotted against the Ball-Berry index and compared to data from other authors.

The canopy conductance to water vapour (g_c) was calculated as:

$$\frac{1}{g_c} = \frac{1}{g} - \frac{1}{g_a} \qquad \text{eq. 6}$$

where the total conductance (g) was calculated using the inverted Penman-Monteith formula.

$$\frac{1}{g}=\frac{r_a}{\gamma}\left(\frac{\Delta(Rn-G)+\rho_a c_p\dfrac{(e^*(T)-e_a)}{r_a}}{\lambda E}-\Delta\right) \qquad \text{eq. 7}$$

where r_a = aerodynamic resistance (s m^{-1})
γ = psychometric constant (Pa K^{-1})
Δ = rate of change of saturation vapour pressure with temperature (Pa K^{-1})
ρ_a = density of dry air (g m^{-3})
c_p = specific heat of air (J g^{-1} K^{-1})
$e^*(T)$ = saturated air vapour pressure (at air temperature °C)
e = ambient air vapour pressure (Pa)
Rn = net radiation (W m^{-2})
G = soil heat flux (W m^{-2})
λ = latent heat of vapourization (J g^{-1})
E = water flux (kg m^{-2} s^{-1})

The aerodynamic conductance (g_a) to water, with similar conductance to CO_2 assumed, was calculated as:

$$\frac{1}{g_a}=\frac{1}{g_e}+\frac{1}{g_b}=\frac{u}{u_*^2}+6.2u_*^{-0.67} \qquad \text{eq. 8}$$

where g_e = eddy diffusive aerodynamic conductance between the canopy surface and the measurement height (m s^{-1})
g_b = excess aerodynamic conductance estimated through Thom's empirical equation for heat and water vapour transfer to crops (Monteith and Unsworth 1990) (m s^{-1})
u = wind speed (m s^{-1})
u_*= friction velocity (m s^{-1})

The calculation of canopy conductance (eq. 6) is the difference between total conductance (eq. 7) and the aerodynamic conductance (eq. 8). The calculation of the aerodynamic conductance (eq. 8) uses a simplified model for the excess aerodynamic conductance (Thom equation as presented in Monteith and Unsworth 1990) that was arrived at empirically. Since turbulence is generated by mechanical action of the wind moving over a rough surface, as the wind speed and surface roughness increase so should turbulence (Campbell and Norman 1998). This is addressed in the aerodynamic conductance calculation (eq. 7) with the eddy diffusivity term (u/u_*^2). Buoyancy of eddies can also affect turbulent transport. Strong heating of the surface can increase mixing and transport while cooling of the surface can suppress mixing and transport (Campbell and Norman 1998). The buoyancy issue is addressed by the empirical Thom equation ($6.2u_*^{-0.67}$). A more rigorous alternative model for calculating aerodynamic conductance was tested against the simpler Thom model.

The rigorous method of calculating the excess aerodynamic conductance requires the establishment of several intermediate values (Campbell and Norman 1998). A measure of the form drag and skin friction called a roughness length (z_m) is required for the model. This was interpolated from a plot of empirical data from Shaw and Pereria (1982) presented in Campbell and Norman (1998). The more rigorous model requires the calculation of atmospheric stability from the ratio of convective to mechanical production of turbulence. This calculated ratio of stability was used to establish the diabiatic correction factors for heat and momentum under stable and unstable conditions. The rigorous method required a determination of a zero plane displacement (d), or the height above the surface where the drag from that surface is equivalent to the force of the wind. These correction factors were used to calculate an excess aerodynamic conductance canopy surface conductance (Campbell and Norman 1998). As is shown in Appendix 1, the rigorous model estimated about 5% higher conductance in 1999 than the Thom equation. The comparison indicates that the simplified calculation returns an acceptable estimation of boundary layer resistance to heat and vapour movement. The slight over estimation of canopy conductance that results from the use of the Thom empirical equation affects the absolute value but does not affect the trends or diurnal patterns observed.

To estimate the degree of stomatal limitation of ecosystem carbon gain, the ratio of intercellular CO_2 concentration (C_i) to the ambient CO_2 concentration (C_a) was calculated, as described in Field *et al.* (1989):

$$\frac{C_i}{C_a} = 1 - \frac{1.6A}{gC_a} \qquad \text{eq. 9}$$

where A = gross photosynthesis (μmol m^{-2} s^{-1})
g = total conductance (mol m^{-2} s^{-1})
1.6 = ratio of diffusion coefficients for water vapour and CO_2
C_a = ambient CO_2 concentration (μmol mol^{-1})

An alternative estimation of C_i/C_a is possible through the use of carbon isotope data ($\delta^{13}C$‰). The biomass $\delta^{13}C$‰ values represent a time integrated measurement of plant response to environmental conditions. In C_3 plants the $\delta^{13}C$ value provides information about the ratio of molar concentrations of intercellular CO_2 (C_i) to ambient CO_2 (C_a). The C_i/C_a ratio changes in a leaf because of changes in stomatal conductance and/or changes in photosynthetic capacity. If the stomatal conductance is high relative to photosynthetic capacity then plant tissue tends to show more discrimination against the heavier isotope so there is a depletion in $\delta^{13}C$. If the stomatal conductance is low relative to photosynthetic capacity then there is less discrimination so there is an enrichment in $\delta^{13}C$. A model has been developed by Faquhar *et al.* (1982) that relates the $^{13}C/^{12}C$ composition of plant tissue and C_i/C_a.

$$\Delta = a\frac{C_a - C_i}{C_a} + b\frac{C_i}{C_a} = a + (b - a)\frac{C_i}{C_a} \qquad \text{eq. 10}$$

where $\Delta = \delta^{13}C_{air} - \delta^{13}C_{leaf}$ (‰) ($\delta^{13}C_{air} = -7.8‰$)
a = fractionation due to diffusion of CO_2 in air (4.4‰)
b = fractionation caused by the major carboxylating enzyme, rubisco (27‰)
C_i = intercellular CO_2 concentration (µmol mol^{-1})
C_a = ambient CO_2 concentration (µmol mol^{-1})

2.5.1 Energy Balance Closure

A measure of the quality of the data collected by an eddy covariance system was determined by testing for energy balance closure.

$$Rn - G = S + \lambda E \qquad \text{eq.11}$$

The net radiation input must be dissipated by the soil heat flux, sensible heat flux and latent heat flux. Net radiation (Rn) was measured by a net radiometer and soil heat flux (G) was measured by soil heat flux plates, two separate and different data gathering instruments from the sensible (S) and latent heat (λE) flux that were measured and calculated by the eddy covariance system. In this study the energy closure indicated that the eddy covariance underestimated sensible and latent heat flux by about 13% for 1998, and 20% for 1999 (Fig. 2). The energy balance closure reported for this grassland (Fig. 2) was within the same range as other grassland studies (Valentini *et al.* 1995) and results from some forested Euroflux sites (Aubinet *et al.* 2000). The decreased slope of the drier 1999 season (Fig. 2) when compared to the wet 1998 season was most likely due to an underestimation of the water flux during very dry periods, this would affect the calculated latent heat flux. The soil did not have a greater heat storage capacity in 1999 and the net radiation was similar when comparing the two years.

2.5.2 GAP FILLING STRATEGY

There was a very large amount of data collected when using half hour averages for 24 hours over 16 months. There was very little down time for the eddy covariance system, however, there were times when data was not collected or was rejected. Missing or rejected data occurred when the system was turned off for calibration, for mechanical failure or when sensor output was out of range due to external factors (frost, birds, etc.). The total amount of data that was missing or rejected amounted to approximately 16%. To estimate the total carbon gain on an annual basis it was necessary to fill the gaps in data that exist or remove data that was suspect. The data gaps may be filled in different ways: linear interpolation, mean day course and semi-empirical regressions. These strategies were chosen after a review of the Appendix "Gap Filling Strategies" on the AmeriFlux 2000 web page. Linear interpolation was used for short periods (2-3 half-hour averages) where there appeared to be a linear relationship between the data before and after the gap (<1%). Longer gaps where filled by a Mean Day Course based on half-hourly data where the averages were calculated for a calendar week (7%). This method was used when the period to be filled had similar meteorological conditions as the majority of the week used to calculate the average. During the early growing season of 1999, missing NEE was estimated as a function of PAR during the day (1%). There was a period of time in mid-winter when no flux or meteorological data was available. To fill this gap an average of the 2 weeks previous and the 2 weeks following the gap was used to estimate the flux that occurred during the missing period (7.5%). The low and less variable flux that occurs in the winter (<1 μmol m^{-2} s^{-1}) made this approach appear adequate for this period. There was some likelihood that, during stable nighttime conditions, CO_2 exchange was underestimated by the eddy covariance measurements (Aubinet *et al.* 2000). A correction was done on nighttime net ecosystem flux where the atmosphere was not well mixed. The night periods of the growing season with low friction velocities (below 0.4 m s^{-1}) were corrected for the inaccurate flux that was observed, due to stable stratification. The simulated efflux calculated from the multiple linear regression of CO_2 flux versus soil temperature/soil moisture, for that time period, was added to the storage flux for the column of air below the sonic anemometer and used as the corrected night-time net ecosystem flux.

To calculate the daily integrated carbon gain, the half-hourly values of NEE from the eddy covariance data, with the gaps filled, was summed for the day and converted to a carbon equivalent.

Table 1. Soil Profile Characterization of Rood Grassland.

Horizon	Textural class	Horizon thickness (m)	N ($\mu g\ g^{-1}$)	P ($\mu g\ g^{-1}$)	K ($\mu g\ g^{-1}$)	S ($\mu g\ g^{-1}$)	pH	Salt Hazard (ms/cm)
A	Clay loam	0.09	4	24	774	4.89	7.1	0.8
B	Clay	0.16	2			3.76	7.3	0.7

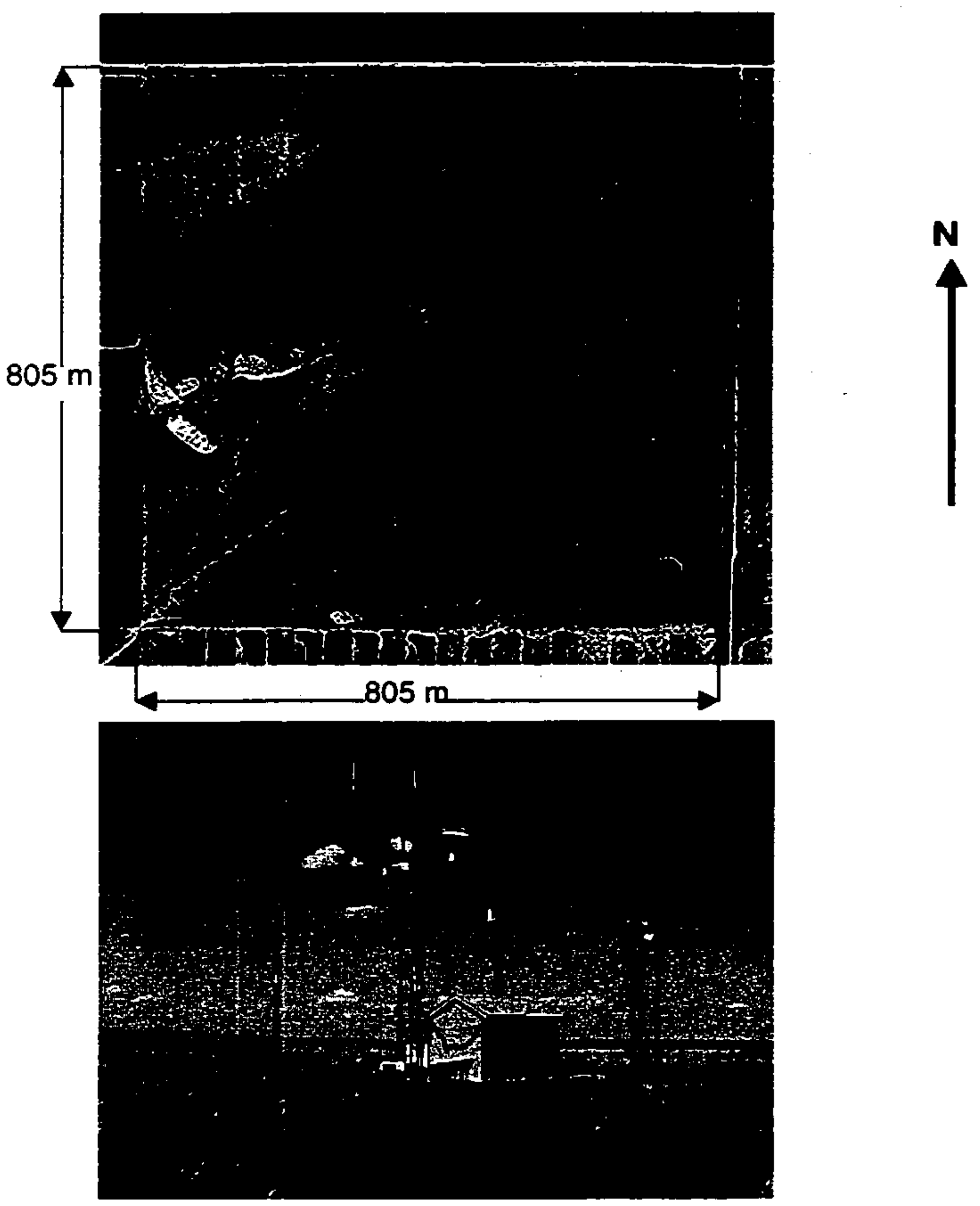

Figure 1. Top picture is an aerial photograph of the study site taken in 1961, showing trails that have existed. The lower picture is the instrument hut and associated micrometeorological equipment at the study site.

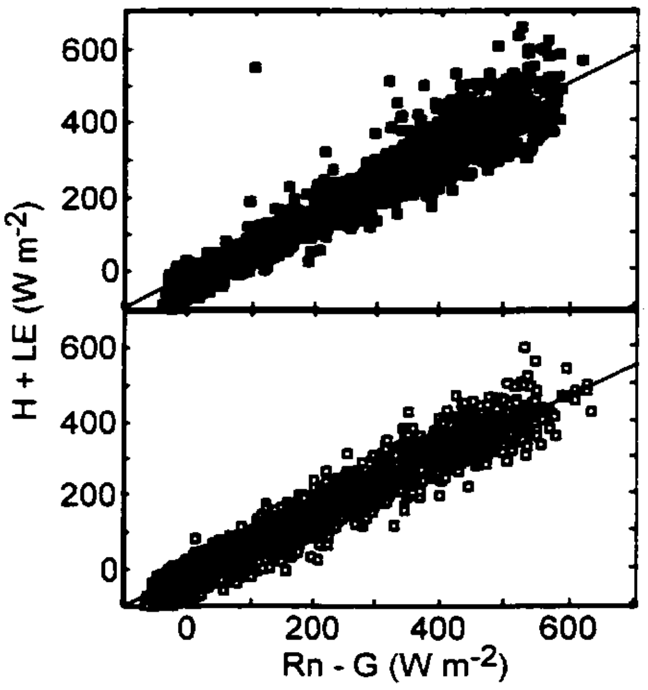

Figure 2. The energy balance closure of sensible heat flux (H) plus latent heat flux (LE) compared to net radiation (Rn) minus soil heat flux (G) for the respective growing season.

1998 (H+LE) = 0.88 (Rn - G) - 20.004 $r^2 = 0.95$, n = 4506

1999 (H+LE) = 0.81 (Rn - G) - 14.008 $r^2 = 0.95$, n = 6202

3. Results

3.1 Comparison of Environmental Conditions in 1998 and 1999

Mean annual precipitation (1908-1999) for Lethbridge was 401.5 mm, with June being the month with the highest precipitation. May and July are the months with the second and third highest precipitation, respectively, based on the long-term average record (Fig. 3). During 1998 precipitation input was similar to the long-term average values for May and July. However, June 1998 was a very wet month, with twice the normal precipitation. In contrast, precipitation during 1999 was similar to the long-term average for the months of May through July.

Because of the excess precipitation during June of 1998, soil moisture remained high at a value of approximately 0.4 (volumetric content) the entire month of June (Julian Days 151-181). In the more typical conditions of 1999, soil moisture content was lower than 0.25 (volumetric content) for much of June (Fig. 4). For the purposes of this study, 1998 can be considered a very wet year, which provides a nice contrast to the approximately normal conditions observed in 1999.

Soil temperature trends (at 4 cm depth) and air temperature trends appear to be similar for the two years (Fig. 4), indicating that shallow soil temperature and air temperature were unconnected to soil moisture variation.

3.2 Plant Species Composition and Abundance

The Rood Grassland had a similar plant species composition in both years, however, the relative abundance of species was quite different between years. The site was dominated by Wheatgrasses (*Agropyron sp.*) and the biennial forb Yellow Goats Beard (*Tragopogon dubius*) (Table 2). The grasses present were *Agropyron smithii* (Rydb.), *Agropyron dasystachyum* [(Hook.) Scrib.] , *Stipa viridula* (Trin.), *Stipa comata* (Trin. and Rupr.) and *Agropyron cristatum* [(L.) Gaertn.], *Bouteloua gracilis* [(H.B.K.) Lag.] and *Koeleria cristata* [(L.) Pers.]. There was one sedge present, *Carex filifolia* (Nutt.). The forbs present were *Tragopogon dubius* (Scop.), *Artemisia frigida* (Willd.), *Taraxacum officinale* (Weber), *Achillea lanulosa* (Nutt.), *Vicia americana* (Nutt.), *Sphaeralcea coccinea* [(Pursh) Rydb], and *Eurotia lanata* [(Pursh) Moq.]. *Agropyron sp.* were dominant through out the summer season, while *Tragopogon dubius* declined in abundance in mid-summer, but was present throughout all the sampling periods. At peak biomass in 1998, the non-dominant grasses and forbs represented 20% and 28% of ground cover respectively. At peak biomass in 1999, the non-dominant grasses and forbs represented 10% and 16% ground cover respectively. There was a decrease in ground cover in 1999, which was most evident for *Agropyron sp.* and *Tragopogon dubius.* Bare ground was just about three times more abundant in 1999 than in 1998 at the time of peak biomass.

3.3 Biomass Production and Leaf Area Index

The amount and timing of biomass production was very different between the two study years. Biomass production was substantially reduced in 1999, with maximum biomass production of only 114 grams m^{-2}, compared with 207 grams m^{-2} in 1998 (Fig. 5). The maximum value of leaf area index (LAI) for 1999 was 0.55 m^{2} m^{-2}, while the maximum LAI for 1998 was 0.89 m^{2} m^{-2} (Fig. 5). In 1998 the peak value for LAI occurred on July 1 and biomass peaked on July 14. In

1999 the peak value for LAI occurred on June 15 and biomass peaked on June 21. These peaks were about 2-3 weeks earlier in 1999 than in 1998.

3.4 Net Ecosystem Carbon Dioxide Exchange

3.4.1 DAILY, SEASONAL AND INTER-ANNUAL PATTERNS

The pattern and amount of net ecosystem carbon dioxide exchange (NEE) was very different between the two study years. The peak NEE of 1998 occurred in mid-July (Julian Days 199-205) (Fig. 6). After this period there was a decline in CO_2 uptake, from a mid-season high of approximately -13 μmol m^{-2} s^{-1}, to approximately -4 μmol m^{-2} s^{-1} by Julian days 234-240. In July the mid-day peak values of NEE occurred at 2 PM, by early August (Julian Days 220-226) the peak mid-day values occurred at 11 AM and by the end of August (Julian Days 234-240) the peak NEE was occurring at 10 AM. The decrease of peak NEE indicates the effect of declining soil moisture due to the onset of the seasonal late-summer drought and leaf senescence. The shift in mid-day peak NEE to earlier in the day indicates the effect of the hot and dry summer afternoons. In 1999, for the same three weeks (Julian Days 199-240), the peak net ecosystem CO_2 exchange was uniformly low at approximately -1 μmol m^{-2} s^{-1} indicating that the ecosystem had effectively gone dormant. In fact the total daily photosynthetic uptake was not quite replacing the total daily respiratory loses for a net CO_2 loss of about 0.5 μmol m^{-2} d^{-1}. The period of peak net ecosystem CO_2 exchange in 1999 occurred in early June (Julian days 157-163). In 1999 the NEE never exceeded approximately -6 μmol m^{-2} s^{-1} and within two weeks of its peak values it had declined to approximately -1 μmol m^{-2} s^{-1} and remained at this rate for the rest of the summer. The shift in the mid-day peak NEE is not as clearly evident in 1999 but the mid-day peak does occur before 12 PM in the three weeks presented (Fig. 7). The relatively low rates of NEE in 1999 are a result of the effect of low soil moisture at the critical leaf expansion period. The presence of the mid-day NEE peak before noon showed that the greatest CO_2 uptake occurred during the morning period when relative humidity was high.

3.4.2 NET ECOSYSTEM CO_2 EXCHANGE AND PHOTOSYNTHETIC EFFICIENCY

In a comparison of the two study years photosynthetic efficiency and the controlling environmental factors were different. Photosynthetic efficiency was defined as the initial slope of NEE (μmol CO_2 m^{-2} s^{-1}) to incident PAR (μmol photons m^{-2} s^{-1}). Half-hourly measurements of NEE for selected periods, were plotted against average PAR for the same periods (Table 3). In 1998 the photosynthetic efficiency for the Rood Grassland showed an increased slope of the NEE/PAR relationship from June through to the peak photosynthetic uptake at the beginning of July (Table 3). In June of 1998, with high soil moisture and relatively low vapour pressure deficient (VPD), the photosynthetic efficiency was 0.014. In July and August of 1998 there was an effect of VPD on the photosynthetic efficiency. In July of 1998 there was an increased efficiency at VPD of <1.1 kPa, indicated by the steeper slope, but as VPD increased to >1.1 kPa the slope of the relationship declined to an efficiency similar to June. In August the photosynthetic efficiency changed not only in response to VPD, but there was some effect due to different soil moisture contents. At a VPD of <1.1kPa and volumetric soil moisture above 16%, the photosynthetic efficiency was approximately 0.014, however the efficiency for the same low VPD and a soil moisture below 16% was much lower, approximately 0.0086. At VPD values >1.1kPa the photosynthetic efficiency was the same at all soil moisture contents and similar to the low VPD/low soil moisture value for August 1998.

In 1999 the photosynthetic efficiencies were lower than in 1998 and they were affected by the volumetric soil moisture content but not by VPD. In the month of May there was a lower slope of NEE/PAR for soil moisture above 24% and a higher slope for soil moisture below 24%. Soil moisture content was higher at the beginning of May and declined to the end of May (Fig. 4). In the month of June this was reversed with the highest photosynthetic efficiency occurring when soil moisture was above 24%. The photosynthetic efficiency during low soil moisture in June was similar to the photosynthetic efficiency during low soil moisture in May.

The differences in controlling factors of photosynthetic efficiency, between 1998 and 1999, were reflective of the soil moisture content during CO_2 uptake. In 1998, the effect of VPD on photosynthetic efficiency was apparent when soil moisture was not limiting. When soil moisture became limiting, the VPD effect was less obvious, as was observed in the late summer season. In 1999, only the effect of soil moisture content was apparent because it was the most limiting factor for the entire season.

3.5 Ecological and Physiological Controls on Net Ecosystem Exchange

3.5.1 RESPIRATION

A multiple linear regression model of nighttime CO_2 flux (Fig. 8) using the 4 cm soil temperature and volumetric soil moisture was used to calculate a total ecosystem respiration value. Turbulent conditions (friction velocities > 0.4) were chosen to ensure a thorough mixing of the air so that the measurements used represented a CO_2 flux without unmixed layers (Clark *et al.* 1999; Grace *et al.* 1998). In 1998 this model explained approximately 71% of the variation in the night CO_2 flux observed under turbulent conditions. In 1999 a model using the same parameters explained approximately 31% of the variation in the night CO_2 flux observations under turbulent conditions. The soil temperature at 4 cm and the volumetric soil content were chosen as the two parameters that provided the best fit in data regressions. The range of nighttime NEE values suitable for use in the multi-linear regression of respiration to soil moisture and soil temperature was much smaller in 1999 compared to 1998. The high soil moisture content of 1998 allowed for a better correlation between the observed and modeled respiration because of the greater range of nighttime ecosystem respiration rates measured in 1998.

3.5.2 GROSS PHOTOSYNTHESIS

There were marked differences in the gross photosynthesis light response curves for the mid-June to mid-August periods of 1998 and 1999 (Fig. 9). In 1998 the highest rates of gross photosynthesis, approximately 15 μmol m^{-2} s^{-1}, occurred at the end of June (weeks 171-185). The light response remained at approximately the same rates, although with more downward variability, for the middle of July (weeks 186-203). By the end of July to Mid-August (weeks 204-224) there was a decline in the light response, which continued until the end of the summer season. There was less evidence of light saturation in the response curve through the most active growth period, weeks 171-203. The reduction in gross photosynthesis over the summer season indicated the effect of declining soil moisture due to the onset of the seasonal late-summer drought and leaf senescence.

In 1999 the light response curves for the period, end of June through to mid-August, had only low rates of gross photosynthesis, <5 μmol m^{-2} s^{-1}, reflecting the water stressed nature of the ecosystem (Fig. 9). The rate of gross photosynthesis declined further by the end of August and there were similar values for both years by early September, Julian days 242-247. The rate of gross photosynthesis was increasing from May to mid June of 1999 (Fig. 10). The rate of gross photosynthesis went from <5 μmol m^{-2} s^{-1} for Julian days 122-135 to >5 μmol m^{-2} s^{-1} by Julian days 152-170. After Julian day 170 the rate of gross photosynthesis declined. There was evidence of light saturation at quite low rates of PAR, approximately 600 μmol m^{-2} s^{-1}, by the middle of May (days 136-151) and continuing for the rest of the summer season.

Gross photosynthesis was approximately 3 times higher in 1998 than in 1999 during the peak of the growing season. This higher rate of gross photosynthesis was due to the greater biomass and leaf area, which in turn were due to the higher soil moisture conditions during the peak of the growing season in 1998.

3.5.3 PLANT NITROGEN

Plant nitrogen content, expressed as a percentage of plant dry weight, was similar in 1998 and 1999 (Fig. 11). Both years also showed a similar seasonal variation ($P<0.002$) in plant N content. A regression of % Plant N versus Julian Day for the 1998 data has a slope of -0.0108 and an intercept of 4.104 ($r^2=0.91$). The same regression for the 1999 data had similar results ($y= -0.0102x + 4.0413$, $r^2=0.65$). The general decline in N concentration was consistent for both years except for day 215 of 1999. The higher value on this day was the result of a single replicate with a relatively high dry matter containing new growth of *Tragopogon* after a rain shower on day 199. Despite this anomaly, the data indicate that the ecosystem plant N was similar in both years on any given day.

However, there were differences between 1998 and 1999 when plant nitrogen content was expressed as g N m^{-2} (Fig. 12). Because of the much higher live aboveground biomass in 1998, the amount of plant N (g N m^{-2}) was significantly higher in 1998 than in 1999. In both years there was a similar rate of increase in nitrogen content until Julian day 146 (May 26), by day 166 (June 15) there was approximately two fold more g N m^{-2} in the 1998 biomass compared to 1999 biomass. There was a 23 day difference in peak live aboveground biomass g N m^{-2}, with the 1999 peak being only 60% of 1998 values.

3.5.4 CANOPY CONDUCTANCE AND THE RATIO OF INTERCELLULAR CO_2 CONCENTRATION TO AMBIENT CO_2 CONCENTRATION

The rate and diurnal pattern of canopy conductance (g_c) was very different between the two study years (Fig. 13). Shown are the diurnal pattern of monthly average canopy conductance for the hours 9-19, from peak biomass of each year and following through the decline in production. The compared time periods also have similar declining volumetric soil moisture levels. The peak rate of g_c for 1998 occurred in July, approximately at the same time as the peak rate of NEE. After this period there was a decline in g_c, from the mid-season high of approximately 180 mmol m^{-2} s^{-1}, to approximately 80 mmol m^{-2} s^{-1} by August. The highest rate of g_c was seen before 12:00 hours for the months shown, and the peak rate of canopy conductance shifted to earlier in the day as the season progressed. The decreased rate of g_c and the shift in the peak g_c indicates the effect of declining soil moisture and increased VPD on sustainable transpirational water loss. In 1999, the peak rate of g_c was lower than in 1998 and occurred in June, approximately at the same time as the peak rate of NEE (Fig. 13). After this period there was a decline in g_c, from mid-season high of approximately 100 mmol m^{-2} s^{-1}, to approximately 40 mmol m^{-2} s^{-1} by July. The highest rate of g_c was seen before 12:00 hours for the months shown. However, unlike 1998, there did not appear to be a shift of peak rate of canopy conductance to earlier in the day as the season progressed. The low rates of g_c were a result of the lower soil moisture conditions that occurred in 1999. The decrease of peak g_c as the season progressed indicated the effect of a decline in soil moisture. However, the maintenance of peak rates of g_c for about the same period of the day, infers an accommodation by the plants of the ecosystem to the lower soil water availability in 1999 such that changes in VPD had less effect on controlling canopy conductance.

The monthly average diurnal pattern of C_i/C_a ratio for the periods corresponding to the g_c was plotted (Fig. 13). The diurnal pattern of C_i/C_a was similar for both years. In Figure 13, g_c was reduced for the peak period of 1999 compared to peak 1998 and yet the C_i/C_a for that period was similar. In the comparison of August 1998 to July 1999, despite differences in canopy conductance, the C_i/C_a was very similar.

The C_i/C_a ratio calculated from the biomass ^{13}C measurements showed a different result, with seasonality of the C_i/C_a ratio evident in both years of the study (Fig. 14). The above normal precipitation of June 1998 resulted in a higher average C_i/C_a by Julian day 200. The normal precipitation of 1999 resulted in a lower average C_i/C_a by Julian day 190. The generally lower g_c rates of 1999 did result in a lower average C_i/C_a ratio.

An investigation was conducted into the relationship between observed canopy conductance and the empirical Ball-Berry model using parameter inputs from eddy covariance measurements (gross photosynthesis, rh and ambient $[CO_2]$). In this analysis the observed daytime values of canopy conductance on days with no rainfall were used to avoid a wet canopy. Other selection criteria included observed water flux above 0.05 mmol m^{-2} s^{-1} to avoid unrealistically low fluxes, and U_* values above 0.1 m s^{-1} for well mixed atmospheric conditions. In June and early July of 1998 there were higher canopy conductance values reported than at any other period, but all of the 1999 data and the late season of 1998 data are at the low end of the scale. The slope parameter (*m*) of approximately 10 with small intercept value and relatively good r^2, indicated that a larger range of canopy conductance values can improve the predictive powers of this model (Fig. 15).

3.6 Ecosystem Carbon Gain

The amount of net carbon gain was very different between the two study years (Table 4). The daily integrated carbon gain in g C m^{-2} d^{-1} showed that there was more uptake in 1998 compared to 1999 (Fig. 16). The net ecosystem exchange measurements (NEE) were integrated to determine the daily carbon balance. The daily carbon balance for 1998 showed the highest variability in daily C gain during the peak of the growing season with some days even recording a net loss of C during this time. There was a general downward trend in C gain and less variability after soil dry down around day 203. The peak LAI occurred on day 182 and peak biomass occurred on day 195, these were well within the period of peak C gains for 1998. In 1999 the seasonal pattern (Fig. 16) showed peak daily carbon gain was much lower and occurred much earlier than in 1998. The peak C gain occurred on day 164, coincidentally the day of peak LAI. The highest C gain of 1999 occurred about 2 weeks after the peak in soil moisture, unlike 1998. The variability seemed to continue throughout the season perhaps reflecting the ecosystem response to rain events. The large fluctuations in C gain occurred during the most active growth period, which was similar to 1998. A period of approximately 40 days (190-230) occurred at the end of the growing season when the C gains were very small or carbon losses were measured, this would represent the period of dormancy. In 1998 the eddy covariance measurements did not begin until Julian day 171 (mid June) so that approximately 6 weeks of the early growing season was not measured. An estimate of net carbon exchange for the missing period (Julian days 110-170) was made based on the early growing season net carbon exchange that occurred in 1999. This estimating procedure appeared justified based on the similarity of LAI and biomass between the two years for that period (Fig. 5). The estimated net carbon exchange for the missing period of 1998 now allowed for an estimate of total growing season net carbon exchange to be made for both years of the study. The estimated total seasonal net C exchange (Julian days 110-250) includes slightly less net C exchange losses in the late season because of the earlier cut off date of September 7 compared to September 30 for the measured seasonal C gain. There is, however, more of the early season net C exchange included. This total estimated period more effectively represents the increase and decline of net C exchange for the most active growth periods of both years (Fig. 16).

The results of a comparison of the carbon gain calculated from biomass harvest to the carbon gain calculated from a daily-integrated net ecosystem CO_2 flux are similar, granting certain assumptions. In 1998, the peak aboveground live biomass was 207.03 g m^{-2} on Julian day 195. The below ground biomass was sampled once on Julian day 202 and the average of four replicates was 529.93 g m^{-2} (±104.7) to the 20 cm depth. This sampling date was very close to the peak aboveground biomass and near the beginning of the dry season of this grassland. Several grassland studies have indicated that the peak of below ground biomass occurs at or around the same time as peak aboveground biomass (McNaughton *et al.* 1998, Pandey and Singh 1992, Sims and Singh 1978a). This would give about 737 g m^{-2} of biomass to account for on the Rood Grassland for 1998. If there was about 50% of root material (265 g m^{-2}) that over winters from the previous year (McNaughton *et al.* 1998, Pandey and Singh 1992, Sims and Singh 1978), then there was about 472 g m^{-2} of biomass added in 1998. A daily-integrated net ecosystem carbon gain, from the eddy covariance measurements, indicated that there was 145 g C m^{-2} taken up between Julian day 171 and 250. If we assume that the eddy covariance carbon gain for the unsampled growing period of 1998 was similar to the same period of 1999, based on a similar LAI and biomass trend (Fig. 4), then there would have been another approximately 45 g C m^{-2} gained (Julian day 110 and 170). This would give a total carbon gain of 190 g C m^{-2} taken up between Julian day 110 and 250 for 1998. The 190 g m^{-2} carbon would be equivalent to about 422 g m^{-2} of biomass if the plant tissue was 45 percent carbon. This estimate is 50 g below the biomass estimated as added in 1998. This discrepancy could be due to greater than 50% over-wintering root biomass, or an over estimation of root biomass. In 1999 the below ground biomass was not sampled. There was a peak of 114.37 g m^{-2} of aboveground live biomass harvested on Julian day 172. The daily integrated net ecosystem carbon gain for the period Julian day 110 to 250 showed a gain of 46.8 g C m^{-2}, which at 45 percent carbon content, would be 104 g m^{-2} of biomass. There would then be a short fall of 10.37 g m^{-2} between the biomass harvest and the estimate from the eddy covariance data. This would imply that there was no net root growth or a small loss of root material, and all of the carbon taken up went to aboveground biomass. In a study of intra-seasonal dynamics of 10 North American grassland sites, Sims and Singh (1978) had several sites over different years that had no net root growth or even a net loss of root material yet there was a small aboveground biomass reported.

The carbon gain estimated from the eddy covariance measurements appears to about 10% less than that estimated from biomass collections for both 1998 and 1999.

Table 2. Inter-annual comparison of major plant species composition (%ground cover) for the Rood grassland. Point frame survey done at peak biomass of respective year (July 5, 1998 and June 20, 1999).

% ground cover	1998	1999
Agropyron spp. (Wheat grasses)	44.75	32.00
Tragopogon dubius (Goats beard)	32.75	24.50
Vicia americana (Wild vetch)	8.50	2.00
Koleria cristata (June grass)	5.25	2.00
Artemisia frigida (Pasture sage)	4.50	1.00
Taraxacum officinale (Dandelion)	3.75	6.00
Eurotia lanata (Winter fat)	2.75	0.00
Stipa comata (Needle-and-thread)	1.75	3.00
Bouteloua gracilis (Blue grama)	1.50	2.50
Stipa viridula (Green needle)	1.25	2.00
Carex spp. (Sedge)	0.00	10.00
Phlox hoodii (Moss phlox)	0.75	0.50
Sphaeralcea coccinea (Scarlet mallow)	0.25	0.00
Achillea lanulosa (Yarrow)	0.00	3.50
Bare ground	14.25	42.00

Species composition, as a percent ground cover, was estimated by sampling 400 points using a 10 point frame randomly placed.

Table 3. A comparison of the seasonal and inter-annual variation in photosynthetic efficiency in the Rood Grassland for selected months of 1998 and 1999.

Year	month	VPD kPa	Vol. Soil moisture %	Slope mol NEE mol^{-1} PAR	Intercept mol NEE	r^2
1998	June	All	All	0.0144	-2.298	0.83
	July	<1.1	All	0.022	-3.909	0.76
		>1.1	All	0.0137	-2.443	0.86
	Aug	<1.1	>16%	0.0132	-1.491	0.63
		<1.1	<16%	0.0086	-2.02	0.71
		>1.1	All	0.0073	-2.001	0.65
1999	May	All	>24%	0.0031	-0.61	0.50
		All	<24%	0.0055	-0.638	0.77
	June	All	>24%	0.0077	-1.502	0.72
		All	<24%	0.0054	-0.899	0.49

Data consists of the initial slope of the half-hourly averaged NEE response to incident PAR <600.

Table 4. Comparison of the daily integrated net carbon exchange for the growing seasons of 1998 and 1999.

Net Carbon Exchange	1998	1999
Maximum (grams C m^{-2} d^{-1})	4.95	2.50
Minimum (grams C m^{-2} d^{-1})	-2.88	-1.47
Daily seasonal average (grams C m^{-2} d^{-1})	1.29	0.21
Measured seasonal C gain (grams C m^{-2} $season^{-1}$)	134.48	38.33
Total seasonal C gain (grams C m^{-2} $season^{-1}$)	190.0	46.8

Measured 1998 season: Julian days 171-274 (June 19-Sept. 30)

Measured 1999 season: Julian days 91-274 (April 1-Sept. 30)

Total seasonal C gain: Julian days 110-250 (April 20-September 7). This time period includes plant emergence, active growth, and decline within the season for this grassland. There was an estimate of net C exchange that occurred before measurement began in 1998. An estimate was necessary in order to compare a full growing season from this grassland to other grasslands studies and to a full growing from 1999 of this study.

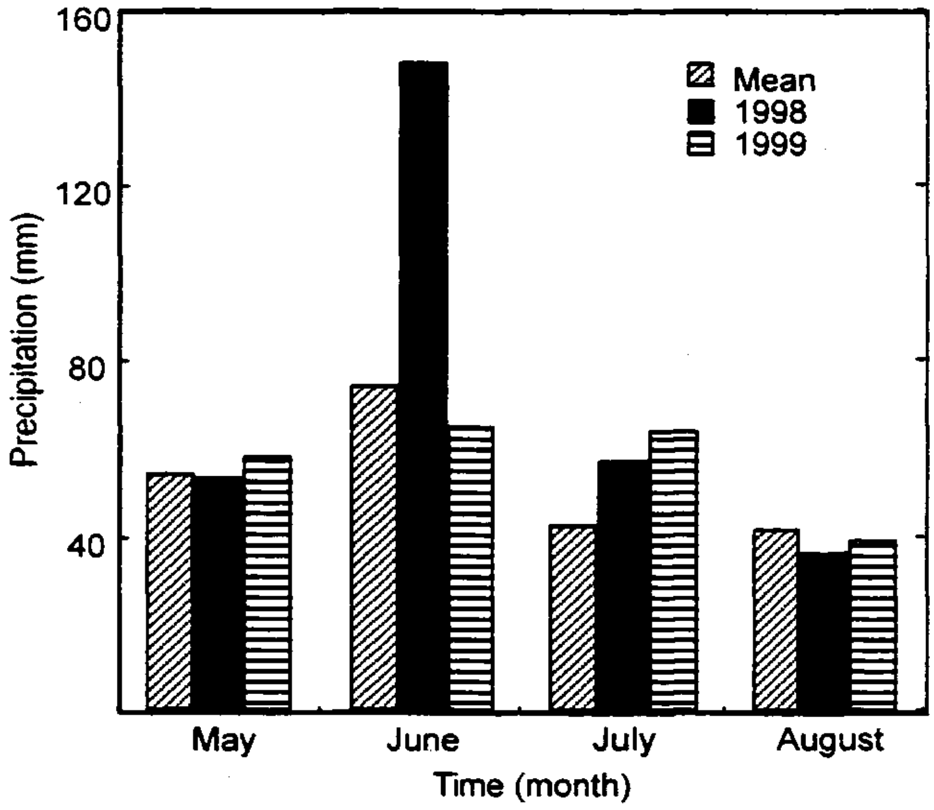

Figure 3. Comparison of the measured monthly precipitation (millimeters) for the years of 1998 and 1999 to the 11 year running mean monthly precipitation for Lethbridge Alberta.

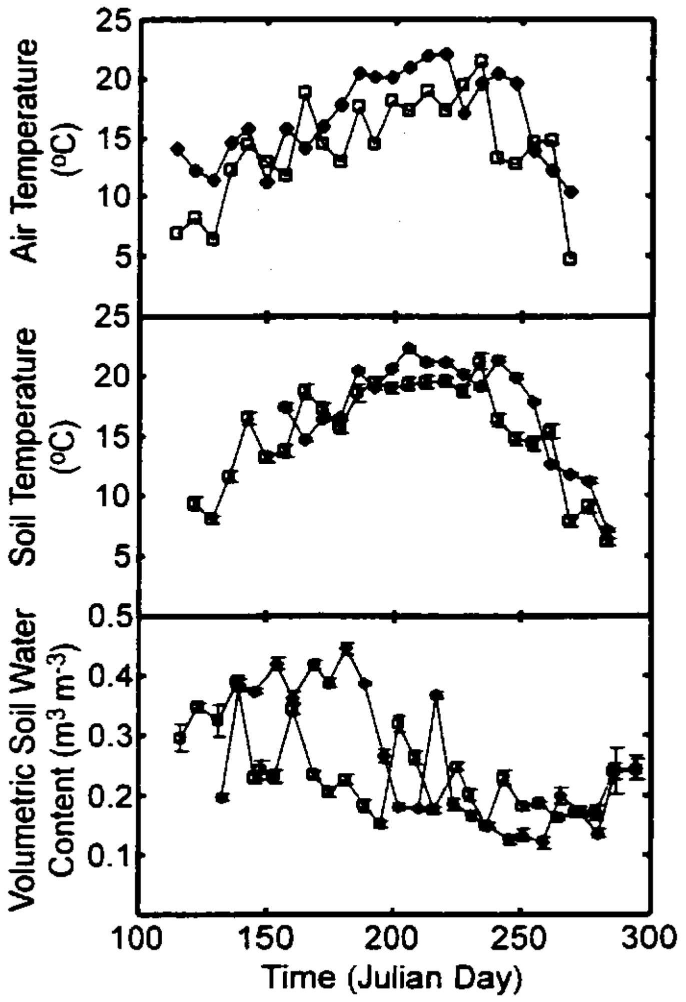

Figure 4. Comparison of seasonal and inter-annual variation of air temperature, soil temperature and volumetric soil water content for the years ◆ 1998 and ☐ 1999.

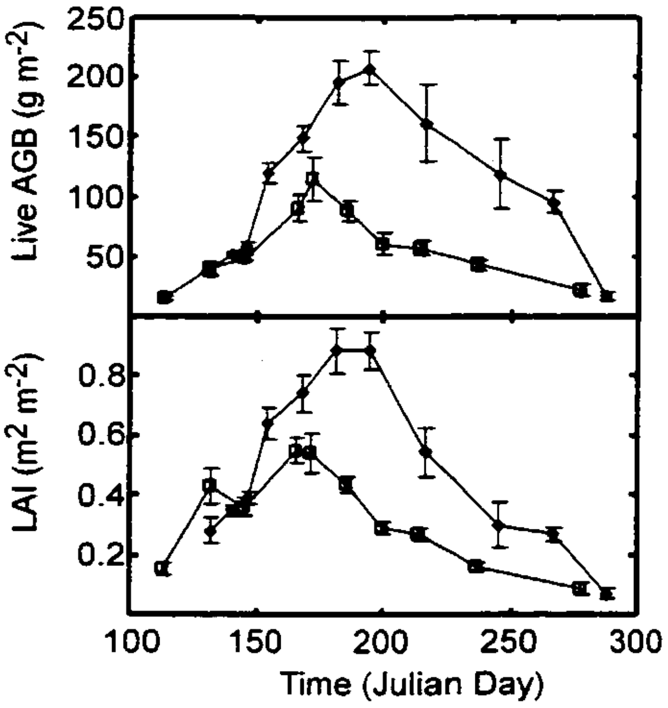

Figure 5. Comparison of seasonal and inter-annual variation of live above ground biomass (AGB) and leaf area index (LAI) for years ◆ 1998 and ☐ 1999. Standard error of the mean as error bars.

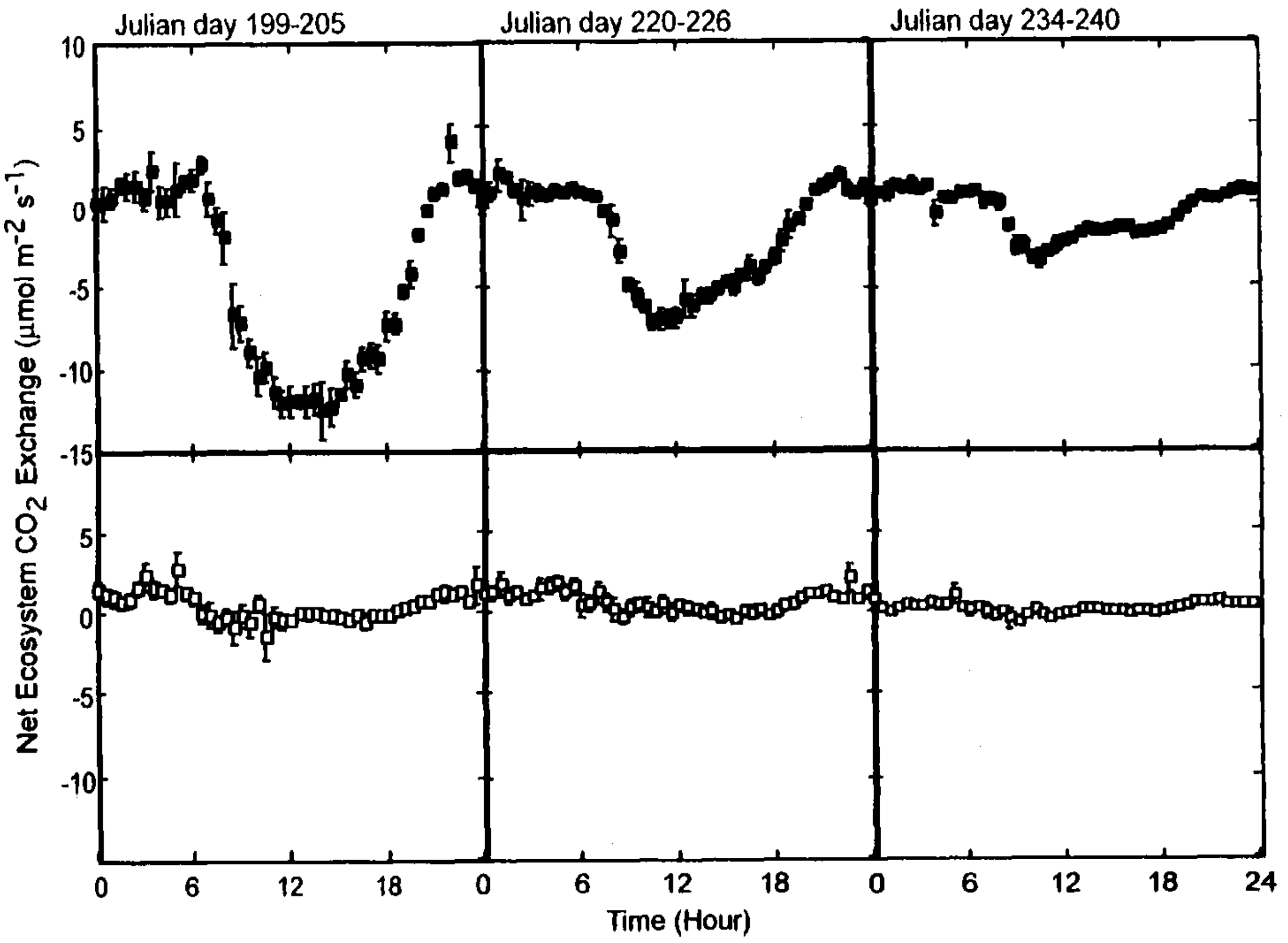

Figure 6. Comparison of seasonal and inter-annual diurnal variation of net ecosystem CO_2 exchange. Points are half hourly values averaged over the selected weeks. Standard error of the mean as error bars.

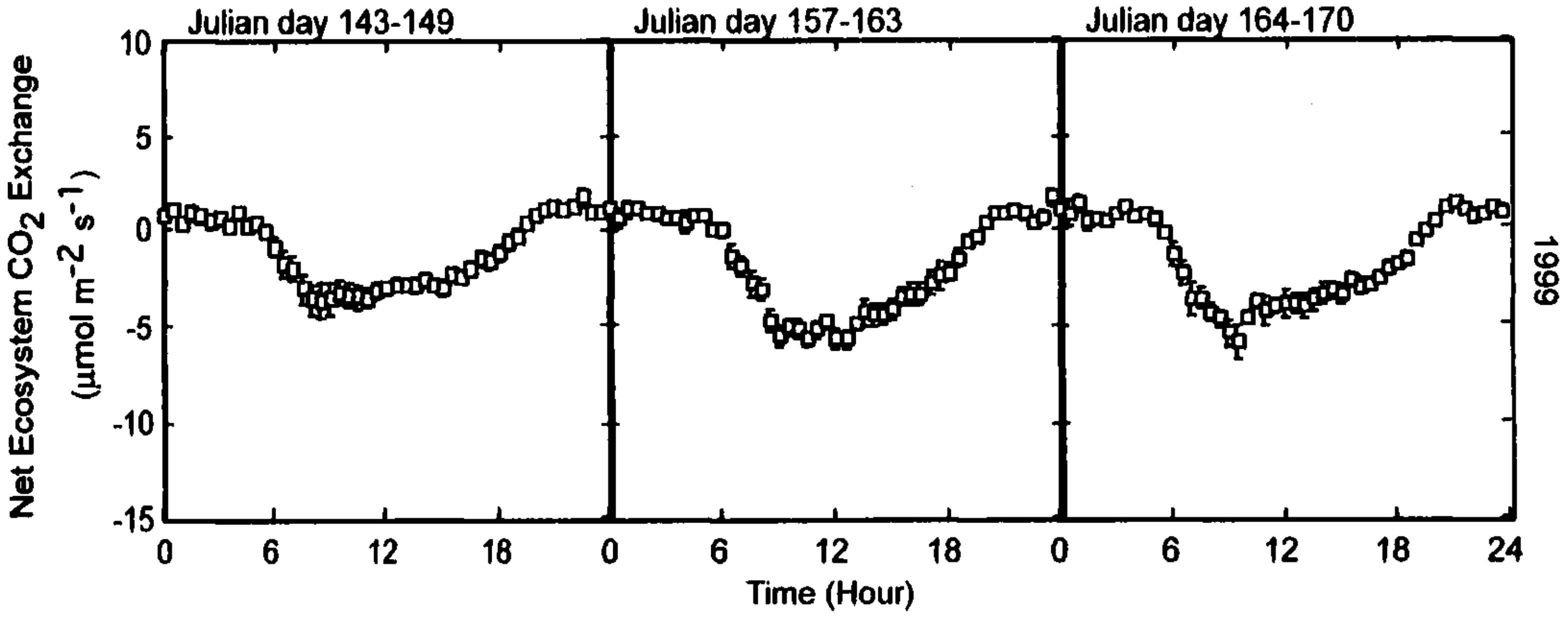

Figure 7. Comparison of seasonal diurnal variation of net ecosystem CO_2 exchange for selected weeks of early growing season 1999. Points are half hour values averaged for the selected weeks 1999. Standard error of the mean as error bars.

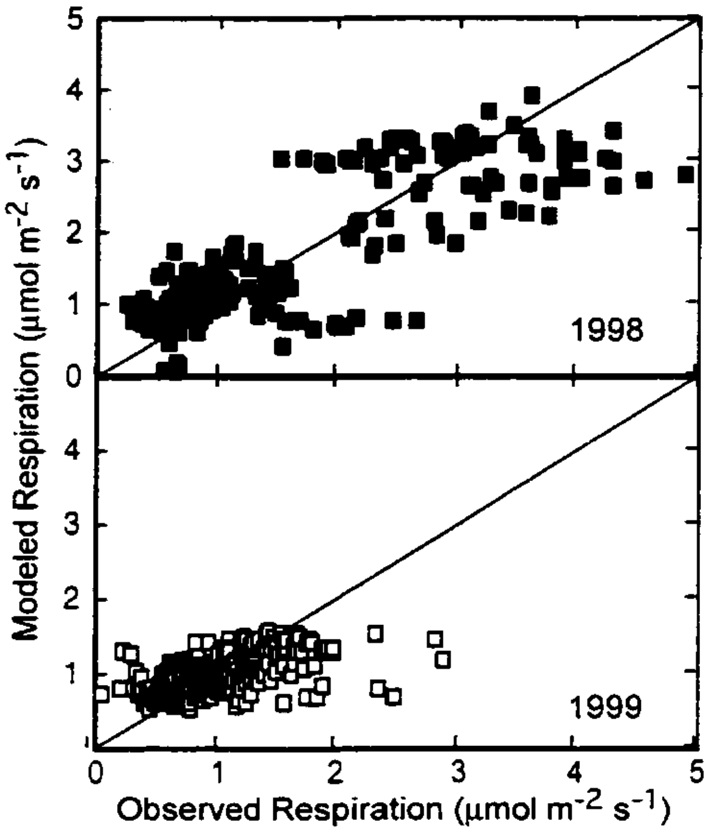

Figure 8. Comparison of modeled respiration to observed respiration. Modeled respiration is calculated from a multi-linear regression of soil moisture and % soil moisture (Respiration = a[soil temperature] + b[soil moisture] + y intercept). Observed respiration is the measured night time net ecosystem CO_2 exchange in conditions of >0.4 friction velocity. The dark line is the 1:1 line. The correlation coefficients are r = 0.84 for 1998, r = 0.56 for 1999.

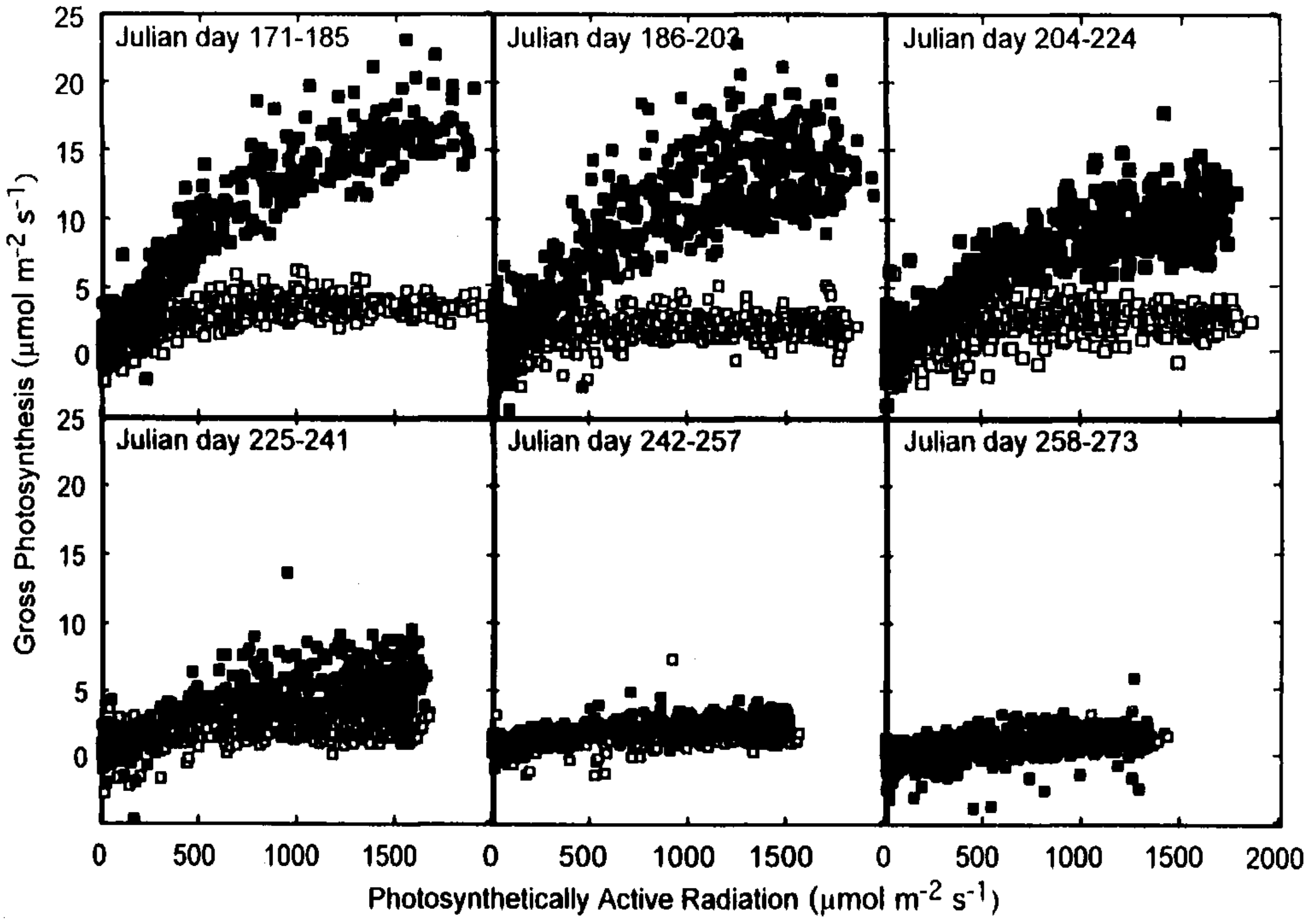

Figure 9. Comparison of seasonal and inter-annual variation of gross photosynthesis to changes in photosynthetically active radiation (PAR). Points are half hourly values averaged for the selected weeks of ■ 1998 and □ 1999.

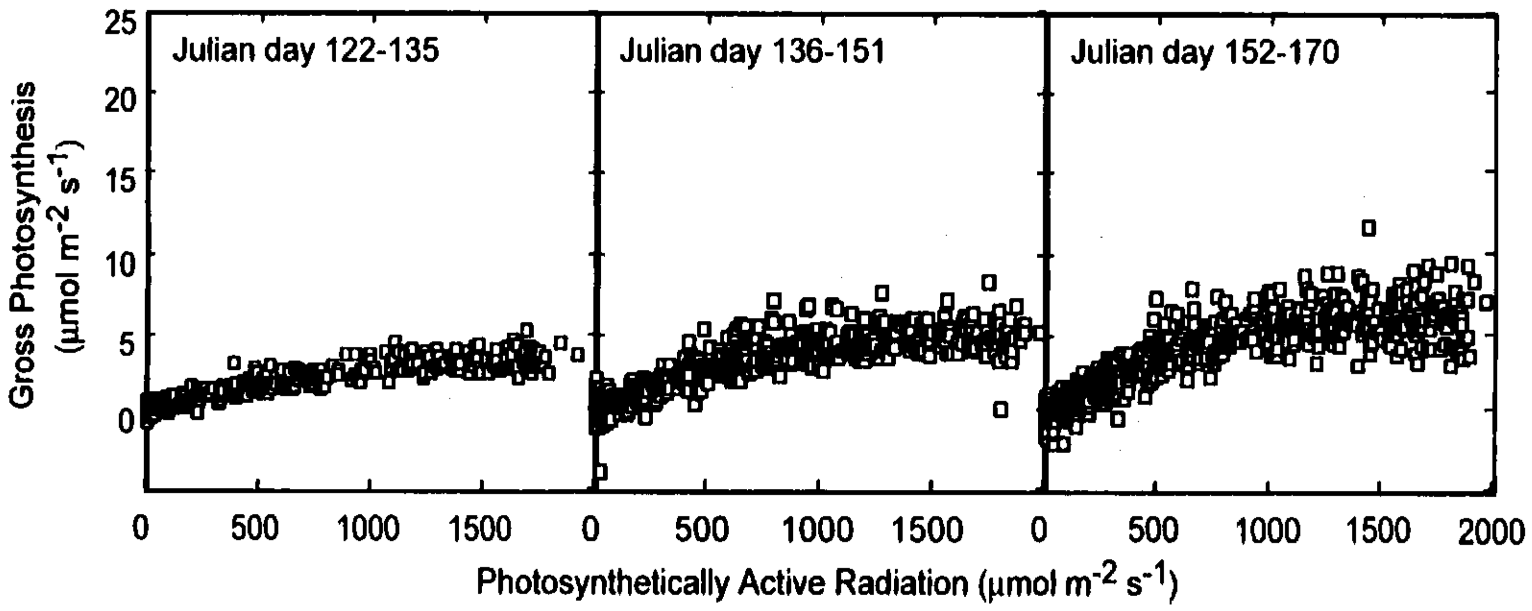

Figure 10. Comparison of seasonal variation of gross photosynthesis to changes in photosynthetically active radiation (PAR). Points are half-hourly values averaged for the selected weeks of □ 1999.

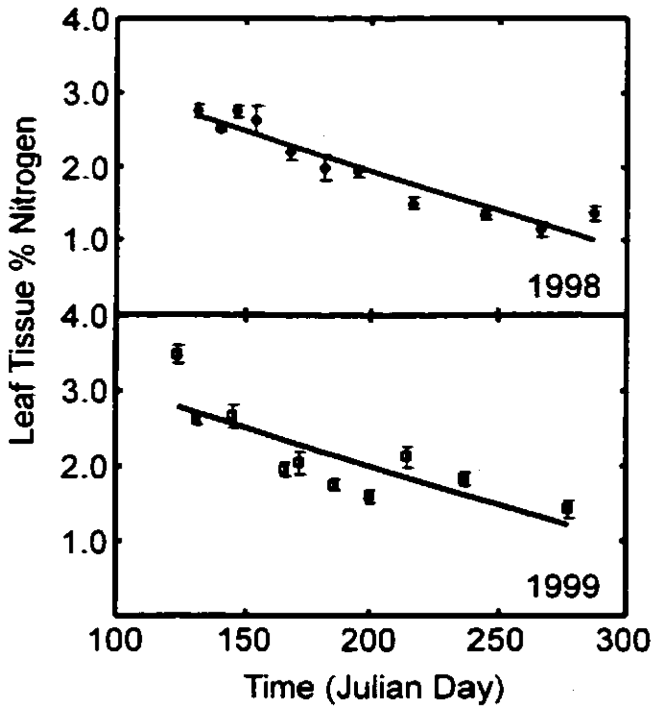

Figure 11. Comparison of seasonal variation of leaf tissue nitrogen content for 1998 (top box, ■) and 1999 (bottom box, ❐). Points are averages of six replicates with standard error of the mean as error bars.

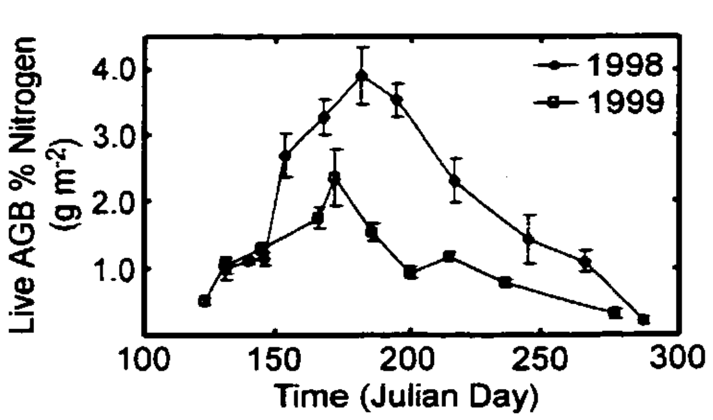

Figure 12. Comparison of seasonal and inter-annual variation of live above ground biomass nitrogen content (g m^{-2} ground area). Points are averages of six biomass replicates per sample date, with standard error of the mean as error bars.

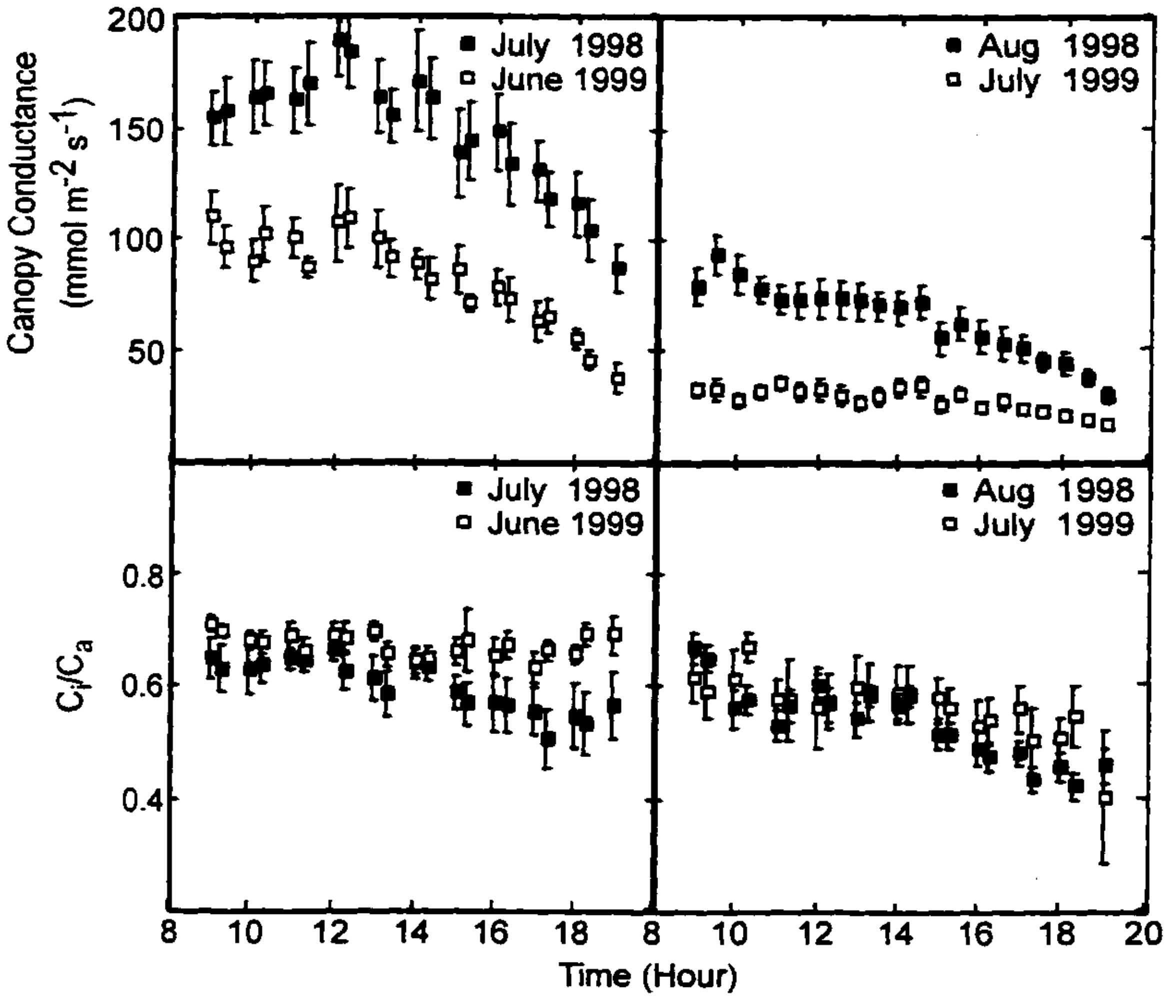

Figure 13. Comparison of seasonal and inter-annual daily variation of canopy conductance to water vapour and the ratio of intercellular CO_2 concentration (C_i) to ambient CO_2 concentration (C_a). Points are averaged half hours, for the hours between 9:00 and 19:00. Comparisons begin at peak LAI of the respective year and progress through the seasonal soil moisture decline. Standard error of the mean as error bars.

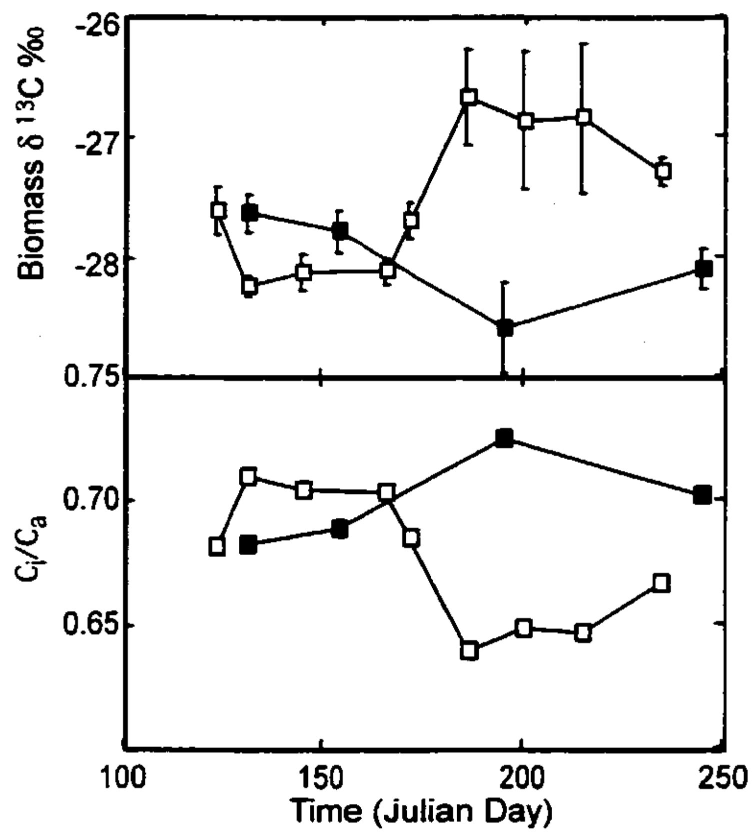

Figure 14. The upper figure is the inter-annual and seasonal variation in the stable isotope carbon isotope value of the harvested biomass. The lower figure is the inter-annual seasonal variation of the ratio of intercellular CO_2 to ambient CO_2 calculated from the $\delta^{13}C$ biomass values (Faraquhar *et al.* 1982). The solid boxes (■) are the 1998 values and the empty boxes (□) are the 1999 values. The error bars are standard error of the mean.

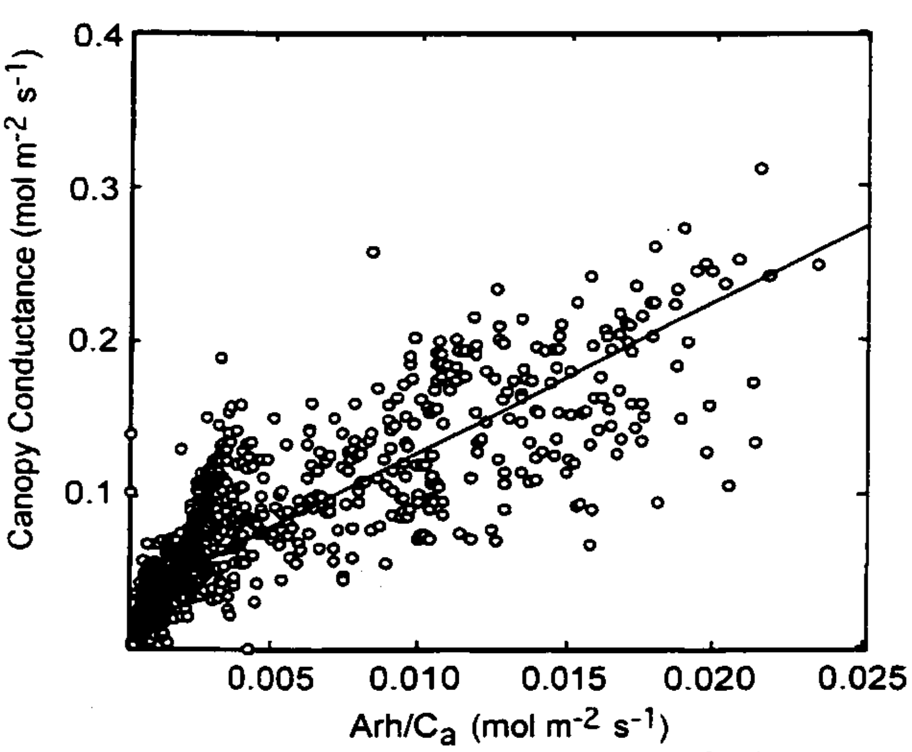

Figure 15. The observed canopy conductance (mol m^{-2} s^{-1}) versus Arh/C_a (Ball-Berry index) for 1998 and 1999. A is canopy gross photosynthesis (calculated as the sum of net ecosystem CO_2 exchange and ecosystem respiration, µmol m^{-2} s^{-1}), rh is relative humidity and C_a is the carbon dioxide concentration (µmol mol^{-1}). Ball-Berry index parameters were taken from eddy covariance measurements.

Canopy conductance = 9.76(Arh/C_a) + 0.031, r^2 = 0.72

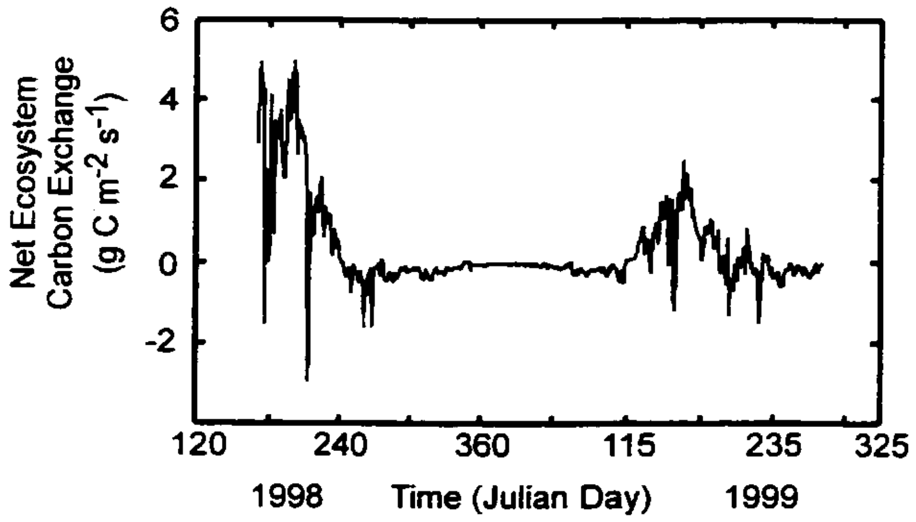

Figure 16. Seasonal and inter-annual daily integrated net ecosystem carbon exchange for Julian day 170 of 1998 through to Julian day 275 of 1999.

4. Discussion

4.1 Patterns in Net Ecosystem CO_2 Exchange, Gross Photosynthesis and Respiration

The daily and seasonal change in NEE was largely a result of changes in gross photosynthesis (GP). The daily-integrated GP (Fig. 17) had a greater range of seasonal variation than the rate of daytime respiration (R_d). The greater range of variation in daily and seasonal GP compared to R_d has also been noted by other authors (Vourlitis *et al.* 2000, Lloyd *et al.* 1996). The maximum values of NEE for this grassland (5-13 μmol m^{-2} s^{-1}) compare to those for a mixed grass prairie in Saskatchewan (11.5 μmol m^{-2} s^{-1}; Ripley and Saugier 1974) and to a subalpine grazed pasture in Austria (7 μmol m^{-2} s^{-1}; Tappeiner and Cernusca 1996). The maximum NEE values were lower than values observed for a tall grass prairie in Kansas (23 μmol m^{-2} s^{-1} ; Ham and Knapp 1998), but higher than those for a coastal tundra in Alaska (2.5 μmol m^{-2} s^{-1}; Vourlitis and Oechel 1997).

The shift of peak NEE to earlier in the day was a result of stomatal response to increasing VPD. Baldocchi (1997b) has also noted the shift of peak uptake to earlier in the day in association with drought conditions in the study of a temperate broad-leaved forest. In contrast, it has been suggested by Clark *et al.* (1999), that high air temperature in the afternoon caused an associated increase in the respiration rates, which resulted in lower rates of net CO_2 exchange, and this was the cause of a shift in peak uptake in a Florida forest. In this study, water vapour conductance values during peak CO_2 uptake in 1999 (Julian days 152 to 170) indicate that the period of peak conductance for the day occurs at about the same time as the peak CO_2 uptake. This suggests that the reason for the shift in peak NEE was a stomatal response to increased water loss driven by the increasing VPD, rather than an increase in temperature causing more respiration.

The multiple linear regression used to estimate ecosystem respiration from the relationship between CO_2 efflux, soil temperature and soil moisture worked quite well when there was a large range of soil moistures from which to select data with high friction velocities. It was less effective under the low soil moisture conditions of 1999 because of the low ecosystem respiration fluxes observed. This could raise the question of the accuracy of using night-time respiration flux to estimate day-time respiration. Lavigne *et al.* (1997) concluded that eddy covariance measurements at night were consistently lower than ecosystem respiration rates by 20-40% in the study of a boreal forest. In a comparison to chamber measurements done in 1999 at our site, the eddy covariance-calculated respiration was about 74% of chamber-observed respiration. The calculated respiration ranged from 52% to 100% (data not shown) of observed respiration, but consisted of only a small data set (4) of controlled chamber respiration comparisons. The nighttime CO_2 flux measured in 1999 had a very small range of variation and this small range gives undue influence to outliers. In 1998, the fit of calculated to observed night-time CO_2 flux was quite good using the two soil parameters, although there were no controlled chamber measurements for comparison. The larger range of observed respiration allows for a better fit for the calculated data. This method for calculation of ecosystem respiration is imperfect, but it does provide an estimate of daytime respiration, although respiration is likely underestimated.

The seasonal change in the rate of gross photosynthesis appears to be connected to the amount of leaf area available to carry on photosynthesis (LAI). The highest rate of GP occurred during the period of greatest LAI for both years, and GP declined as LAI declined (Fig. 18). The relationship between GP and LAI has been demonstrated by other authors (Saigusa *et al.* 1998, Tappeiner and Cemusca 1996). In order to compare CO_2 fluxes from other grassland studies with different LAI, GP was normalized by expressing it on a leaf area basis (Ruimy *et al.*1995). A comparison of the GP/LAI for the period of peak CO_2 uptake, showed that canopy photosynthesis per unit leaf area was higher in 1998 (499 mmol m^{-2} d^{-1}) than in 1999 (344 mmol m^{-2} d^{-1}). However, the individual leaf area of 1998 was not more efficient than that of 1999 as indicated by the similar values of %N content in the biomass (Fig. 11). This supports the idea that a higher LAI can optimize the capture of incident radiation. The GP/LAI values calculated for this grassland are similar to values estimated from Saigusa *et al.* (1998) (341-487 mmol m^{-2} d^{-1}) but higher than those reported in Tappeiner and Cemusca (1996) (85-122 mmol m^{-2} d^{-1}) where the highest values of GP/LAI occurred in stands with the highest LAI (6.2 m^2 m^{-2}). In the Tappeiner and Cemusca (1996) study, the total ecosystem respiration during daylight hours (day respiration) was only 6 to 15% of the GP, while for this grassland the day respiration (R_d) was 30-50% of GP. The R_d/GP for this grassland was in the range of that reported for forested sites (Baldocchi *et a*l. 1997) and would account for the higher GP/LAI values found.

4.2 Environmental Controls on Grassland Net Carbon Exchange

Ecosystem carbon budgets are controlled by the balance between carbon uptake during photosynthesis and carbon loss during respiration. The environmental controls on photosynthesis and respiration operate in distinct ways for these two processes. In addition, in different ecosystems net carbon exchange can be predominantly controlled by changes in one of these two major components. For example, among mature forests in Europe, differences in total ecosystem respiration were responsible for the latitudinal gradient observed for net ecosystem carbon exchange (Valentini *et al.* 2000). Annual gross photosynthesis was very similar in forests ranging across a large latitudinal gradient from Italy (45° lat.) to Sweden (60° lat.). The higher annual respiration costs in the northern forests reduced the net carbon gain compared to forests in more southern locations (Valentini *et al.* 2000). In contrast, the senescence of above ground biomass in this grassland results in much less inter-annual variation in total ecosystem respiration. The yearly variation in net carbon exchange was more strongly controlled by differences in gross photosynthesis.

Soil and air temperature have been established as major environmental controls on respiration for a wide range of ecosystems (Ruimy *et al.* 1995). In a Tennessee deciduous forest the CO_2 efflux was governed by litter and soil temperature (Baldocchi and Meyers 1991). In a Florida pine forest, the likely cause of similar summer and winter net CO_2 exchange was given as seasonal changes in the temperature-dependent rates of respiration (Clark *et al.* 1999). Soil water content has also been implicated as a control in an Arctic tundra, where CO_2 efflux followed changes in soil temperature when soil moisture content was highest but became limited by soil, moss and lichen hydration at mid-season (Oberbauer *et al.* 1996). In this study, no single environmental factor could adequately predict the changes in respiration rate. In 1999 the highest observed respiration rates were approximately half of the highest observed rates in 1998 (Fig. 8). The 1999 biomass was roughly half of the biomass of 1998, which suggests a large contribution from plants to ecosystem respiration. A combination of the soil water content and soil temperature parameters appeared to be the governing factors for this grassland and proved to be the best at predicting nighttime respiration rates.

The environmental controls on ecosystem photosynthesis include: temperature, nutrients, atmospheric water vapour, and soil water. These factors are interrelated with light intensity, which is the overriding controller of photosynthetic activity (Ruimy *et al.* 1995). Air temperature has been shown to have some control on photosynthesis when temperatures rise above the optimum for that ecosystem (Hollinger *et al.* 1994, Baldocchi *et al.* 1997). Nutrient status of the plants in an Amazonian grassland has been suggested as a control on photosynthesis by placing constraints on photosynthetic capacity (Grace *et al.* 1998). In addition, net nitrogen mineralization plays a role in limiting aboveground net primary productivity across the central grasslands of the U.S. (Burke *et al.* 1997). The vapour pressure deficit (VPD) has also been shown to affect CO_2 uptake. Grace *et al.* (1995) found that bulk stomatal conductance decreased as the leaf to air vapour pressure deficit increased in an Amazonian forest. Smedley *et al.* (1991) inferred from a decline in ^{13}C discrimination that there had been a decline in leaf conductance in response to drought in a Utah grassland. Stomatal closure in response to decreasing soil water content was given as the likely cause of a decrease in photosynthesis in a broad-leaved forest in Tennessee (Baldocchi 1997b). The seasonal variation of net ecosystem exchange was closely related to leaf expansion and soil water content during a dry year in a Beech forest in France (Granier *et al.* 2000). Vourlitis *et al.* (2000) found that temporal variation in CO_2 flux could be predicted from: radiation, air temperature, soil water content and normalized difference vegetation index (NDVI) on tundra in Alaska. It is clear from these examples that many environmental factors, or combination of factors, can affect photosynthesis but what are the most important factors for this grassland?

The environmental factors controlling photosynthesis in this grassland were primarily soil moisture content, through its effect on LAI, and to some degree vapour pressure deficit. Air temperature did not appear to have an independent effect on photosynthesis in this grassland. Instead air temperature was involved in the control of photosynthesis through the relationship between air temperature and VPD. The nitrogen content of the bulk aboveground biomass was important in controlling photosynthesis because of its relationship to leaf area index (LAI). However bulk aboveground biomass nitrogen differences were not the result of a limitation of soil available nitrogen, because leaf nitrogen was not significantly different between the years of comparison. The interrelations of these environmental factors with photosynthetically active radiation (PAR) in controlling photosynthetic activity are discussed in the remainder of this section.

4.2.1 ECOSYSTEM PHOTOSYNTHETIC EFFICIENCY COMPARISONS

This grassland had a similar seasonal change in photosynthetic efficiency as a grassland in California (Valentini *et al.* 1995). Table 5 lists the comparison of photosynthetic efficiencies calculated as the ratio of daily integrated NEE to daily integrated incident PAR (PAR_o) for these two ecosystems. The data comparison indicated that quite different grasslands, with few common species and different seasons of growth, have comparable photosynthetic efficiencies.

In a Brazilian cerrado (Miranda *et al.* 1997) the initial slope of NEE to PAR_o for in the wet and dry seasons was reported as 0.015 and 0.013, for LAI values of 1.0 and 0.4, respectively. These values are similar to the initial slope (0.013-0.022) observed during the high soil moisture period of 1998 in this grassland (Table 5). A Florida pine forest had an initial slope of 0.044 in the most active season and a slope of 0.038 in the winter, with LAI values of 6.5 and 3.7 respectively (Clark *et al.* 1999). In contrast, a wet cypress forest in the same study had a slope of 0.027 in the active growing season and a slope of 0.002 under a leafless over-story, LAI values of 5.0 and 1.5, respectively. The photosynthetic efficiency of this grassland increased as the LAI increased (Fig. 19). This was also true of the other diverse ecosystems used in this comparison (Fig. 19), because the inherent leaf-level photosynthetic efficiency is very constant across species and growth forms (Ehleringer and Pearcy 1983). The inference was that individual leaves have a relatively low level of photosynthetic efficiency and the ecosystem photosynthetic efficiency was determined by the cumulative total leaf surface available to harvest light.

The effect of vapour pressure deficit (VPD) on the photosynthetic efficiency of the ecosystem in evident in 1998 but was not evident in 1999 (Table 5). The effect of VPD on photosynthetic efficiency was evident in July of 1998 at all soil moisture contents, which suggests that this effect was more important than soil moisture content constraints at this time. However, the soil moisture content was >0.24 m^3 m^{-3} for most of July 1998. In August of 1998 the effect of VPD was evident only for a brief period of time with higher soil moisture contents. This indicates that soil moisture content had become the dominant control of photosynthetic efficiency. In 1999 the same water vapour deficit effect was not apparent, but rather the photosynthetic efficiency appeared to be affected only by soil moisture content. This is because soil moisture content was above 24% for only very brief periods in the early season. This suggests the dominance of soil moisture content as the control on photosynthetic efficiency in years of normal precipitation.

Meinzer (1993) put forth the idea that stomata react to the rate of water loss rather than the water vapour deficit itself. Meinzer's explanation was that the maintenance of a near constant leaf water status was achieved by modulation of the stoma in response to hormonal signals from the roots, this would couple the vapour phase to the liquid phase conductance and consequently to the hydraulic capacity of the soil. This would make the capacity of the soil to deliver water an important controlling factor in transpiration. The increase in VPD would increase the driving gradient for water movement, this in turn would exert a greater negative pressure on the soil water. As the driving gradient increases, or the soil dries out, the plant could either exert a greater negative pressure, and risk embolism, or reduce the water loss to a rate that can be delivered from the soil. As the stomata close to decrease the rate of water loss, there would be less latent heat flux and an increase in sensible heat flux and as a consequence there would be an increase in leaf temperature. This rise in leaf temperature would result in an increase in photorespiration there-by lowering the photosynthetic efficiency (Lambers *et al.* 1998).

There was over all less efficiency in 1999 because the hydraulic capacity of the soil to deliver water decreased during active leaf expansion and became the overall controlling environmental factor. The lower initial slope for NEE/PAR in May 1999, when volumetric soil moisture content was >24% (Table 3), was a result of initial leaf expansion just beginning, so that PAR_o could not be used as efficiently. This was similar to the situation in June 1998, when soil moisture was high but leaf expansion was not complete. There was a lower slope in June 1998 than in July 1998 when peak LAI occurred (Fig 5). In this example, the light use efficiency changed due to the increase in leaf area. The slope of the relationship then declined after peak biomass in concert with the decrease in LAI.

An investigation of the effect of diffuse and direct radiation on the apparent photosynthetic efficiency was conducted. An increase in ecosystem light efficiency under diffuse radiation has been noted in several studies of forested sites (Hollinger *et al.* 1994, Baldocchi *et al.* 1997a, and Baldocchi 1997b). The probable causes put forward for the increased efficiency were; the decreased radiation load on leaves and/or the increased contribution from the lower parts of the canopy, that are normally shaded. In 1999 for this grassland I speculated that the decreased radiation load in diffuse light on cloudy days might cause an increased photosynthetic efficiency. An analysis of light response curves (data not shown) under normal growing season temperatures, however, showed no clear indication of improved efficiencies. The slope of the NEE/PAR_o relationship generally did increase from a low in clear conditions to as much as a ten fold increase in slope for overcast conditions, but the coefficient of determination (r^2) was very low for one or all of the described relationships. The relatively low leaf area of this grassland probably precludes any efficiency increase possible from reduced radiation loads.

4.2.2 CANOPY CONDUCTANCE

Canopy conductance was a very important controlling factor in plant/ecosystem assimilation on a diurnal basis as evidenced by the diurnal variation seen in Figure 13. There was a seasonal decrease in canopy conductance that was concurrent with a decline in soil water content. Saigusa *et al.* (1998) found that daily photon flux density and VPD became dominant factors for canopy CO_2 flux in a Japanese grassland at the seasonal peak of precipitation and with LAI of approximately 3. Hollinger *et al.* (1994) found that approximately 40% of the afternoon decline in net ecosystem CO_2 exchange rate was due to an increase in VPD for a New Zealand forest with a LAI of 7 and under minimal water stress. These examples indicate an effect of VPD on net CO_2 exchange but under moist soil conditions. In a young beech forest (LAI=5.6), increases in VPD decreased net ecosystem production by closing stomata, until late summer when ecosystem C fixation decreased because of decline in PAR and a drying of the soil (Granier *et al.* 2000). In this grassland, VPD had more affect on CO_2 assimilation for the period of high soil moisture content, when soil moisture was low there was little effect of changes in VPD.

In the comparison of C_i/C_a ratio between the two years (Fig. 13) the diurnal pattern of change was evident and has been noted in other studies (Knapp 1993, Zhang and Nobel 1996). However, a comparison of both canopy conductance and C_i/C_a for peak growth periods in the two study years shows that, despite the significantly lower canopy conductance in 1999 the C_i/C_a ratio for the two years was similar. This was also evident in the next comparison period of August 1998 and July 1999. This would suggest that the lower canopy conductance had less effect on the intercellular supply of CO_2 for the plants of the ecosystem than might be expected, because even with the reduced canopy conductance the C_i/C_a was held relatively constant (Anderson *et al.* 1995, Wong *et al.* 1979). This departs from the expected leaf level response, where C_i should decline with a decline in stomatal conductance because the demand for CO_2 would remain the same (Lambers *et al.* 1998). However, the C_i/C_a ratio calculated from the carbon isotope data of the biomass samples indicated that the decreased canopy conductance of 1999 did result in a lower integrated C_i/C_a as the season progressed (Fig. 14). This suggests that relatively small differences in short term C_i/C_a ratio can have an affect on the seasonally integrated C_i/C_a ratio.

If in the short term the intercellular supply of CO_2 was only slightly affected by lower canopy conductance, then the demand for CO_2 must have been lower in 1999 compared to 1998. The inference then, was that with 45% less leaf area in 1999 compared to 1998, there was less demand for CO_2 so that a lower canopy conductance could supply the demand. Because of this, VPD was less important as a controlling factor of photosynthesis when soil moisture was limiting canopy conductance. This points out the importance soil moisture content, through its relationship to LAI, as a control on photosynthesis.

4.2.3 BALL-BERRY INDEX

When observed canopy conductance was compared to the Ball-Berry index, the slope (*m*) of the relationship was 9.76 with an r^2 of 0.72 (Fig. 15). The relative humidity parameter in the Ball-Berry model suggests a more direct influence of VPD on canopy conductance than appeared to actually occur in this grassland. In contrast, the mechanism for soil moisture to exert effects on canopy conductance in the Ball-Berry model is via changes in A, assimilation rate (or gross photosynthesis). Therefore, soil moisture has indirect effects on canopy conductance, primarily through changes in LAI, in the Ball-Berry model formulation. Despite these limitations the Ball-Berry model could predict canopy conductance reasonably well in this grassland (Fig. 15). The slope parameter (*m*) was similar to the reported "cardinal value" of 10 in Baldocchi and Meyers (1998). However, a caveat in that same study was that *m* can deviate significantly under conditions of moderate to severe soil moisture conditions, which are common in this grassland. The value of *m* for this grassland was lower than the range reported (approximately 20-40) for the late growing season in a California serpentine grassland (Valentini *et al.* 1995).

4.2.4 PLANT NITROGEN

The nitrogen content of plant material can be considered as a surrogate for photosynthetic capacity. Approximately 50% of the nitrogen content of plants is involved in the photosynthetic apparatus (Lambers *et al.* 1998), so that nitrogen content would represent the capacity of the plants to carry on photosynthesis. The generally similar values of leaf nitrogen content indicate that the photosynthetic capacity of the leaves for the 2 study years was about the same and that it changed in a similar way over the growing season. There was, however, a large difference between the absolute amount of plant nitrogen per unit ground area (g N m^{-2}) between 1998 and 1999 (Fig. 12). This was due to the increased leaf area (LAI) of the ecosystem in 1998 (Fig. 5). This indicates that the ecosystem in 1999 as a whole had a lower photosynthetic capacity even though the individual leaves had about the same photosynthetic capacity. The changes in ecosystem photosynthetic capacity appear to contribute to the general decline in assimilation as the season progresses. Environmental stress (i.e. drought) caused smaller amounts of plant material to be developed but with the same individual leaf photosynthetic capacity. While the leaves have the same photosynthetic capacity the whole plant and therefore the ecosystem have a very different photosynthetic capacity because there is less photosynthetic material available in 1999. This is supported by Hirose and Bazzaz (1998) where they found a strong linear relationship between canopy photosynthesis and total canopy leaf nitrogen in the C_3 plants of their greenhouse experiment.

At about 2 times as much g N m^{-2} in 1998 compared to 1999 the ecosystem can assimilate about 3 times as much CO_2 and this holds true until late in the growing season. The reduced leaf area in 1999 limits the photosynthetic capacity of the ecosystem and the stomatal conductance that was necessary, or possible, to meet the demand for CO_2. This points out the importance of soil moisture content in determining the photosynthetic capacity of the ecosystem.

4.3 Ecosystem Carbon Gain

In comparison to other grasslands, this grassland had relatively high daily carbon uptake in the summer season when soil moisture was high. In 1998 there was a maximum net C exchange of 4.95 g C m^{-2} d^{-1}, a minimum of –2.88 g C m^{-2} d^{-1} with the average of 1.81 g C m^{-2} d^{-1} for the growing season (Table 4). In 1999 the maximum net C exchange was 2.50 g C m^{-2} d^{-1}, the minimum –1.47 and the average was 0.34 g C m^{-2} d^{-1} for the growing season (Table 4). This compares with a daily net C exchange of 2.86 g C m^{-2} d^{-1} for a Saskatchewan grassland (Ripley and Saugier 1974), a Caucasus sub alpine pasture with a daily net C exchange of 2.13 g C m^{-2} d^{-1} (Tappeiner and Cernusca 1996), and a tall grass prairie in Kansas with a daily net C exchange of 4.85 g C m^{-2} d^{-1} (Ham and Knapp 1998). In Grace *et al.* (1998) the average daily flux of CO_2 for a C_4 pasture in Amazonia, would represent 1.92 g C m^{-2} d^{-1}. In Miranda *et al.* (1997), the reported wet season carbon flux of a Brazilian savanna was about 2.1 g C m^{-2} d^{-1}. In Baldocchi *et al.* (1997), a typical daily net C exchange for a boreal jack pine forest was estimated to be between –4 to 2 g C m^{-2} d^{-1}. The daily net C exchange for this grassland was similar to a pine forest ecosystem in Florida that had an estimated mean daily net CO_2 exchange of 0.7 to 3.0 g C m^{-2} d^{-1} (Clark *et al.* 1997) and higher than a flooded Cypress ecosystem from the same study which ranged from -0.9 to 1.2 g C m^{-2} d^{-1}. The grassland of this study had a maximum daily net C exchange that compares favorably with many different ecosystems. Under conditions of decreased soil water content, as in 1999, the maximum daily net C exchange is still comparable to some forest systems and tropical grasslands.

This grassland had seasonal net C exchange comparable to another Canadian grassland when precipitation was above normal, and even comparable to a boreal jack pine forest when precipitation was normal. The summer season (Julian days 110-250) net C exchange for this grassland, estimated from the eddy covariance measurements, was 190 g C m^{-2} in 1998, and was 46.8 g C m^{-2} in 1999. The yearlong gain (summer and winter) for 1998 was 149 g C m^{-2} and for 1999 was 5.81 g C m^{-2} (winter and summer). A Saskatchewan grassland was estimated to have a growing season gain of 224 g C m^{-2} (Ripley and Saugier 1974). In a study of grasslands across all of North America, desert grasslands were estimated to gain from 101 to 171 g C m^{-2} yr^{-1}, and mixed grasslands gained from 235 to 641 g C m^{-2} yr^{-1} (Sims and Singh 1978b). A boreal jack pine forest was reported to assimilate only 47 g C m^{-2} during the heart of the growing season (Baldocchi *et al.* 1997). The C gain values for a pine forest ecosystem in Florida gained between 608-740 g C m^{-2} yr^{-1} over a two year study (Clarke *et al.* 1999). A flooded Cypress ecosystem from the same Florida study had C gain values of 37-84 g C m^{-2} yr^{-1}. Alaskan tundra has been reported to assimilate 18 g C m^{-2} in a growing season (Vourlitis *et al.* 2000). The yearly C gain of this grassland appears low and highly variable when compared with many other ecosystems.

The range of peak total aboveground biomass for this grassland (114-207 g m^{-2}) was within the ranges reported from other North American grasslands. Mountain grasslands ranged from 124-220 g m^{-2}, the mixed grasslands ranged from 101 to 270 g m^{-2}, shortgrass prairie ranged from 62 to 236 g m^{-2}, desert grasslands ranged from 34 to 134 g m^{-2}, with the highest peak biomass occurring on a tall grass prairie at 336 g m^{-2} (Sims and Singh 1978a). A Saskatchewan grassland ranged from 86 to 186 g m^{-2} (NPP database 2000). A Swedish limestone grassland was reported to have a live aboveground biomass of 247 g m^{-2} (van der Maarel and Titlyanova 1989) and a North India savanna ranged from 367 to 700 g m^{-2} (Pandey and Singh 1992). This grassland appears to produce aboveground biomass within the expected range for comparable grasslands.

There have been some estimates of carbon gain, using broad general assumptions, which provide a surprisingly good "rough" estimate of the actual carbon gain. In Valentini *et al.* (1995) an estimate of 11.1 mol CO_2 m^{-2} of annual photosynthesis was made for the serpentine grassland. Assumptions of a ratio of carbon to biomass of 1:2 and a ratio of photosynthesis to net primary production of 2:1 allowed a prediction of an annual net primary production of 133 g biomass m^{-2}. They considered this low for an estimate that includes root production but it could allow for up to 33 g m^{-2} for new root production which is with in range of one study of root biomass productivity in the Serengeti (McNaughton *et al.* 1998). Using a similar method and the same assumptions for the 1999 growing season of this grassland, there would have been a net primary production of 146 g m^{-2}. The measured maximum live aboveground biomass of this grassland was 114.37 g m^{-2} (±18 sem) for the 1999 season. This relatively simple exercise appears to provide an estimate of carbon gain for this grassland that is close to the estimate from the biomass harvest, and could prove useful in giving quick estimates of carbon sequestration.

The biomass harvest estimates of carbon gain suggest that in periods of high moisture there can be a relatively large gain in aboveground biomass, and in periods of low moisture all or most of the carbon gain occurs in the aboveground biomass with little root growth. The average below ground biomass for this study (530 g m^{-2}) appears to be at the low end of the range of below ground biomass reported for mixed grasslands, 668-1150 g m^{-2} (Sims and Singh 1978a). The minimal replicates and difficulties of estimating the below ground biomass could account for a large portion of the discrepancy. In Sims and Singh (1978b), the mixed grass prairie was reported as having the least dynamic root turnover, with an average turnover of only 18% but as low as 10%. In addition, van der Maarel and Titlyanova (1989) reported that the ratio of below ground to aboveground phytomass was reported to increase from 1.7 to 6.5, as aridity increases in a gradient of European to Asian grasslands. The ratio of below ground biomass to aboveground biomass in 1998 for this grassland was 2.6, and if there was no net root growth the ratio would increase to 4.6 in 1999. This would suggest that the plants of this ecosystem maintain the existing root biomass and decrease the aboveground growth in response to lower soil moisture content. This supports the assumption made, of no net root growth in 1999, in reconciling the carbon gain estimated from eddy covariance with the carbon gain estimated from biomass harvest.

The two years of study for this site represent an above average and an average growing season on the basis of precipitation. The ecosystem carbon budget for this grassland also showed the wide range of carbon gain that can occur. The carbon gain appeared to have some predictability based on a relationship to LAI (Fig. 20). The LAI is controlled primarily by the soil water content, especially that resulting from early growing season precipitation. This ecosystem was a relatively large carbon sink in a year of above average precipitation, with sequestration rates that approach those of an Aspen woodland (Black *et al.* 2000). Under conditions of soil moisture deficit this grassland can replace the respiratory losses of carbon that occur during the winter and even gain a small amount, making it a small carbon sink in a year of normal precipitation.

Table 5. Comparison of Photosynthetic Efficiency of grasslands.

	Date	GP mol m^{-2} d^{-1}	PAR$_o$ mol m^{-2} d^{-1}	Photosynthetic Efficiency mol A/mol PAR$_o$	Relative Soil Moisture
California Serpentine Grassland 1991	February 26	0.0683	22.09	0.0031	wet
	April 3	0.1577	41.46	0.0038	
	May 6	0.1384	48.86	0.0028	
	May 15	0.0128	47.68	0.0003	dry
Rood Grassland 1998	June	0.3909	32.64	0.0120	wet
	July	0.4232	42.14	0.0100	
	August	0.2059	40.17	0.0037	
	September	0.0671	29.48	0.0023	dry
1999	May	0.1209	37.30	0.0032	wet
	June	0.1535	36.39	0.0042	
	July	0.0830	40.88	0.0020	
	August	0.0701	35.95	0.0019	dry

California Serpentine from Valentini *et al.* (1995)

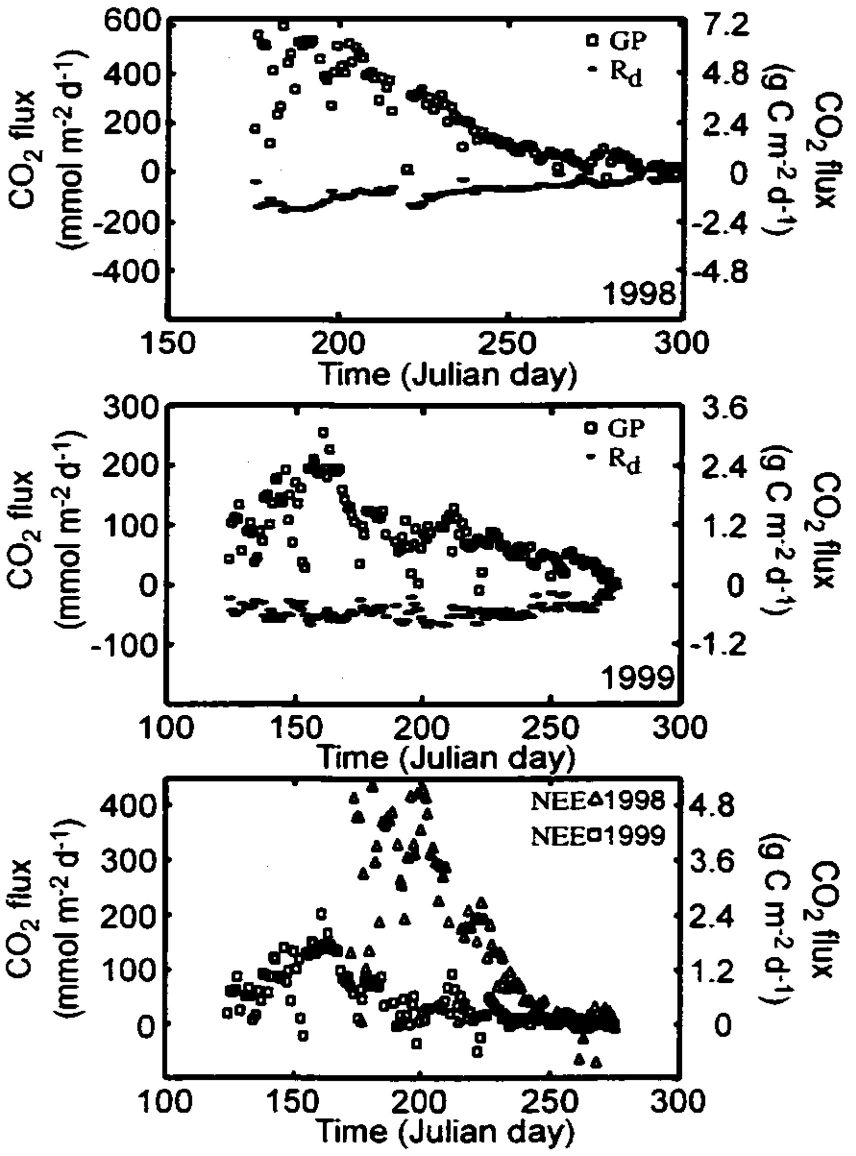

Figure 17. Comparison of seasonal and inter-annual variation in daily integrated ecosystem gross photosynthesis (GP), ecosystem daylight respiration (R_d), and net ecosystem CO_2 exchange. (NEE) Note scale differences between 1998 and 1999.

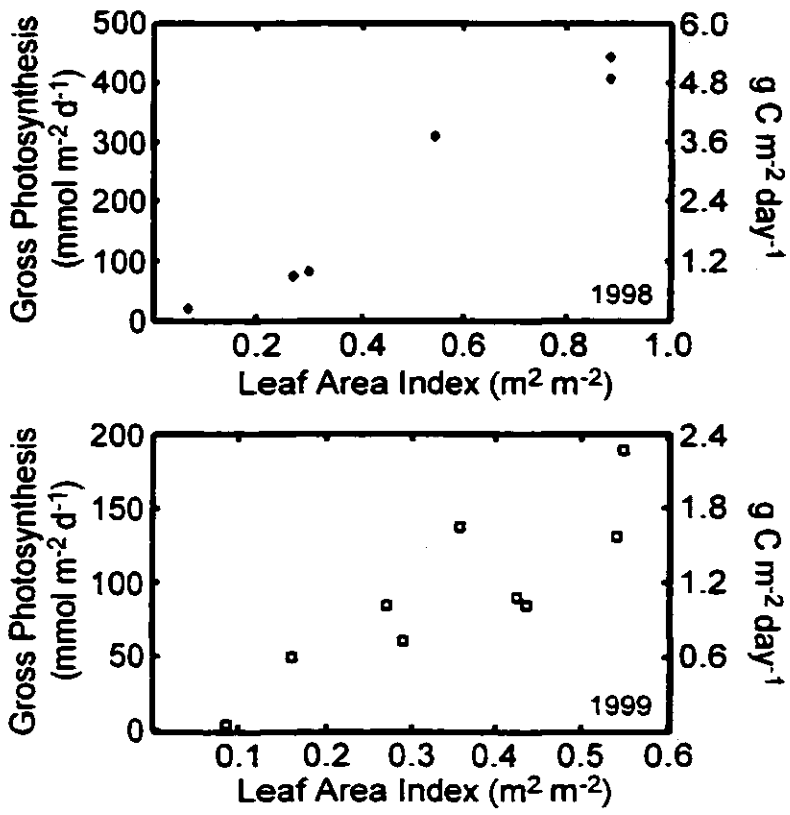

Figure 18. Comparison of variation of gross photosynthesis with changes in leaf area index (LAI) for 1998 and 1999. Note scale differences between 1998 and 1999. The 1998 figure shows GP from peak LAI through to decline, while the 1999 figure shows GP from emergence to peak through to decline in LAI.

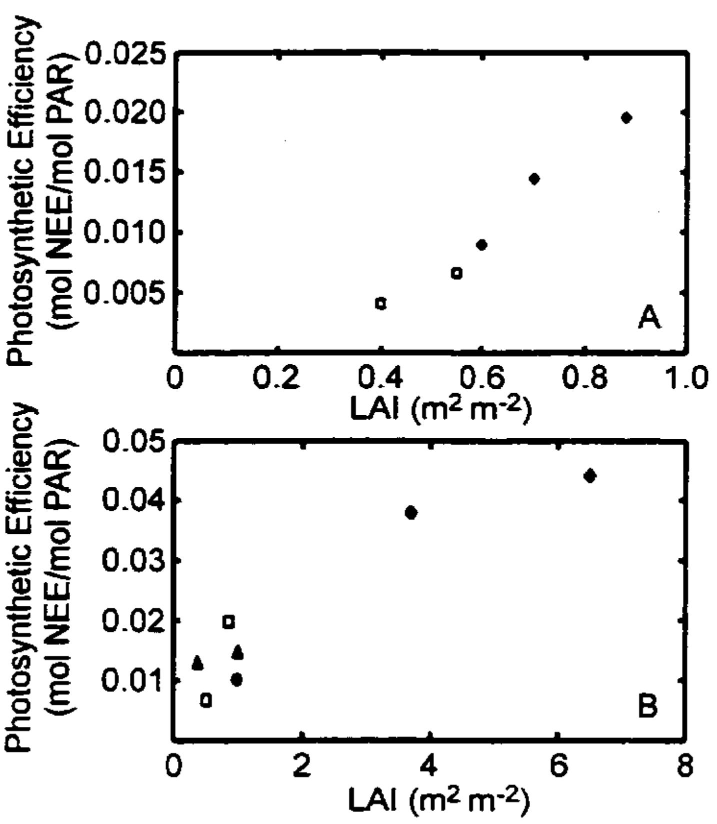

Figure 19. Variation of photosynthetic efficiency with changes in leaf area index (LAI). Upper box figure (A) data consists of monthly average photosynthetic efficiency and LAI. 1998 ◆ June, July and August; 1999 May and June. Lower box figure (B) data consists of photosynthetic efficiency and LAI at peak periods of season or year for the respective study. ◆ Clark *et al.* 1999, ▲ Miranda *et al.* 1997, ● Valentini *et al.* 1995, ☐ this study for 1998 and 1999.

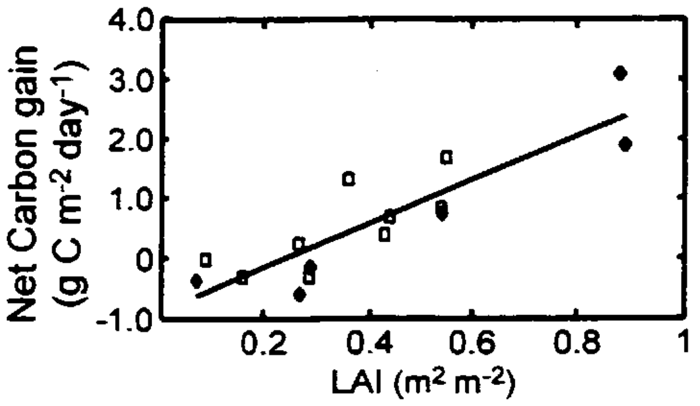

Figure 20. Comparison of variation of net carbon gain with changes in leaf area index (LAI) for ◆ 1998 and □ 1999. Net carbon gain was taken as the 7 day average around the corresponding LAI value. Data consists of peak LAI through to the decline in LAI at the end of season.

5. Conclusions

There are very different patterns of net ecosystem exchange in this grassland when comparing 1998 and 1999. Ecosystem CO_2 exchange peaks in June in a year of normal summer precipitation and then declines in response to the seasonal drought. NEE peaked in mid-July in a year of above normal June precipitation. The inter-annual variation in gross photosynthesis can be as much as three times greater in a year of high June precipitation compared to a year of normal precipitation.

There was one environmental factor common to both uptake and loss of CO_2 in this grassland. Ecosystem respiration was primarily controlled by soil temperature and soil moisture content. Photosynthetic CO_2 uptake was controlled by soil moisture content, through its effect on LAI. There was evidence of stomatal limitation on CO_2 uptake from VPD effects during periods of high soil moisture. Soil moisture deficit is the most important environmental factor controlling carbon sequestration in this grassland.

Production in this grassland was comparable to other North American grasslands and some forested sites. This grassland can be a large sink for carbon in conditions of high soil moisture. This grassland can replace the over winter CO_2 respiratory loss in conditions of normal precipitation. The annual carbon budget calculated from the eddy covariance measurements were somewhat less than the budget estimated from plant biomass harvests. The carbon gain for this grassland can be predicted based on a relationship to leaf area index.

It is difficult to make definitive predictions based on only two years of data. However, it would appear that monitoring the soil moisture content for the six weeks after plant emergence could give a reasonable estimate of biomass and LAI for grasslands of this type. Knowing these two parameters, the seasonal carbon budget could be estimated. The timing and amount of rainfall appear to be of great importance since soil moisture deficit is the controlling environmental factor for LAI and biomass. The rain events large enough to affect soil moisture, and those events which occur during the critical leaf expansion period, appear to be the most important for measurement.

Given the demonstrated importance of soil moisture to production on this grassland, irrigation studies would be a logical research direction to develop next. The determination of the minimum soil moisture content and the critical time period for that soil moisture would be of benefit to the estimation of CO_2 exchange and carbon sequestration. Grazing studies of this undisturbed prairie would add further to the literature on effects of clipping and how that effects CO_2 exchange and carbon sequestration. Litter interception of rain, fire effects on plants and litter, along with studies of the effects of nitrogen deposition would all supply data to help elucidate some of these controversial topics.

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Appendix

Aerodynamic Resistance

The stability correction method (Campbell and Norman 1998) for calculating canopy resistance or conductance when compared to a less rigorous method (Thom [1972] as cited in Monteith and Unsworth [1990]) indicated that the differences were minimal under neutral or unstable conditions. The stability effects were most important in stable conditions and low wind speeds (Campbell and Norman 1998). The diabatic corrections for convective production or suppression of turbulence do not have a great effect on the calculated canopy resistances or conductances in this grassland. It is generally assumed that stability corrections were not important for wind speeds greater than 3-4 m s^{-1} (Campbell and Norman 1998). The approximation of the additional boundary layer resistance (r_b) taken from Thom's empirical equation presented in Monteith and Unsworth (1990) gives an adequate estimation for heat and water vapour transfer even over a wide range of friction velocities (u_*). This grassland tends to have unstable conditions and higher wind speeds through much of the growing season. Use of the less rigorous method of calculation of canopy conductance should not cause serious estimation errors.

In Figure 20 aerodynamic resistance as calculated with the Thom empirical equation was plotted against the aerodynamic resistance as calculated by the rigorous method that uses diabatic correction factors. The slope of the relationship indicates that the empirical Thom equation just slightly under estimates the aerodynamic resistance. This translates into a slight over estimation of canopy conductance (Fig. 20).

To calculate the rigorous model of aerodynamic resistance several intermediate calculations are required. A measure of the form drag and skin friction called a roughness length for momentum (z_m) is required. This was interpolated from a plot of empirical data from Shaw and Pereria (1982), presented in Campbell and Norman (1998). The plot was z_m/h (canopy height) to plant area index (PAI). The PAI was defined as the area of leaves and stems per unit ground area and it was assumed to be the same as the LAI, because for this study all above ground plant material was measured as leaf area. This interpolation of the plot allowed a relationship to be established:

$$z_m = 0.12h \qquad \text{eq. 12}$$

Where h is the height of the canopy that was taken as 0.4 m.

Therefore the z_m was calculated as 0.05 m for this grassland. The assumption for momentum roughness length (z_m) relationship to the roughness length for heat (z_h) and vapour (z_v) is taken from Campbell and Norman (1998)

$$z_h = z_v = 0.2z_m \qquad \text{eq. 13}$$

The roughness length for heat was 0.01 m.

With these parameters defined, a measure of atmospheric stability (ζ) can be calculated. This is taken from a ratio of convective to mechanical production of turbulence (Paulson 1970).

$$\zeta = \frac{z}{\left[\frac{-u_{*}^{3} c_{p} \rho T}{k g H}\right]} \qquad \text{eq. 14}$$

where: z= measurement height (m)
u_* = friction velocity (m s^{-1})
c_p = specific heat at constant pressure (J mol^{-1} C^{-1})
ρ_a = molar density of dry air (mol m^{-3})
T = temperature (K)
k = von Karman constant (0.4)
g = acceleration due to gravity (10 m s^{-2})
H = sensible heat flux (W m^{-2})

The calculated ratio of stability is used to establish the diabatic correction factors for (Ψ_H) heat and momentum (Ψ_M) under stable (negative sensible heat flux) and unstable conditions (positive sensible heat flux) (Campbell and Norman 1998).

For unstable conditions:

$$\Psi_H = 2\ln\left[\frac{1+(1-16\zeta)^{0.5}}{2}\right] \qquad \text{eq. 15}$$

$$\Psi_M = 0.6\Psi_H \qquad \text{eq. 16}$$

For stable conditions:

$$\Psi_M = \Psi_H = 6\ln(1+\zeta) \qquad \text{eq. 17}$$

The diabatic correction factors can be used to estimate an aerodynamic resistance (r_a) accounting for atmospheric stability and the differences between roughness lengths, z_m and z_h (Grace *et al.* 1995).

$$r_a = \left(\frac{u}{u_{\cdot}^{2}}\right) + \frac{1}{ku_{\cdot}}\left[\ln\left(\frac{z_m}{z_h}\right) + \Psi_M - \Psi_H\right] \qquad \text{eq. 18}$$

where: r_a = aerodynamic resistance (s m^{-1})
u = horizontal windspeed (m s^{-1})
$u_{\cdot}$ = friction velocity (m s^{-1})
k = von Karman's constant (0.4)
z_m = roughness length for momentum (m)
z_h = roughness length for heat (m)
Ψ_M = diabatic correction factor for momentum
Ψ_H = diabatic correction factor for heat

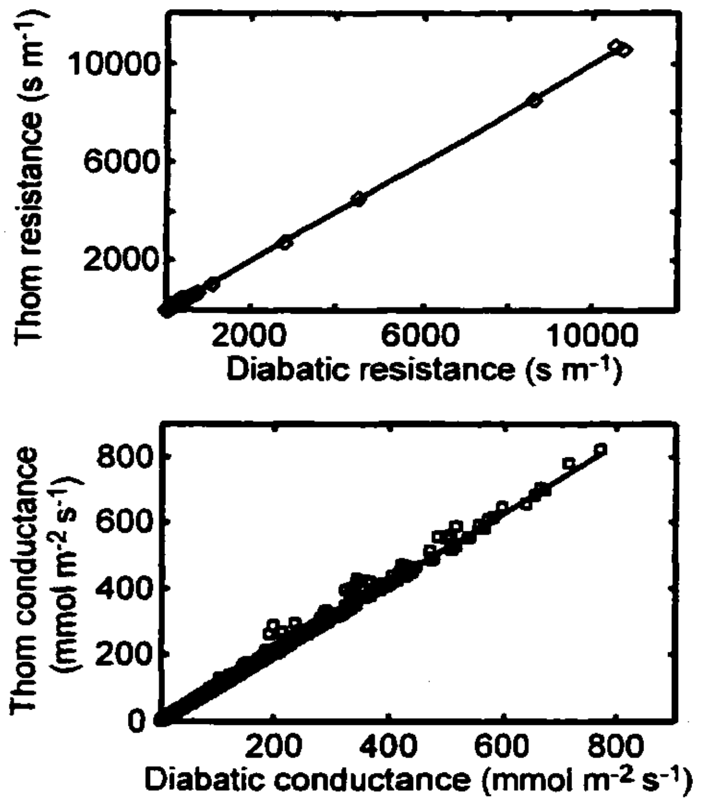

Figure 21. (Top figure) The Thom aerodynamic resistance versus diabatic aerodynamic resistance. Thom as calculated by the empirical equation and the diabatic aerodynamic resistance as calculated using diabatic correction factors.

Thom resistance = 0.996 diabatic resistance + 4.395 $r^2 = 0.99$

(Bottom figure) The Thom canopy conductance versus the diabatic canopy conductance. thom as calculated by the empirical equation and the diabatic canopy conductance as calculated using correction factors

Thom conductance = 1.051 diabatic conductance - 2.227 $r^2 = 0.99$