

SEASONAL AND INTERANNUAL VARIATION IN WATER VAPOR FLUXES  
AND ENERGY BALANCE IN A MOIST MIXED GRASSLAND

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## Abstract

Fluxes of sensible and latent heat were measured over a grassland during 1998 and 1999 using the eddy covariance technique. The study objectives were to document seasonal and interannual variation in evapotranspiration and energy partitioning and to examine what factors influenced evapotranspiration. Bowen ratios were lower in 1998 (0.5-3.0) than in 1999 (2.5-8.5) due to lower evapotranspiration rates (E). Maximum E also occurred later in 1998 than in 1999: Day 188 ( $10.4 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) versus Day 152 ( $5.6 \text{ mmol m}^{-2} \text{ s}^{-1}$ ). Daily evapotranspiration rates were positively correlated with net radiation, canopy conductance, plant nitrogen content, leaf area index and soil moisture. Based on calculations of the decoupling coefficient ( $\Omega$ ), evapotranspiration was more constrained by canopy conductance in 1999 ( $\Omega < 0.2$ ) than in 1998 ( $\Omega > 0.3$ ). Evapotranspiration and energy partitioning in this grassland were sensitive to seasonal changes in soil moisture and interannual variation in spring precipitation. Annual evapotranspiration was 300 mm.

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## List of Symbols and Abbreviations

### Roman Alphabet

CMI	Climatic Moisture Index (cm)
$c_p$	Specific heat of air ( $J g^{-1} K^{-1}$ )
$e_a$	Actual vapor pressure of the ambient air (Pa)
$e_s$	Saturation vapor pressure (Pa)
E	Evaporation rate ( $mmol m^{-2} s^{-1}$ )
ET	Evapotranspiration
G	Soil heat flux ( $W m^{-2}$ )
$g_{aerodynamic}$	Aerodynamic conductance to water vapor ( $m s^{-1}$ or $mmol m^{-2} s^{-1}$ )
$g_{canopy}$	Canopy conductance to water vapor ( $m s^{-1}$ or $mmol m^{-2} s^{-1}$ )
H	Sensible heat flux ( $W m^{-2}$ )
JD	Julian Day
LAI	Leaf area index
PAR	Photosynthetically active radiation ( $\mu mol m^{-2} s^{-1}$ )
q	Water vapor concentration ( $mmol mol^{-1}$ )
$r_a$	Aerodynamic resistance ( $s m^{-1}$ )
$r_e$	eddy diffusive aerodynamic resistance for mass transfer ( $s m^{-1}$ )
$r_b$	boundary layer resistance for mass transfer ( $s m^{-1}$ )
$R_n$	Net Radiation ( $W m^{-2}$ )
s	Slope of the relation between saturation vapor pressure and temperature ( $kPa K^{-1}$ )
u	Average wind speed ( $m s^{-1}$ )

List of Abbreviations and Symbols Continued

$u_*$	Friction velocity ( $\text{m s}^{-1}$ )
VPD	Vapor pressure deficit (kPa)
$w$	Vertical wind speed ( $\text{m s}^{-1}$ )
Greek Alphabet	
$\beta$	Ratio of sensible to latent heat flux
$\Delta$	Rate of change of saturation vapor pressure with temperature ( $\text{Pa K}^{-1}$ )
$\varepsilon$	Ratio of molecular weights of water vapor and air
$\gamma$	Psychrometric constant ( $\text{Pa K}^{-1}$ )
$\lambda E$	Latent heat flux ( $\text{W m}^{-2}$ )
$\Omega_{\text{canopy}}$	Decoupling coefficient of a canopy
$\rho_a$	Density of dry air ( $\text{g m}^{-3}$ )

## **1. Introduction**

### *1.1 Global change*

The evidence is irrefutable. Humans are modifying the environment more than any other species in Earth's recent history. Historically, effects were only local and regional (e.g. burning biomass and cultivating relatively small pieces of land). Two hundred and fifty years after the start of the Industrial Revolution, it is apparent that our actions, past and present, have global consequences. It has been estimated that we have altered as much as one-half of the Earth's land surface (Vitousek, *et al.* 1997). This in turn, has caused dramatic changes in the abundance and distribution of flora and fauna in addition to unparalleled increases in extinction rates. Over 20% of bird species alone have disappeared (Vitousek, *et al.* 1997). We have also substantially altered the chemistry of the atmosphere; for example, the atmospheric concentration of carbon dioxide has increased by over 30% (Friedli *et al.* 1986; The Climate Monitoring Diagnostics Laboratory (CMDL) 2000). Due to this and other increases in greenhouse gases, the average global surface temperature is expected to increase 1 to 3.5 °C relative to 1990 by 2100 (U.S. Global Change Research Information Office (USGCRIO) 2000). The nitrogen and water cycles have also been modified. Human activity now accounts for over 50% of terrestrial nitrogen fixation while 6% of river runoff is lost via evaporation as a result of man-made water impoundments and diversions (Vitousek, *et al.* 1997). Coupled with a rapidly growing population, expected to be 9.3 billion by 2050 (U.S. Census Bureau 2000), our unquenchable thirst for goods and services will place even more demands on our planet. The proper functioning of ecosystems, the key to

meeting basic human requirements, may be endangered by these and other global changes (USGCRIO 2000).

### *1.2 The water cycle*

The global water cycle is the movement of water through the land, atmosphere and ocean (USGCRIO 2000). Together with gravity, energy from the sun drives the cycle (Dingman 1994). Evaporation, precipitation and stream flow are chiefly responsible for transmitting the water between the three systems (Singh 1992) (Figure 1a). While the water cycle is a closed system globally, on any smaller scale, it is open (Singh 1992). For example, water evaporated off the Pacific Ocean may fall as precipitation in the Great Plains. In terrestrial systems there are three main components to the water cycle: land, subsurface and aquifer (Figure 1b). These three systems are interconnected by processes of infiltration, deep percolation and upward movement of water (Singh 1992). Precipitation, surface runoff, infiltration and evapotranspiration are the dominant processes by which water moves in the land system (Singh 1992).

### *1.3 Evapotranspiration*

Evapotranspiration is the sum of all water vapor leaving the biosphere. In addition to evaporation from wet surfaces of the soil or the outside surface of vegetation, it also includes transpiration, or the evaporation of water from the moist, internal surfaces of leaves (Lambert *et al.* 1998). The study of gas exchange, evapotranspiration in particular, is critical to understanding the processes that control ecosystem productivity. Soil water availability, assimilation of CO<sub>2</sub> by plants, and nutrient cycling are all linked to evapotranspiration (Pielke *et al.* 1998).

Evapotranspiration is an important determinant of soil water availability (Hodkinson *et al.* 1999). In most terrestrial ecosystems, the soil serves as the primary water storage component (Aber & Melillo 1991). This store of water is recharged by precipitation and depleted by evapotranspiration. The availability of water, or lack thereof, has important consequences on species distribution, spatial pattern, and community composition (Kelliher, Leuning & Schulze 1993). The amount of water available for plant growth is particularly important. Per unit biomass, water is required more than nutrients in all terrestrial systems (Aber & Melillo 1991). This is, in large part, due to the fact that transpiration and CO<sub>2</sub> assimilation in plants are inextricably linked. The two processes share a common physical pathway. Stomatal conductance, and therefore, transpiration, is a "slave of photosynthesis" (Baldocchi & Vogel 1996), so that high rates of CO<sub>2</sub> assimilation are accompanied by high water vapor fluxes (Baldocchi & Meyers 1998).

Stomata also link the N and H<sub>2</sub>O cycles, as leaf nitrogen content and stomatal conductance are both related to photosynthetic capacity (Baldocchi and Meyers 1998; Wong, Cowan & Farquhar 1979). Köstner *et al.* (1992) found a positive relationship between maximum total conductance and leaf nitrogen content of two *Nothofagus* species. A more direct connection can also be made as the uptake of nutrients from the bulk soil is driven by the movement of water through the soil-plant-atmosphere continuum (Lambers *et al.* 1998). Soil moisture has also been reported as an important factor influencing decomposition rates and therefore nutrient availability. Islam, Mulchi & Ali (2000) reported that the amount of microbial biomass and easily mineralizable carbon was higher under well-watered conditions. In a natural calcareous grassland,

there was a weak but positive relationship between soil moisture and N mineralization and hence nutrient availability (Jamieson, Monaghan & Barraclough 1999). Results from a number of current studies indicate that decomposition is increased under moist conditions (Moorhead *et al.* 1999; Moore *et al.* 1999). Soil moisture was a major factor controlling decomposition along elevational transects of the Sierra Nevada (Wang, Amundson & Niu 2000) and northern Arizona (Murphy, Klopatek & Klopatek 1998).

Evapotranspiration also plays a pivotal role in climate. Latent heat flux (latent heat of vaporization x evapotranspiration rate) is a major component of Earth's surface energy budget. If more energy is dissipated via sensible rather than latent heat flux, a deeper atmospheric boundary layer results (Baldocchi & Vogel 1996; Pielke *et al.* 1998). This in turn influences mesoscale circulation patterns and weather (Kelliher *et al.* 1993). The water budget, a mathematical expression of the water cycle (Singh 1992), is an important ecosystem property. Despite this fact, little is known about processes controlling evapotranspiration at the ecosystem level.

Net radiation, vapor pressure deficit (VPD) and atmospheric turbulence are principal drivers of evapotranspiration. Because the vaporization of water requires energy, evapotranspiration is dependent on the amount of available energy. Consequently, there is a strong positive relationship between net radiation and evapotranspiration. Vapor pressure deficit, the drying power of air (Monteith & Unsworth 1990), is another environmental factor which influences evapotranspiration rates. The ability of a surface to transmit water to the atmosphere, or conductance, (Kelliher *et al.* 1995) also needs to be considered. Aerodynamic conductance is largely a function of wind speed and turbulence. Stomata, however, add an extra resistance.

Canopy conductance, for the most part, is the integration of stomatal conductances across all leaves in a canopy. Canopy conductance, like stomatal conductance, is likely to change with VPD (Hanan & Prince 1997; Berbigier *et al.* 1996) and therefore air temperature and relative humidity. In a study of four Sahelian plant species, VPD was consistently the most significant variable explaining the observed variation in stomatal conductance (Hanan & Prince 1997). Even under ideal conditions of high soil moisture and high light, canopy conductance tends to decline with increasing VPD (Blanken *et al.* 1997; Köstner *et al.* 1992). Soil moisture availability is also expected to influence canopy conductance. One would expect plants to exert tighter control over transpirational water loss when soil moisture becomes limiting. Stomatal conductances of beech, chestnut and oak all declined in response to a drought treatment (Heath 1998). Canopy conductance of a loblolly pine forest in North Carolina was found to decrease with decreasing volumetric soil moisture (Oren *et al.* 1998). Leaf area index (LAI), which represents the transpirational surface of the vegetation, is a strong determinant of canopy conductance on a seasonal and interannual basis (Wilson & Baldocchi 2000). The extent to which plants are able to dictate evapotranspirational fluxes depends on how well the canopy is coupled to the atmosphere (Jarvis 1985; Jarvis & McNaughton 1986). In a canopy uncoupled from the atmosphere, the relative humidity and temperature of the air next to the leaves can be very different from that above the canopy. In contrast, a coupled canopy cannot humidify the adjacent air to the extent that it effectively lowers the vapor pressure deficit (Jarvis 1985). For example, a single leaf exposed to well-mixed air will experience a higher VPD than that experienced by leaves in a dense canopy, where the air is less well mixed and the humidity is higher because of water

transpired from the canopy. The relative contribution of water vapor from soil evaporation will also determine what role stomatal control can exert over evapotranspiration (Field *et al.* 1997).

#### 1.4 Evapotranspiration and global change

Global changes may significantly alter ecosystem functioning.

Evapotranspiration is particularly vulnerable. Due to the increased concentration of greenhouse gases (CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O, chlorofluorocarbons), global surface temperature is expected to increase by as much as 3.5 °C by 2100 relative to 1990 (USGCRIO 2000). The atmospheric concentration of carbon dioxide alone has increased from a pre-industrial concentration of 280 ppm (Friedli *et al.* 1986) to around 368 ppm and continues to rise at an average rate of 1.2 ppm year<sup>-1</sup> (CMDL 2000). Water vapor pressure is temperature dependent. All things being equal, an increase in air temperature would lead to higher VPD, increased evapotranspiration and decreased soil water availability. In gas exchange experiments done by Franks & Farquhar (1999), however, a variety of plant species were shown to differ in their sensitivity to changes in VPD. While the increase in CO<sub>2</sub> may be enhancing the greenhouse effect, ecosystem response to elevated concentrations may be counteractive. Several experiments have shown that exposure to higher than ambient levels of carbon dioxide results in decreased stomatal conductance (Garcia *et al.* 1998; Bettarini, Vacarri & Miglietta 1998). A study of plants growing in a natural CO<sub>2</sub> spring demonstrated lower stomatal conductances even after long-term exposure (Bettarini *et al.* 1998). The mean reduction of stomatal conductance for four of the calcareous grassland species varied from 19 to 52 per cent (Bettarini *et al.* 1998). These changes could not be attributed to significant changes in stomata density

(Bettarini *et al.* 1998). Midday stomatal conductance in spring wheat declined by about 36% (Garcia *et al.* 1998). In whole-plant experiments, potted soybean plants exposed to increased CO<sub>2</sub> concentration lost significantly less water than the control plants, regardless of whether the plants were well-watered or droughted (Serraj, Allen & Sinclair 1999). As technology has improved, larger-scale measurements of water vapor flux are becoming more prevalent. For example, field-grown rice lost 10% less water when exposed to air enriched with carbon dioxide, allowing two extra growing days during drought stress cycles (Baker *et al.* 1997). Midday evapotranspiration in winter wheat declined under elevated CO<sub>2</sub> (Dijkstra *et al.* 1999). Results from an open top chamber experiment with a planted calcareous grassland showed up to a 9% decrease in water vapor flux when exposed to CO<sub>2</sub> enriched air (Stocker *et al.* 1999). When tallgrass prairie was exposed to varying levels of CO<sub>2</sub>, soil water availability was higher in the twice ambient treatment despite increased leaf area (Owensby *et al.* 1999). Likewise, the water content of calcareous grassland soil was higher under elevated CO<sub>2</sub> conditions (Niklaus, Spinnler & Körner 1998).

While experiments with herbaceous plants tend to illustrate strong stomatal closure when exposed to elevated CO<sub>2</sub> concentrations, not all plant communities respond in this manner. For example, in an experiment with field grown pine trees, water use was unchanged even under drought conditions (Ellsworth 1999). There were no significant differences found in pre-dawn and midday water potentials, soil moisture or stomatal conductance (Ellsworth 1999). Trembling aspen, *Populus tremuloides*, likewise showed no significant reductions in stomatal conductance when exposed to high CO<sub>2</sub> concentrations (Curtis *et al.* 2000). Even in grassland studies, there have been conflicting

results. Field *et al.* (1997) report that while the effects of elevated CO<sub>2</sub> on evapotranspiration in sandstone ecosystems were relatively large, there was little or no effect in serpentine ecosystems. Ecosystems, therefore, may respond differently to changes in CO<sub>2</sub>.

The trend of increased N deposition in nutrient limited ecosystems may also have an effect on canopy conductance and evapotranspiration. The nitrogen cycle has been significantly altered by human activity (Vitousek *et al.* 1997). The manufacture of N-based fertilizers and increased cultivation of legumes has resulted in a doubling of the amount of N<sub>2</sub> fixed (Vitousek *et al.* 1997). Fossil fuel combustion has also resulted in enhanced N deposition to terrestrial ecosystems. Furthermore, studies are starting to show that under CO<sub>2</sub> enrichment, N<sub>2</sub>-fixation in association with herbaceous and woody plants increases (Montealegre *et al.* 2000; Hungate *et al.* 1999). It is well established that photosynthetic capacity and productivity are increased under conditions of higher N availability. Few studies, however, have addressed how canopy conductance and evapotranspiration will be affected. In swards of *Danthonia richardsonii*, water use and LAI both increased with increasing N application (Lutze & Gifford 1998). However, the effect was dampened when combined with exposure to above-ambient levels of CO<sub>2</sub> (Lutze & Gifford 1998), suggesting that increased N availability may cancel the antitranspirant effect of elevated CO<sub>2</sub> in herbaceous plants. In a greenhouse study of wheat, increased concentration of root zone NO<sub>3</sub><sup>-</sup> had no statistically significant effect on transpiration, while elevated CO<sub>2</sub> reduced water vapor loss by over 30% (Smart *et al.* 1998). While perturbations in atmospheric chemistry and biogeochemical cycles have the potential to alter the proper functioning of ecosystems, the combined effects of

different global changes are difficult to predict and may have contrasting interactions in different ecosystems.

#### *1.5 Eddy covariance*

Before one can assess the influence that global change might have on the hydrologic balance of various ecosystems, one must first examine how environmental and biological factors control gas exchange between the biosphere and atmosphere at a range of temporal scales (daily, seasonally and interannually). The development of eddy covariance (Baldocchi *et al.* 1998), a micrometeorological method of measuring gas exchange, is making such "ecosystem-level" measurements of gas and energy exchange possible. Additionally, the technique makes measurements at a time scale necessary to examine climatic and biological mechanisms responsible for variation in flux rates (Wilson & Baldocchi 2000). To date, forests have received the most attention by investigators, however, the need to make measurements in a variety of ecosystems and climatic regimes was emphasized in 1996 during an International Geosphere-Biosphere Program workshop (Aubinet *et al.* 2000).

#### *1.6 Grasslands*

Approximately one third of the Earth's land surface is covered by grasslands (Thinkquest 2000). There are two main divisions of grasslands: temperate and tropical (University of California, Berkeley 2000). Grasslands tend to be associated with continental climates (large seasonal temperature extremes between winter and summer with low precipitation) (University of California, Berkeley 2000). There are five major grassland areas: the pampa of South America, the veldt of South Africa, the steppes of Central Eurasia, the Australian grasslands and the prairies of the Great Plains of North

America (Freeman 2000). The Great Plains (Figure 2) cover roughly 2.6 million square kilometers (Ostlie *et al.* 1997). It is the second largest eco-zone in North America (Ostlie *et al.* 1997). It extends from the boreal forest of Canada's prairie provinces south to the semi-deserts of the U.S. and Mexico (Great Plains Homepage 2000; Ostlie *et al.* 1997) and ranges longitudinally from the Rocky Mountain's foothills to the Eastern deciduous forest. The grassland in this study, west of Lethbridge, Alberta, Canada, is located in the northern portion of the Great Plains and is described as moist mixed grassland (Figure 3). The mean annual temperature of this ecoregion is about 2.5 °C (Environment Canada 2000). The mean summer temperature is 15.5 °C while the mean temperature during winter is -11 °C (Environment Canada 2000). The mean annual precipitation ranges from 350 to 400 mm (Environment Canada 2000). The site represents part of the 22.6 million hectares of unimproved or native grassland in Canada (Agriculture and Agri-food Canada (AAFC) 1998).

#### 1.7 Study Objectives

The objectives of this study were two-fold: 1) to document how evapotranspiration and energy partitioning vary seasonally and interannually in a moist mixed grassland, and 2) to examine how environmental and physiological factors influence evapotranspiration. More specifically, the following questions are addressed:

- a) How do evapotranspiration rate and surface energy balance vary seasonally and interannually?
- b) What are the ecological and physiological processes that control canopy conductance and water loss in this ecosystem?

- c) Is the grassland canopy well-coupled to the atmosphere thereby enabling physiological control of transpiration to be a stronger determinant of water vapor fluxes than radiation input?
- d) Is there a balance between the inputs and outputs of water in this ecosystem, and if not, what accounts for the difference in the ecosystem water budget?

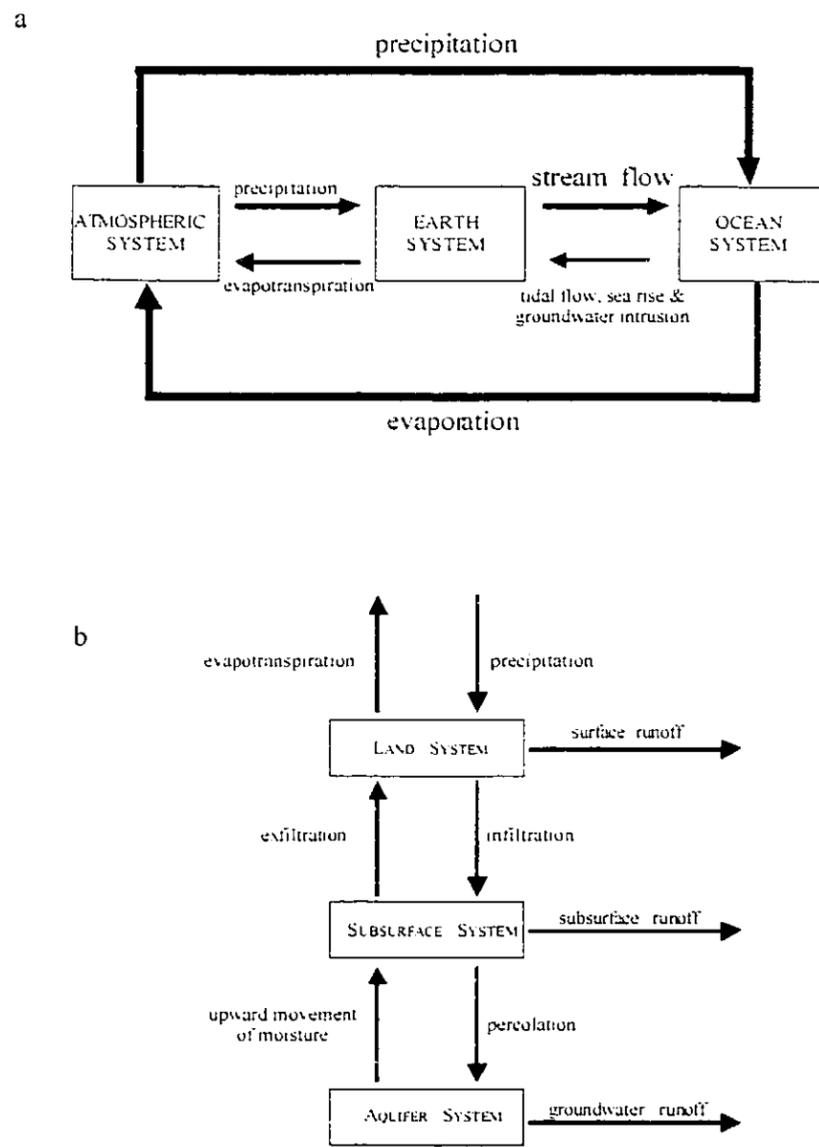


Figure 1. Simplified schematics of the hydrologic cycle: a) global; b) terrestrial (Singh 1992).

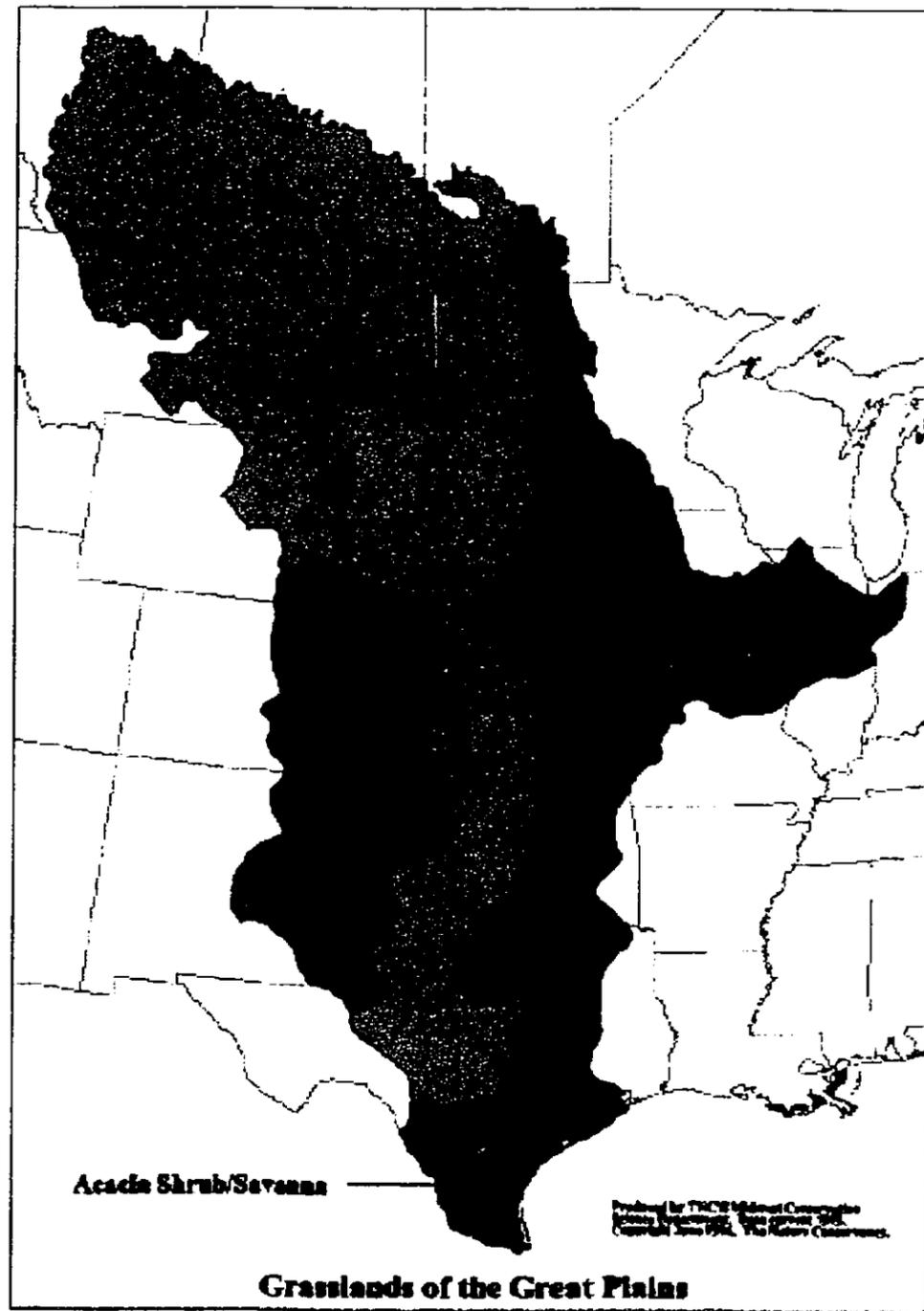


Figure 2. A map of the North American Great Plains (Ostlie *et al.* 1997).

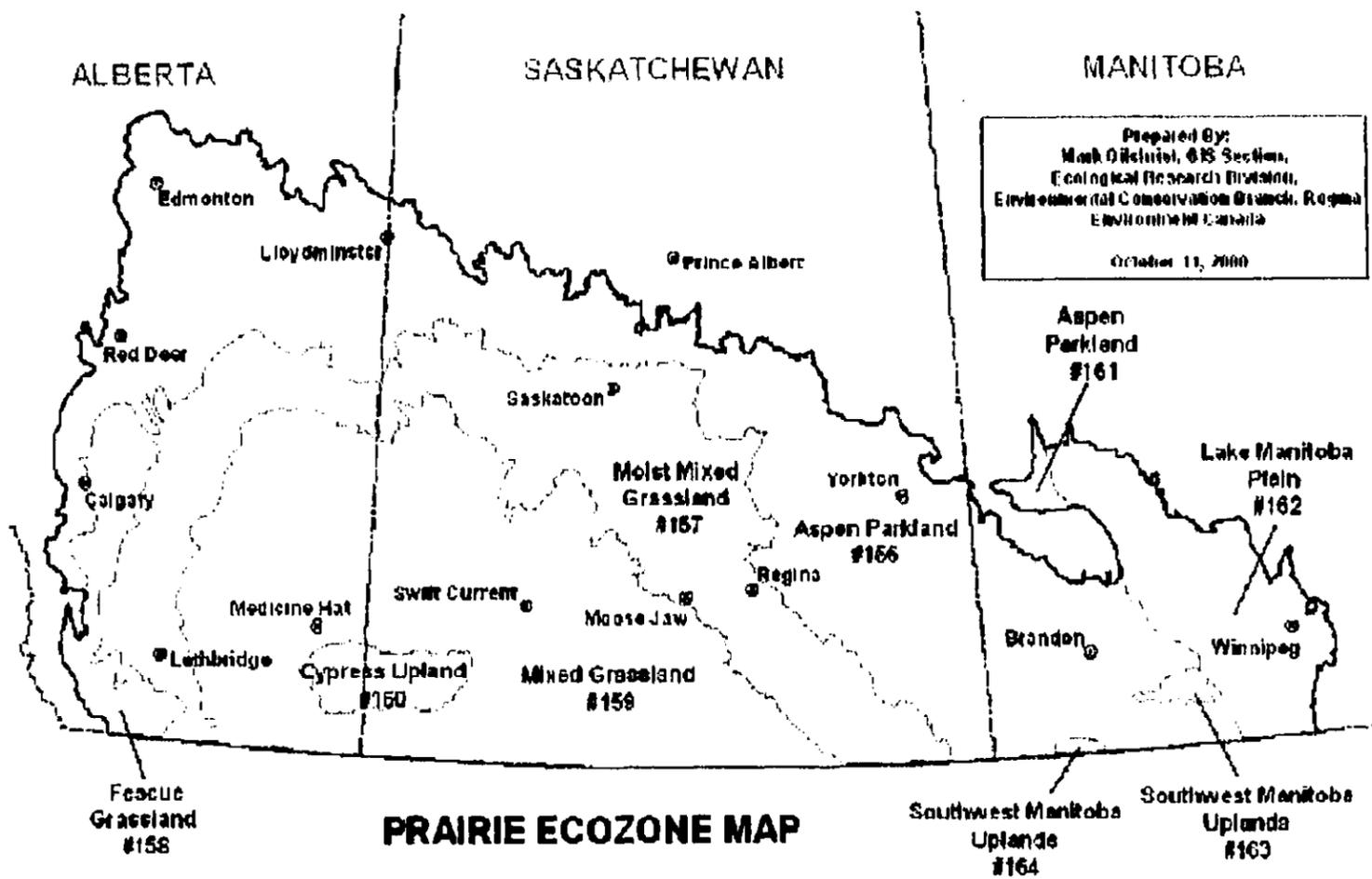


Figure 3. A map of the various prairie ecozones in Canada (Environment Canada 2000)

## 2. Materials and Methods

### 2.1 Study area

The study site, established in June 1998, is located just west of the city limits of Lethbridge, Alberta, Canada (Lat. N:49.43°; Long. W:112.56°, 951 m above sea level). The physiography of the area is described as morainal and gently undulating (Kocaoglu & Pettapiece 1980). The study area is relatively flat with slopes equal to or less than 2 per cent grade. The soils are Orthic Dark-Brown Chernozems (Agriculture Canada 1987) with a clay loam to clay texture and a bulk density of 1.24 g cm<sup>-3</sup>. The dominant grasses are *Agropyron dasystachyum* and *A. smithii* while the dominant forb is an invader species, *Tragopogon dubius* (Carlson 2001). Other major plant species represented to a lesser extent include: *Vicia americana*, *Artemesia frigida*, *Stipa comata*, *Stipa viridula* and *Bouteloua gracilis* (Carlson 2001). The climate is best described as moderately cool and semi-arid. Mean (1908-1999) daily temperatures for January and July are -8.6 °C and 18.0 °C, respectively (AAFC 2000). The mean annual precipitation (1908-1999) for the area is 401.5 mm with 32% falling in May and June (AAFC 2000). During the summer months, average pan evaporation (Class A) exceeds the average precipitation by at least 200% and often 300% (AAFC 2000). The mean annual wind velocity (1928-1999) is 18.8 km hr<sup>-1</sup> out of the west (AAFC 2000).

### 2.2 Continuous measurements

The eddy covariance technique was used to measure the fluxes of water vapor, CO<sub>2</sub> and sensible heat on a continuous basis (Baldocchi, Hicks & Meyers 1988). A three dimensional ultrasonic anemometer (Solent 1012, Gill Instruments Ltd., Lymington, England) was mounted on a one meter boom placed on top of a 6 meter tower and

oriented in the prevalent wind direction (west) to measure wind speed, direction and air temperature. The mid-point of the sonic head was located approximately 6 meters above ground. Changes in water vapor concentration (along with CO<sub>2</sub>) were measured with a closed path, fast response infrared gas analyzer (LI-6262, LI-COR Inc., Lincoln, Nebraska) housed in an insulated instrument hut. Air for H<sub>2</sub>O and CO<sub>2</sub> analysis was drawn through 15 m of 3 mm inner diameter tubing (Bev-A-Line IV Tubing, LABCOR, Concord, Ontario) by a diaphragm pump (Capex V2X 12 VDC, Charles Austen Pumps Ltd., Surrey, England) placed downstream from the infrared gas analyzer (IRGA). The flow rate was 8 L min<sup>-1</sup>. Calibration of the IRGA was done at regular intervals for humidity and CO<sub>2</sub> using a portable dew point generator (LI-610, LI-COR Inc, Lincoln, Nebraska) and a CO<sub>2</sub> cylinder referenced to WHMO CO<sub>2</sub> standard at CMDL NOAA, respectively. Fluxes of water vapor, CO<sub>2</sub>, and sensible heat were computed using the University of Edinburgh EdiSol software (Moncrieff *et al.* 1997). Fluxes (F) were calculated as the product of the mean covariance of vertical wind speed fluctuations (w') and the scalar fluctuations of interest e.g. H<sub>2</sub>O (q') and the density of dry air (ρ<sub>a</sub>).

$$F = \rho_a \overline{w'q'} \quad (\text{Equation 1})$$

where w is the vertical wind speed (m s<sup>-1</sup>), q is water vapor concentration (mmol mol<sup>-1</sup>), and primes denote deviations from a mean. For example,

$$w' = w - \overline{w} \quad (\text{Equation 2})$$

$$q' = q - \overline{q} \quad (\text{Equation 3})$$

The running mean (overbars) was based on a 300 second time constant. Due to the time taken by the air sample to travel to the IRGA, calculations were stored in a buffer until an

appropriate time lag could be determined. The time lag was selected by maximizing the correlation between  $w'$  and  $q'$  after the 30 minute sampling period (Moncrieff *et al.* 1997). The resultant mean fluxes and various wind components (e.g. wind speed and direction) were recorded by a computer every half hour. Transfers of mass and energy to the atmosphere are represented by positive values while negative values signify atmospheric losses.

Along with the eddy flux instrumentation, a weather station was established to provide meteorological data. Unless otherwise stated, instruments are located on the 6 meter tower. Two soil heat flux transducers (REBS HFT-3.1, Radiation Energy Balance System, Seattle, Washington), placed about 2 cm below the soil surface, were used to calculate a mean soil heat flux. Net radiation was measured by a net radiometer (REBS Q\*7.1, Radiation Energy Balance System, Seattle, Washington) mounted on a nearby 3 m tower. A LI-COR Quantum Sensor (LI-190SA, LIC-COR, Lincoln, Nebraska), used to measure photosynthetically active radiation (PAR), was also located on the 3 m tower. Relative humidity and air temperature were measured using a shielded thermistor and a capacitance humidity probe (207 Temperature and Relative Humidity Probe, Campbell Scientific Ltd., Edmonton, Alberta) placed 2 meters above the ground. Additional air temperatures at 1 and 5 meter heights were measured with aspirated thermocouples (Model ASPTC Aspirated Shield with Fine Wire Thermocouple, Campbell Scientific Ltd., Edmonton, Alberta). Copper-constantan thermocouples were used to measure soil temperatures at soil depths of 2, 4, 8 and 16 cm. Total precipitation was recorded in 15 minute intervals by a tipping bucket rain gauge (TE525, Texas Electronics, Inc., Dallas, Texas). With the exception of the rain gauge, all data were recorded as half-hourly

averages. All data were recorded on dataloggers (CR10 and CR10X, Campbell Scientific Ltd., Edmonton, Alberta).

### *2.3 Periodic measurements*

Over the course of the growing season, several periodic measurements were taken. Replicate samples (n=6) for leaf area (and biomass) were collected by clipping vegetation within a 20 cm by 50 cm quadrat. Sampling in 1998 was done on a stratified random basis. In 1999 quadrats were placed in randomly selected 1 x 1.5 m sub-plots located within two larger 20 x 20 m plots, one northeast and the other southeast of the instrument hut. A leaf area meter (LI-3100 Area Meter, LI-COR, Lincoln, Nebraska) was used to determine the total leaf area for all green tissue that was rooted within the metal frame of the quadrat. The total leaf area data were expressed per ground area as a leaf area index ( $\text{m}^2 \text{m}^{-2}$ ). The samples were dried in an oven at 60°C for at least 24 hours and then weighed (Mettler PJ400, Greifensee, Switzerland) for above ground biomass. The biomass samples were freeze-dried using liquid N then ground. Coarse grinding was done with a mortar and pestle. When samples were sufficiently large, a fine grind was performed using a coffee bean grinder to produce a homogeneous sample. An elemental analyzer (NC2500, CE Instruments, ThermoQuest Italia, Milan Italy) determined the total N and C content of the biomass samples as a percent on a weight basis. An average N and C content of all six replicates was calculated for each sample period. Soil samples (0-10 cm depth for 1998 and 0-15 cm for 1999) were collected on a weekly basis using a soil corer. Six replicates were selected using a stratified random method. The known volume of soil was weighed (Mettler PJ400, Greifensee, Switzerland), dried at 105°C for

24 hours, and then re-weighed. The gravimetric moisture content was converted into volumetric measurement using the mean bulk density of the soil.

#### 2.4 Evaluation of eddy covariance

The eddy covariance data were screened for anomalous values outside the range normally encountered. Possible causes for such values can be sensor malfunction due to interference from hoarfrost and birds. To assess the accuracy of the eddy covariance measurements, half-hourly values were used to calculate a surface energy budget

$$R_n = H + \lambda E + G \quad (\text{Equation 4})$$

where  $R_n$  is net radiation,  $H$  is sensible heat flux,  $\lambda E$  is latent heat flux, and  $G$  is soil heat flux. This test for energy closure is particularly robust as  $R_n$  and  $G$  were measured independently of the eddy covariance system. Figure 4 shows the energy balance as  $(H + \lambda E)$  plotted against  $(R_n - G)$  for the 1998 and 1999 growing seasons (JD 171-273 and JD 124-273 respectively). There was a strong correlation between the sensible and latent heat flux with net radiation minus soil heat flux for both years (1998, adjusted  $r^2=0.95$ ; 1999, adjusted  $r^2 = 0.88$ ). According to the slope of the relationships (0.89 for 1998; 0.81 for 1999), eddy covariance underestimated fluxes of sensible and/or latent heat. This has also been reported in other grassland studies using eddy covariance (Twine *et al.* 2000). The results of the energy balance closure, however, were within the range reported and accepted by other eddy covariance investigators (Aubinet *et al.* 2000).

## 2.5 *Gap filling*

Missing data can be problematic when trying to calculate daily, seasonal and annual sums of total evapotranspiration. Breaks in data collection can be attributed to IRGA maintenance and calibration, power outages, and pump failure. The removal of anomalous values also resulted in gaps. Several strategies were used to compensate for missing data. Half hour breaks were filled by calculating an average of the values immediately before and after the data break. In cases in which there appeared to be a linear relationship between water vapor flux and some variable (explained below), linear interpolation was used ( $r^2$  of 0.35 to 0.98). If short breaks occurred before or after midday (when peak values would normally be observed), time of day was used as a predictor variable for water vapor flux. In many other cases, PAR values and a linear relationship between PAR and water flux were used to estimate missing evapotranspiration values. When PAR and other meteorological data were unavailable, a mean diurnal course was used to fill the missing time periods. The size of the data set used to develop these relationships was dependent on the size of the gap. For example, data for 3 days before and after the break were used when the gaps were 5 days or less. In the case of a 32 day data gap occurring in the winter, 4 weeks of data before and after were used. Missing or rejected data occurred for a total of 16% of all possible 30 minute time periods during the study.

## 2.6 Calculating canopy conductance and omega

Mean canopy conductance ( $g_{\text{canopy}}$ ) was calculated using the inverted Penman-Monteith formula:

$$\frac{1}{g_{\text{canopy}}} = \frac{r_a}{\gamma} \left( \frac{\Delta(R_n - G) + \rho_a c_p \left( \frac{e_s - e_a}{r_a} \right)}{\lambda E} - \Delta \right) - r_a \quad (\text{Equation 5})$$

where

$r_a$	aerodynamic resistance ( $\text{s m}^{-1}$ )
$\gamma$	psychrometric constant ( $\text{Pa K}^{-1}$ )
$\Delta$	rate of change of saturation vapor pressure with temperature ( $\text{Pa K}^{-1}$ )
$\rho_a$	density of dry air ( $\text{g m}^{-3}$ )
$c_p$	the specific heat of air ( $\text{J g}^{-1} \text{K}^{-1}$ )
$e_s$	saturation vapor pressure (Pa)
$e_a$	actual vapor pressure of the ambient air (Pa)
$R_n$	net radiation ( $\text{W m}^{-2}$ )
$G$	soil heat flux ( $\text{W m}^{-2}$ )
$\lambda E$	latent heat flux ( $\text{W m}^{-2}$ )

The air temperature at 1 meter was used as the temperature reference.

Aerodynamic resistance ( $r_a$ ) was calculated using the following formulas

$$r_a = r_e + r_b \quad (\text{Equation 6})$$

$$r_a = \frac{u}{u_*^2} + 6.2 u_*^{-0.67} \quad (\text{Equation 7})$$

where

$r_e$	eddy diffusive aerodynamic resistance
$r_b$	boundary layer resistance for mass transfer
$u$	the average wind speed ( $\text{m s}^{-1}$ )
$u_*$	friction velocity ( $\text{m s}^{-1}$ )

Conductances in  $\text{m s}^{-1}$  were converted to  $\text{mmol m}^{-2} \text{s}^{-1}$  using the Ideal Gas Law.

Omega, the dimensionless decoupling coefficient, was subsequently calculated according to Jarvis & McNaughton (1986) as

$$\Omega_{\text{canopy}} = \frac{(\varepsilon + 1)}{\left( \varepsilon + 1 + \frac{g_{\text{aerodynamic}}}{g_{\text{canopy}}} \right)} \quad (\text{Equation 8})$$

where  $g_{\text{aerodynamic}} = 1/\tau_a$

and  $\varepsilon = s / \gamma$

$s$  the rate of change of saturation vapor pressure with temperature (kPa K<sup>-1</sup>)  
 $\gamma$  psychrometric constant (kPa K<sup>-1</sup>)

Because a wet canopy can lead to inaccurate calculations for canopy conductance (and the decoupling coefficient), days with recorded amounts of precipitation and suspected dewfall were excluded from these calculations. Data recorded during periods of low water vapor fluxes (< 0.05 mmol m<sup>-2</sup> s<sup>-1</sup>) and inadequate turbulence ( $u < 0.10$ ), which can also lead to unrealistic values (either underestimating or overestimating of dry canopy conductance), were excluded from calculations of  $g_{\text{canopy}}$ . Due to the dependence of stomatal conductance on PAR, periods with mean PAR less 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  were also removed.

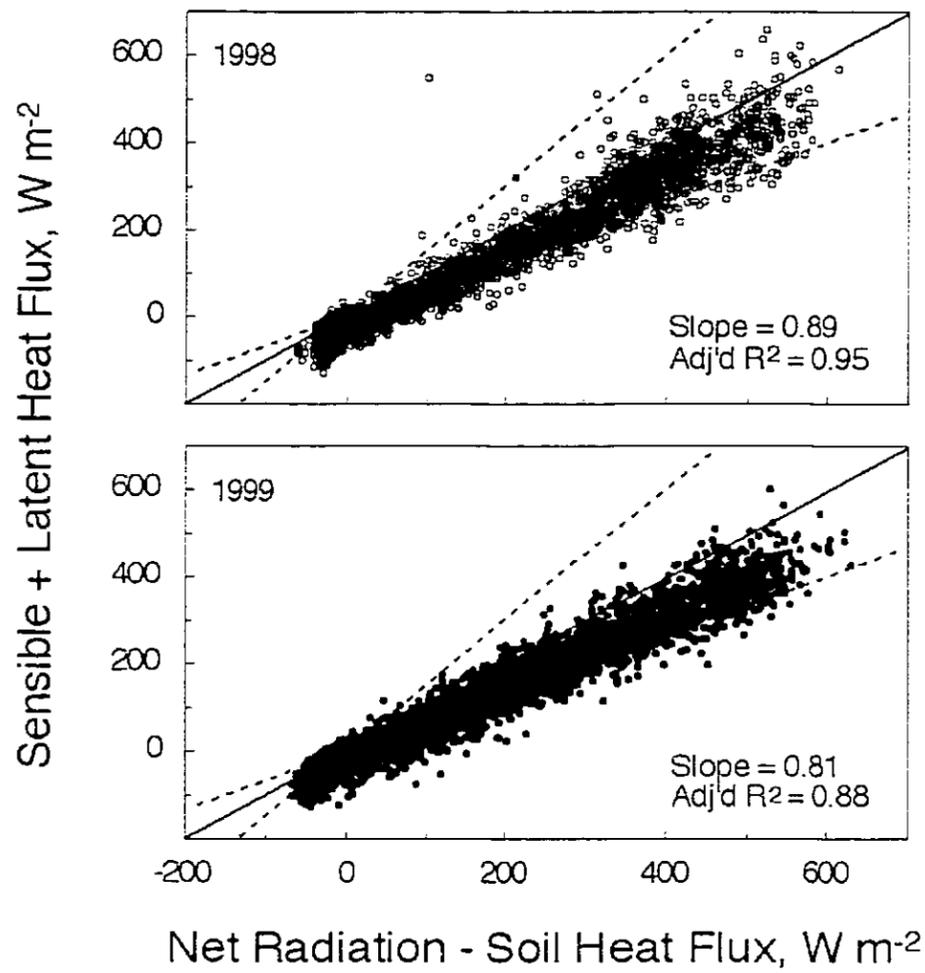


Figure 4. Energy balance for 1998 (days 170-273; n=4506) and 1999 (Days 124-273; n=6203). Fluxes of sensible and latent heat are plotted against net radiation less soil heat flux. Points are half hour intervals. The solid lines represent a 1:1 relationship while the dashed lines represent a 20% deviation from the 1:1 relationship.

### **3. Results**

#### *3.1 Comparison of environmental conditions*

Variation in weather can be a cause of seasonal and interannual variability in ecosystem water flux measurements. Weather conditions for the 1998 and 1999 growing seasons are summarized in Table 1 (AAFC 2000). Daily minimum temperatures increased from May to August on average by at least 5 °C. August was the hottest month with mean daily maximum temperatures of 28.8 °C and 25.9 °C for 1998 and 1999 respectively. August was also the driest month receiving less than 40 mm of precipitation. The highest total solar radiation occurred in July. Class A pan evaporation was also highest in July, 319.6 mm and 305.7 mm, for 1998 and 1999 respectively. Overall, the 1998 growing season tended to be slightly warmer than the 1999 growing season. With the exception of June, total solar radiation and pan evaporation in the 1998 growing season were also greater than those recorded in 1999. Although 1998 was warmer than 1999, wind speed was higher in 1999. Overall, the greatest difference between the two growing seasons was the amount of precipitation received. June 1998 had more than double the amount of rain received in June 1999. A monthly climatic moisture index (CMI) was calculated using meteorological data from the Lethbridge Research Centre. As defined by Hogg (1994), the climatic moisture index is the monthly precipitation minus the monthly potential evapotranspiration (as calculated by the Jensen-Haise method) with units in centimeters. From the CMI values it is evident that the 1999 growing season was more typical of the average conditions for the Lethbridge area (Figure 5). In contrast, June 1998 was much wetter and May, July and August 1998 were drier and/or hotter than average.

### *3.2 Variation in leaf area index (LAI)*

Differences in leaf area index can also account for variation in evapotranspiration within and between growing seasons. In general, LAI steadily increased to a maximum as the growing season progressed, after which a steady decline in LAI was observed (Figure 6a). The maximum LAI recorded in 1999 was approximately 60% of the maximum recorded in 1998. Additionally, the peak value was observed approximately 2 weeks earlier in 1999 than in 1998. This difference was likely due to differences in soil water availability. Soil moisture was high at the start of the growing season but rapidly declined as rain events became less frequent and air temperatures increased (Figure 6b). The extra precipitation received in June 1998 led to a prolonged period of high soil moisture which extended into the first week of July (Day 188) during which peak LAI values were recorded. The decrease in LAI for both years, however, was correlated to a decline in moisture content of the soil. Though summer rainstorms provided water input to the soil in both years, there were no rain events large enough to restore soil moisture to the levels seen in the early spring. With high evaporative demand, soil water availability quickly returned to pre-storm levels.

### *3.3 Seasonal and interannual variation in evapotranspiration*

Under ideal conditions of high soil moisture, sunny conditions, and high LAI, the daily pattern of evapotranspiration could be described as symmetric with peak values corresponding to the pattern of net radiation rather than VPD (Figures 7, 8, and 9). In 1998, there was a strong seasonal decrease in evapotranspiration (Figure 7). Mean maximum rates of evapotranspiration in 1998 declined from  $6.5 \text{ mmol m}^{-2} \text{ s}^{-1}$  during July 18-24 (Days 199-205) to  $2.5 \text{ mmol m}^{-2} \text{ s}^{-1}$  for August 22-29 (Days 234-240). There was

also a slight shift in the occurrence of peak rates of evapotranspiration to earlier in the day. Additionally, the diurnal pattern of water vapor flux became asymmetrical with much lower rates of water flux in the afternoon. The seasonal change in water vapor flux was less apparent in 1999. Nevertheless, peak evapotranspiration rates in 1999 declined by 50% from July 18-24 to August 22-29. Rates of water vapor flux were much higher in 1998 than in 1999. The maximum rate of evapotranspiration in 1998 was  $10.4 \text{ mmol m}^{-2} \text{ s}^{-1}$  (Day 188), but the peak rate of water loss in 1999 was only  $5.6 \text{ mmol m}^{-2} \text{ s}^{-1}$  (Day 152).

#### *3.4 Sensible and latent heat fluxes*

The sensible and latent heat flux components of the energy budget were very different for the 1998 and 1999 growing seasons (Figure 10). In 1998, latent heat flux was much higher than sensible heat flux during days 199-205, with maximum latent heat fluxes of over  $300 \text{ W m}^{-2}$ . During days 220-226, latent and sensible heat fluxes were approximately equal at  $200 \text{ W m}^{-2}$ , but by Days 234-240 sensible heat flux became the dominant component of the surface energy budget, with maximum fluxes of  $250 \text{ W m}^{-2}$ . Peak values of latent heat flux decreased to less than  $100 \text{ W m}^{-2}$ . In contrast, sensible heat flux dominated the energy budget during the entire 1999 growing season, with peak sensible heat fluxes over  $300 \text{ W m}^{-2}$ . Latent heat fluxes in 1999 rarely exceeded  $100 \text{ W m}^{-2}$ . The seasonal and interannual differences in energy budget were further emphasized by differences in Bowen Ratio ( $\beta$ ), the ratio of sensible to latent heat flux. Mean midday values of Bowen Ratio in 1998 increased from 0.5 (Days 199-205) to over 2 (Days 234-240) (Figure 11). For the same time period during the 1999 growing season, Bowen Ratio increased from 2.5 to over 8.5.

### 3.5 Ecophysiological control of evapotranspiration

On a daily basis, dry canopy conductance ( $g_{\text{canopy}}$ ) was highest in the early part of the morning but then tended to decrease with increasing VPD (Figures 12 and 13). The negative relationship between  $g_{\text{canopy}}$  and VPD was evident in both years (Figure 14), though it was not as strong in 1999 owing to the overall lower canopy conductance when periods of peak evapotranspiration were compared (Days 173-211 in 1998 and Days 142-169,  $\text{PAR} > 1400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). On a seasonal basis, a decrease in canopy conductance was also observed in the mean diurnal pattern with the mean values calculated for a 2 week period (Figure 12). In 1998 mean maximum canopy conductance declined from  $190 \text{ mmol m}^{-2} \text{ s}^{-1}$  during days 192-205, to  $110 \text{ mmol m}^{-2} \text{ s}^{-1}$  for days 220-234 (Figure 12). Canopy conductance values in 1999 similarly decreased from  $100 \text{ mmol m}^{-2} \text{ s}^{-1}$  to under  $50 \text{ mmol m}^{-2} \text{ s}^{-1}$  for Days 150-163 and 220-234, respectively. Canopy conductance was much lower in 1999 than in 1998 (Figures 12, 14 and 15). Average canopy conductance calculated on a daily basis was as high as  $200 \text{ mmol m}^{-2} \text{ s}^{-1}$  in 1998 but seldom exceeded  $100 \text{ mmol m}^{-2} \text{ s}^{-1}$  in 1999 (Figure 15). Figure 15 also emphasizes the sharp seasonal decline in canopy conductance in 1998. In 1999, canopy conductance peaked around day 161, followed by a general decline after this date.

The seasonal changes in canopy conductance were related to changes in the physiological state of the plant community. Average daily canopy conductance was positively correlated with canopy nitrogen content and leaf area index (Figure 16a,b). It was also apparent that N content and LAI was much higher in 1998 than in 1999. There was also a positive relationship between canopy conductance and volumetric soil moisture (Figure 16c). Average daily canopy conductance was extremely low during

periods of low water availability. In 1998 when soil moisture was plentiful, daily canopy conductance was as much as 6 times higher.

A dimensionless decoupling coefficient,  $\Omega$ , has been proposed as a means to describe the sensitivity of water vapor flux to a change in canopy conductance (Jarvis 1985; Jarvis & McNaughton 1986). The value of  $\Omega$  ranges from 0 to 1. Zero represents complete stomatal control while 1 indicates total reliance on net radiation in determining water vapor flux. The decoupling coefficient was calculated to determine the relative importance of net radiation and canopy conductance to evapotranspiration rates on a daily, seasonal, and yearly basis. On a daily basis,  $\Omega$  was highest in the morning, then declined to a minimum in the evening (Figure 17) suggesting stronger stomatal control of water loss by plants as the day progressed. Diurnal changes in  $\Omega$ , though present, were much smaller in 1999. A downward seasonal shift in the decoupling coefficient was also observed in both years. In 1998, peak  $\Omega$  values decreased from over 0.35 during days 206-219 to 0.25 during days 220-234. Omega during days 150-163 in 1999 was as high as 0.20, but decreased to below 0.1 during days 220-234. The seasonal variation in the decoupling coefficient was even more striking when the average omega value was plotted as a function of day of year (Figure 18). It also demonstrated that canopy conductance constrained evapotranspiration more in 1999 with omega values consistently below 0.2. In 1998, however,  $\Omega$  did not reach 0.2 until much later in the growing season. There was a positive relationship between omega and evapotranspiration (Figure 19). In other words, when the decoupling coefficient was high and evapotranspiration was limited by net radiation, evapotranspiration rates were higher than times when the canopy was well coupled to the atmosphere (low  $\Omega$  values) and canopy conductance constrained water

vapor flux. There was also a positive relationship between evapotranspiration and net radiation with higher net radiation inputs increasing daily rates of evapotranspiration and thus accounting for some of the day to day variation in water vapor flux.

Evapotranspiration also tended to increase with increasing canopy conductance up to an average canopy conductance of about  $125 \text{ mmol m}^{-2} \text{ s}^{-1}$  after which daily evapotranspiration in 1998 did not increase further. Likewise, evapotranspiration increased with canopy N content, LAI and soil moisture (Figure 19) to a maximum value of  $4.5 \text{ mm day}^{-1}$  in 1998 (under dry canopy conditions). Evapotranspiration rates were much lower in 1999 and showed more variation in the relationships with N content, LAI and soil moisture.

### *3.6 Annual sum of evapotranspiration and the ecosystem water budget*

Total evapotranspiration was calculated on a daily basis (Figure 20). The daily, seasonal and interannual variation in evapotranspiration was very apparent in Figure 20. In 1998, the maximum amount of water loss via evapotranspiration was 4.5 mm, recorded on day 173. In 1999, the greatest rate of daily evapotranspiration was 2.2 mm, which was recorded on day 168. From day 171 to 243 during 1998, the evapotranspirational losses totaled 189 mm of water. Evapotranspiration was much lower in the following growing season despite a longer sampling period. From days 91-243, 134 mm of water evapotranspired in 1999. Between growing seasons [Days 244 (1998) to Day 90 (1999)] the quantity of water lost amounted to less than 40 mm. Calculated rates of evapotranspiration during this fall and winter period were less than  $0.5 \text{ mm day}^{-1}$ . From July 1, 1998 to August 31, 1999 there was a slight positive balance in the water budget of this northern grassland: a total of 332 mm of water was lost via evapotranspiration while

precipitation inputs totaled 346 mm (Figure 21). Because we were not equipped to measure precipitation in the form of snow, precipitation values from the Lethbridge Research Centre were used for the period extending from October to May. Annual evapotranspiration was 300 mm (JD 171 in 1998 to JD 170 in 1999).

Table 1. Comparison of 1998 and 1999 growing seasons in terms of various climatic variables

Variable	Year	May	June	July	August
Temperature, °C					
Mean Daily Maximum	1998	21.3	19.7	27.4	28.8
	1999	17.0	21.0	23.5	25.9
Mean Daily Minimum	1998	6.1	9.1	13.1	11.5
	1999	3.5	8.1	9.3	11.6
Daily Mean	1998	13.7	14.4	20.3	20.2
	1999	10.3	14.6	16.4	18.8
Mean Daily Wind Speed, km h <sup>-1</sup>	1998	16.0	15.0	12.7	12.5
	1999	18.4	17.0	16.4	13.5
Total Solar Radiation, MJ m <sup>-2</sup> month <sup>-1</sup>	1998	707.2	588.1	780.8	691.8
	1999	665.7	654.2	714.9	608.9
Total Pan Evaporation, mm month <sup>-1</sup>	1998	213.2	190.5	319.6	309.5
	1999	249.4	264.4	305.7	264.6
Total Precipitation, mm month <sup>-1</sup>	1998	53.4	148.4	57.4	36.1
	1999	58.3	65.1	64.2	39.3

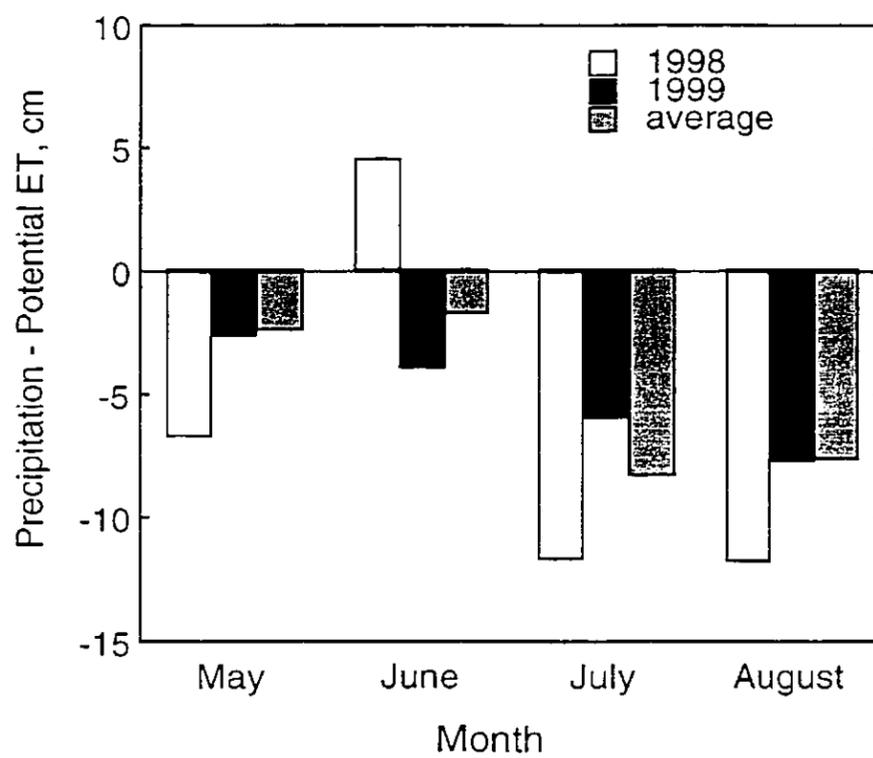


Figure 5. The Climatic Moisture Index for Lethbridge, Alberta, Canada, 1998 vs. 1999 with the 10 year average (1989-1999).

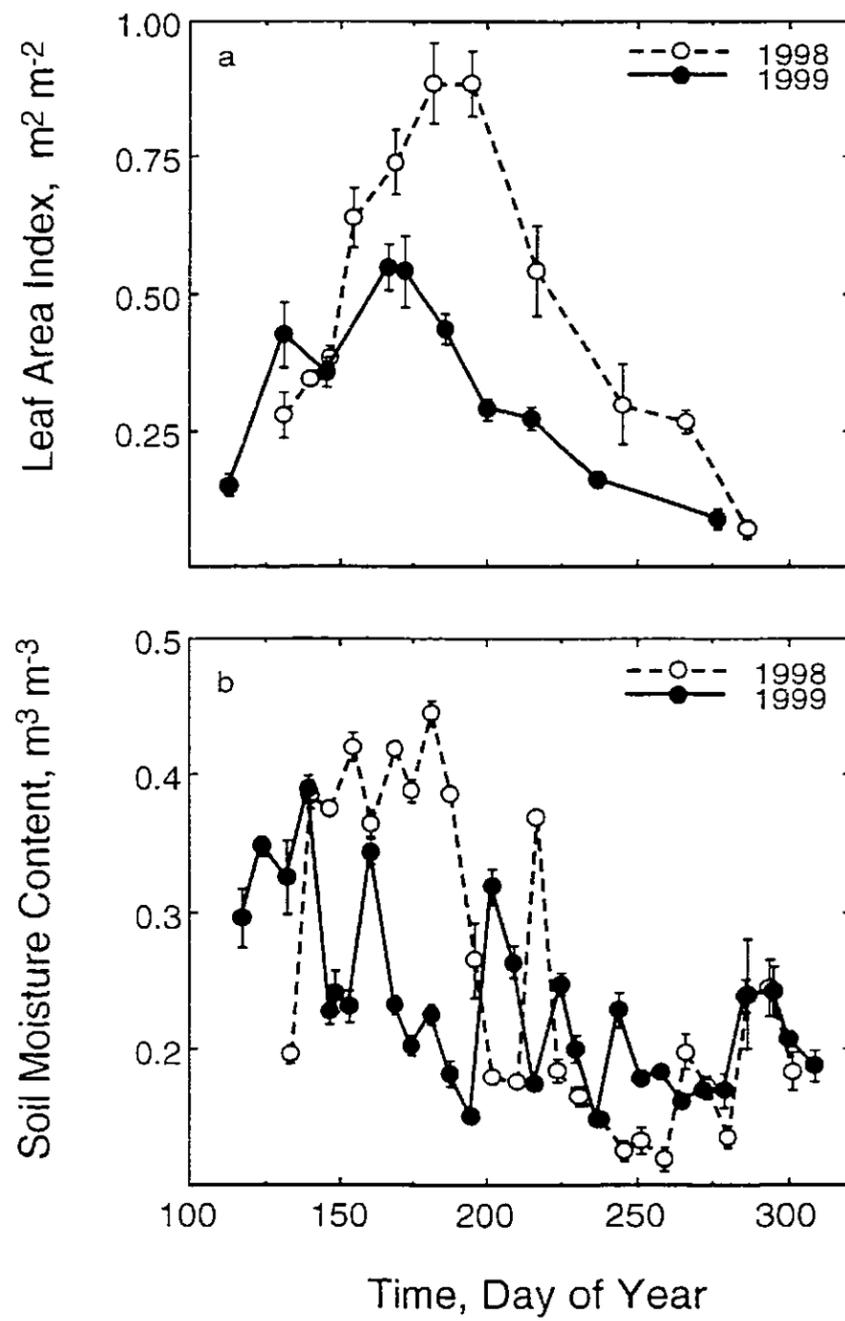


Figure 6. Leaf area index (a) and soil water availability (b) as a function of Julian Day for 1998 and 1999. Y error bars represent the standard error of the mean.

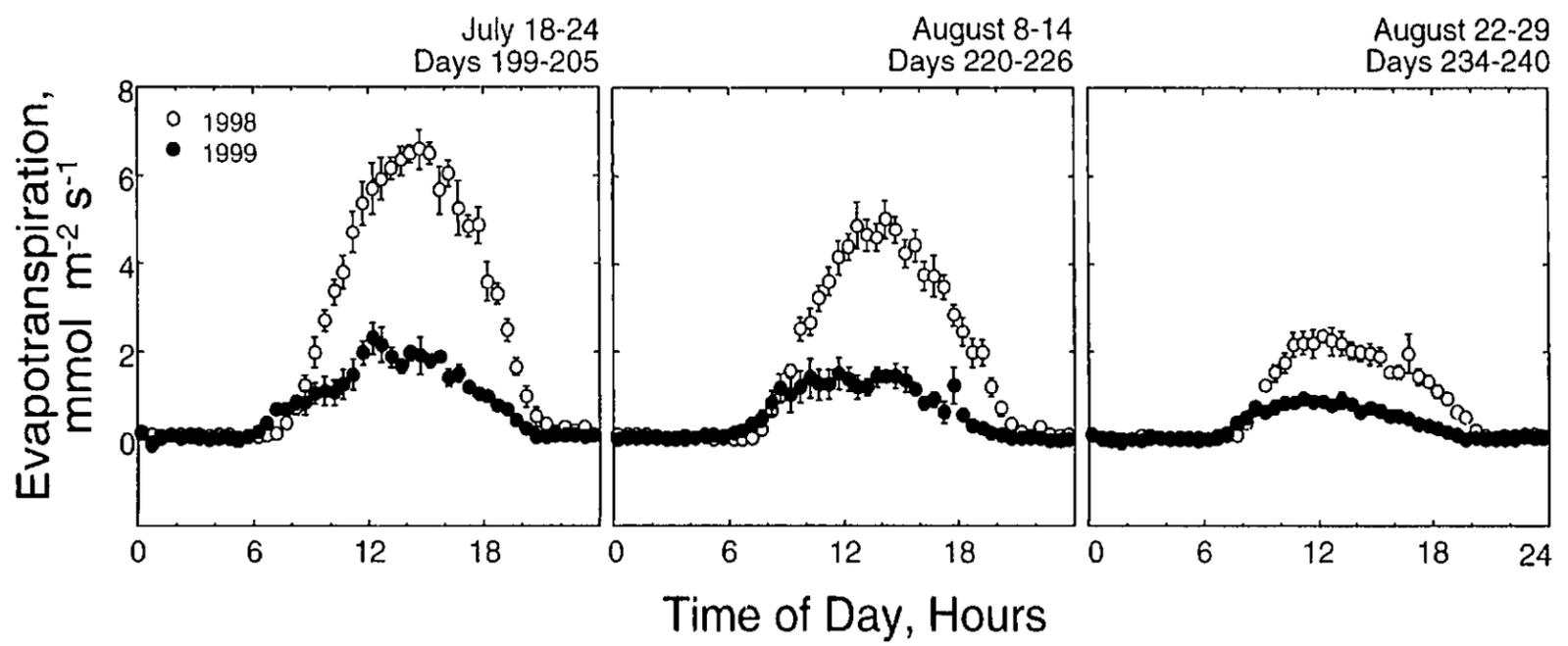


Figure 7. Mean diurnal course of evapotranspiration for days 199-205, 220-226 and 234-240; 1998 (open circles) vs. 1999 (closed circles). Error bars denote standard error of the mean.

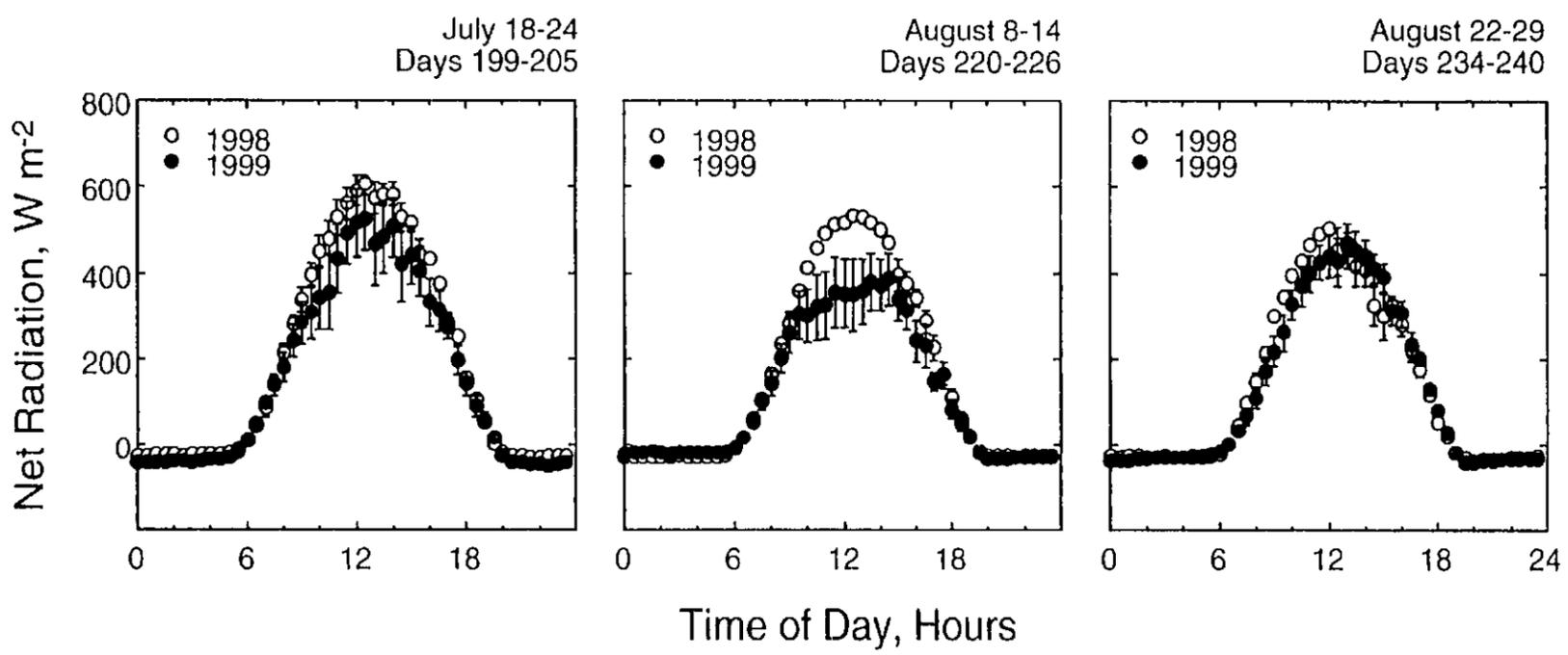


Figure 8. Mean diurnal course of net radiation for days 199-205, 220-226 and 234-240; 1998 vs. 1999. Y error bars represent the standard error of the mean.

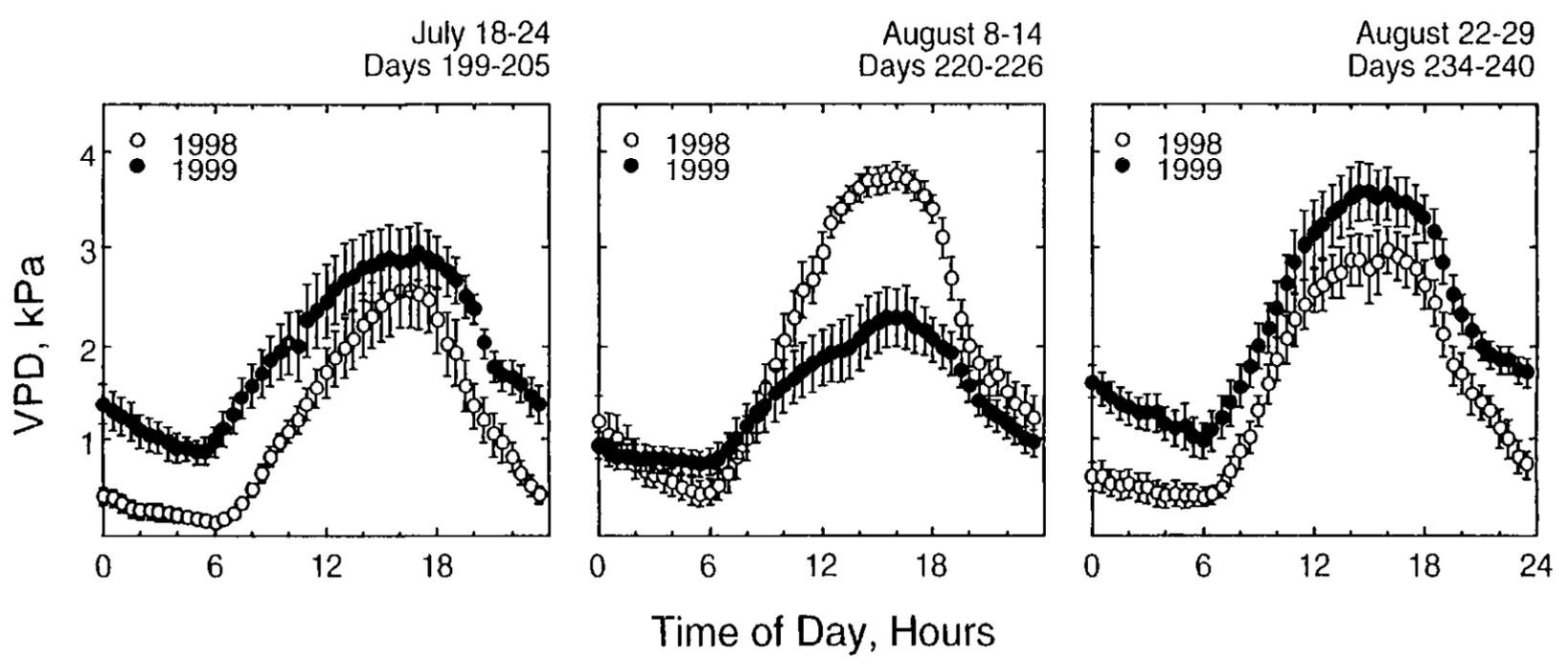


Figure 9. Mean diurnal course of VPD; 1998 (open circles) vs. 1999 (closed circles). Y error bars represent the standard error of the mean.

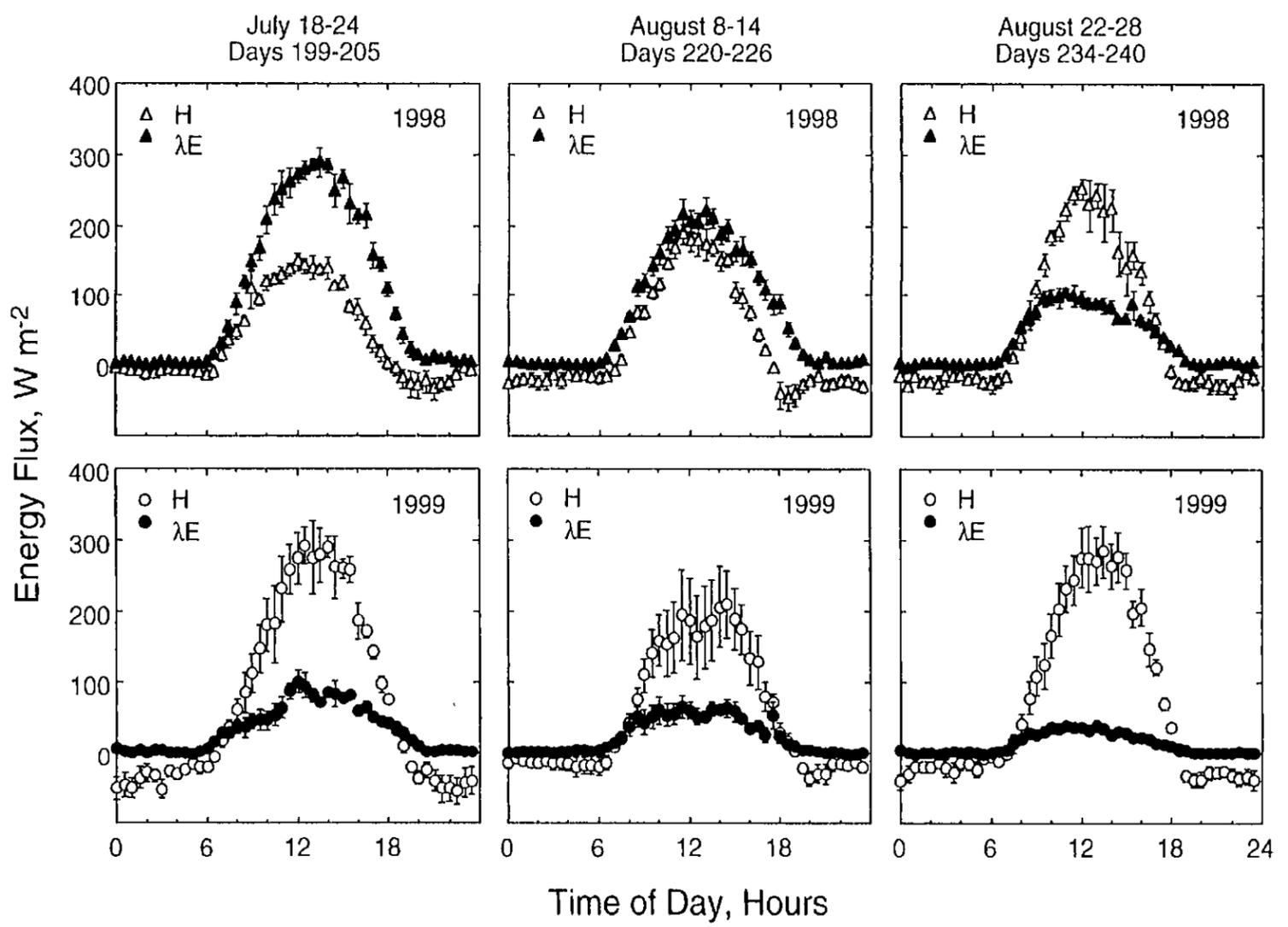


Figure 10. Comparison of mean sensible and latent heat fluxes for 1998 (triangles) and 1999 (circles). Y error bars represent standard error of the mean.

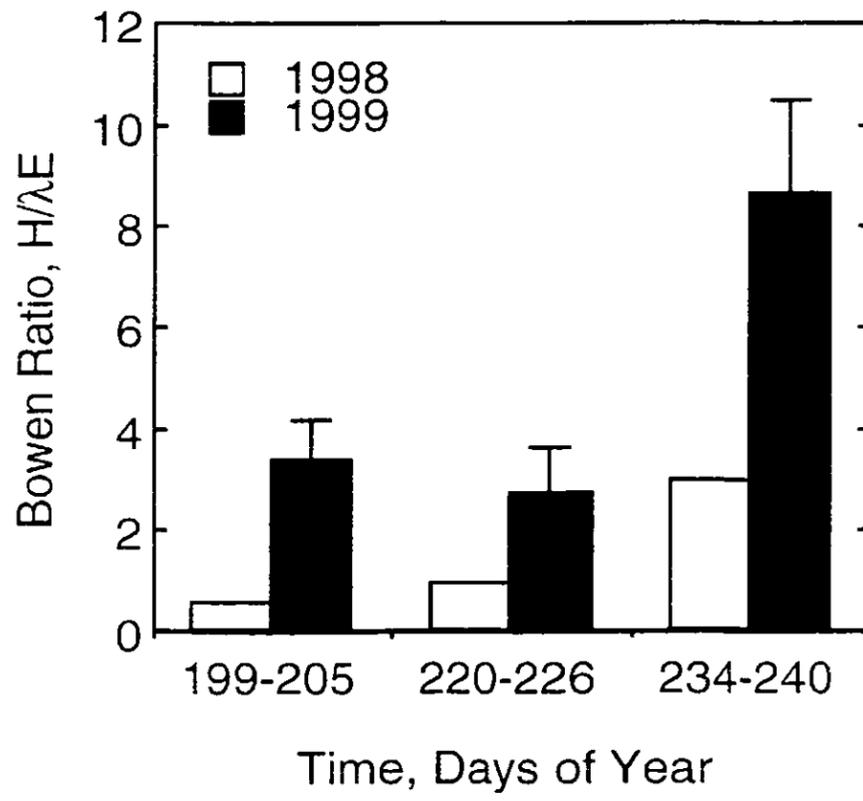


Figure 11. Mean midday Bowen ratios ( $H/\lambda E$ ) for 1998 & 1999. Y error bars represent standard error of the mean.

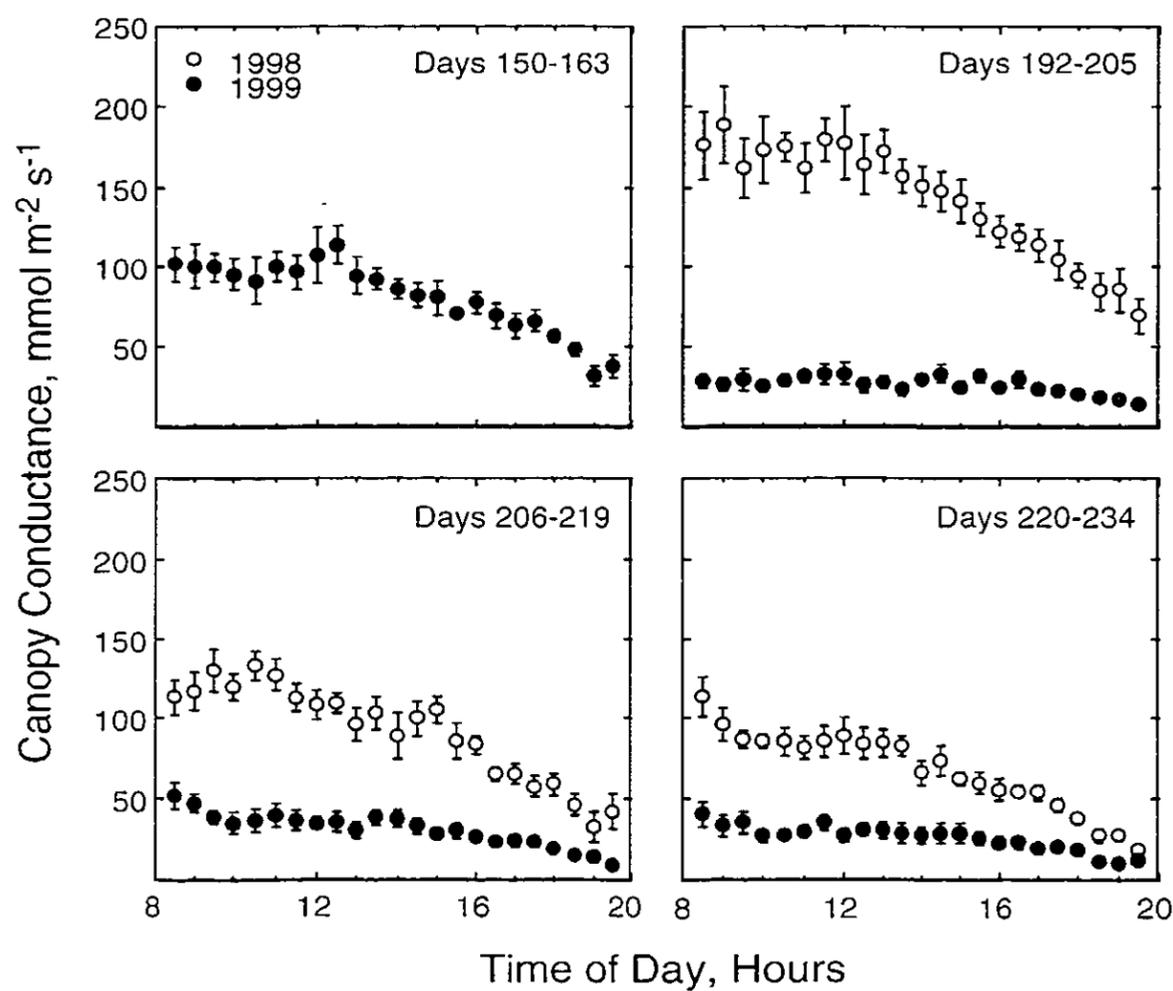


Figure 12. Mean diurnal course of dry canopy conductance to water vapor (2 week averages) for 1998 (open symbols) and 1999 (closed symbols). Y error bars denote standard error of the mean

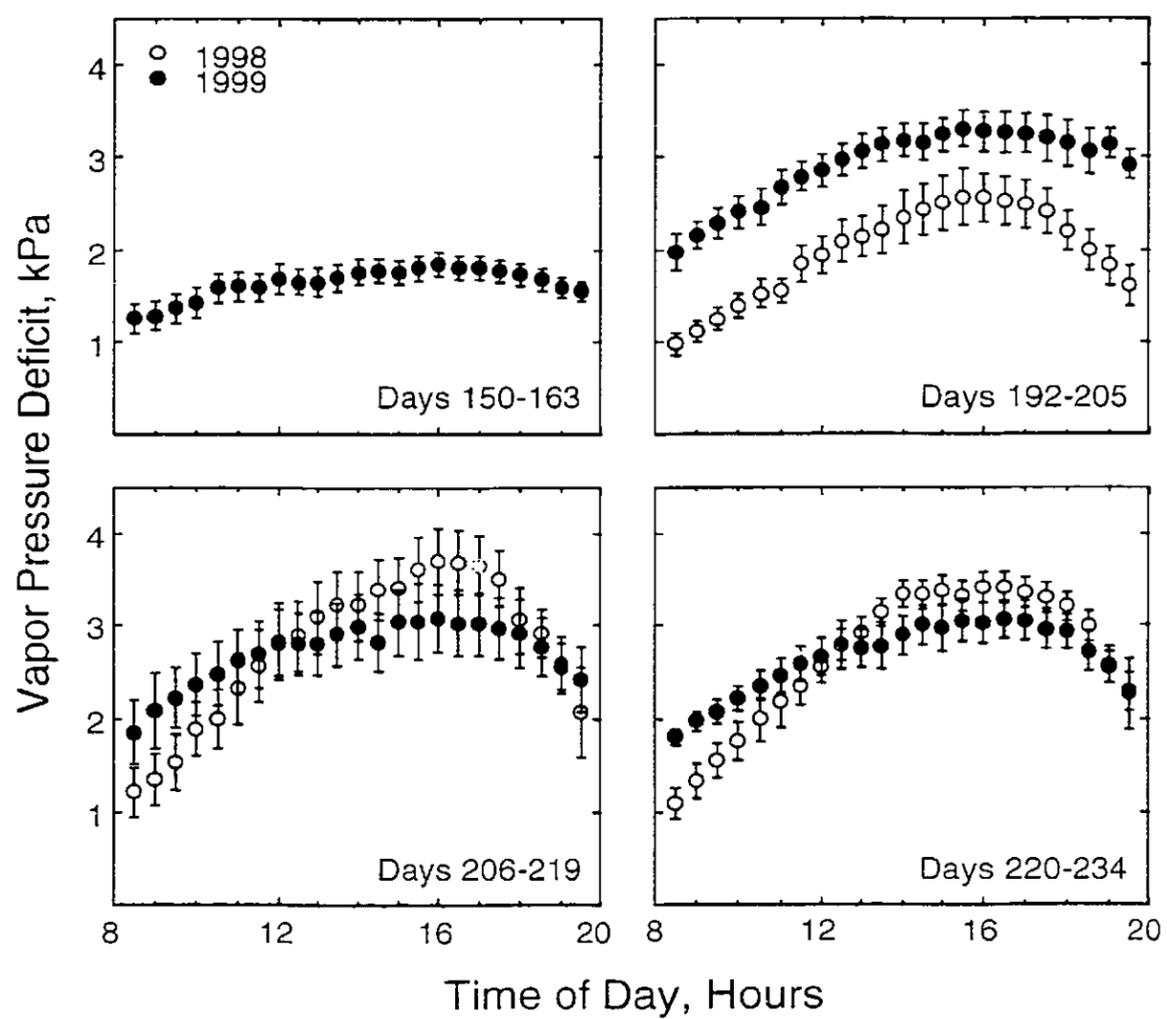


Figure 13. Mean diurnal course of VPD corresponding to calculations of  $g_{canopy}$  under dry conditions for 1998 and 1999 (open and closed symbols respectively). Standard error of the mean is denoted by Y error bars.

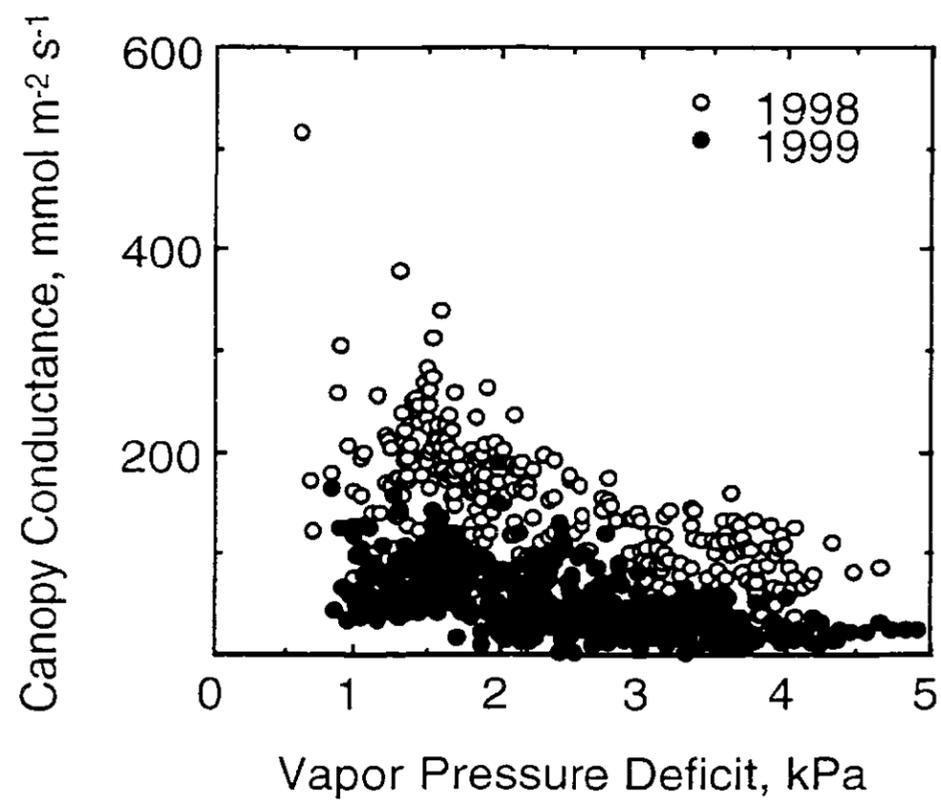


Figure 14. Canopy conductance as a function of VPD for 1998 (Days 173-243) and 1999 (Days 124-243) under conditions of high light ( $\text{PAR} > 1400 \mu\text{mol m}^{-2} \text{s}^{-1}$ )

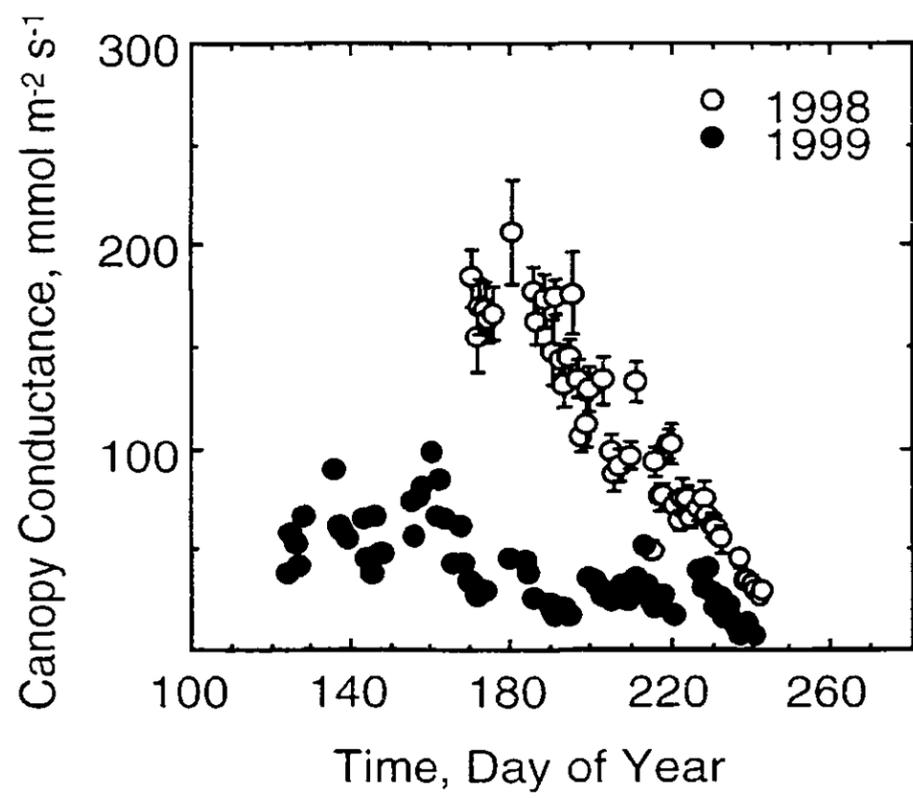


Figure 15. Comparison of average canopy conductance for 1998 (open symbols) and 1999 (closed symbols). Standard error of the mean is denoted by Y error bars.

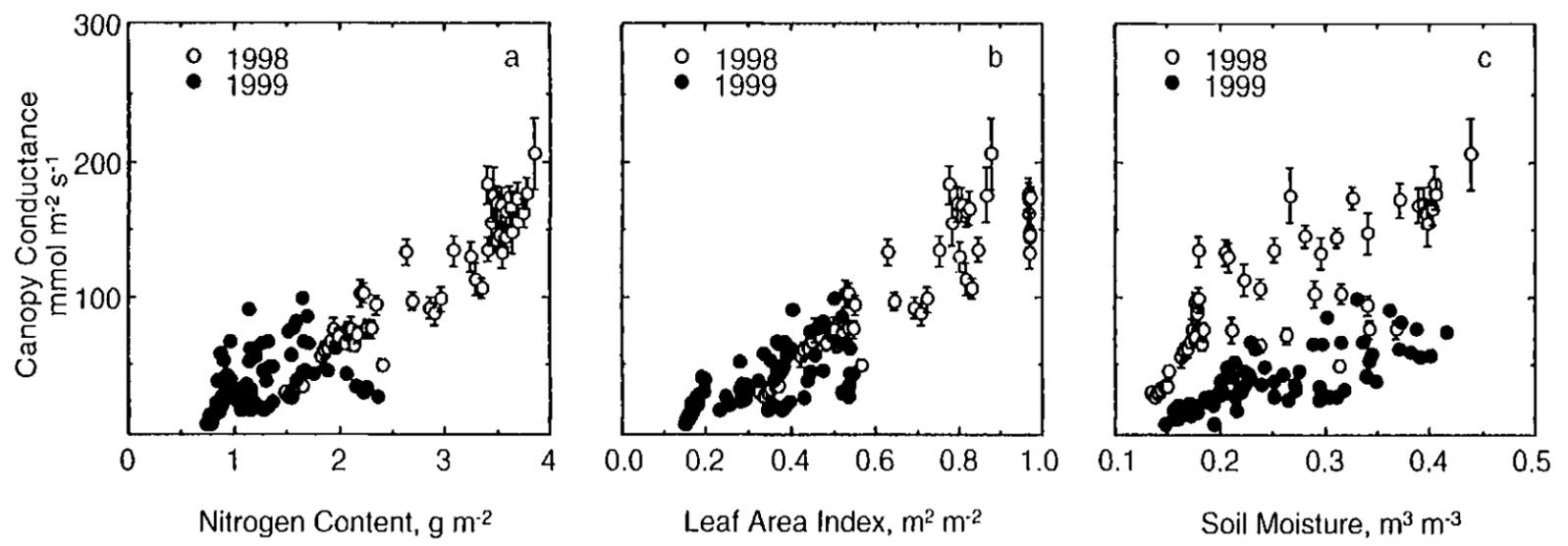


Figure 16. Average daily canopy conductance as a function of canopy N content (a), leaf area index (b) and soil moisture (c) for 1998 and 1999. Y error bars denote standard error of the mean.

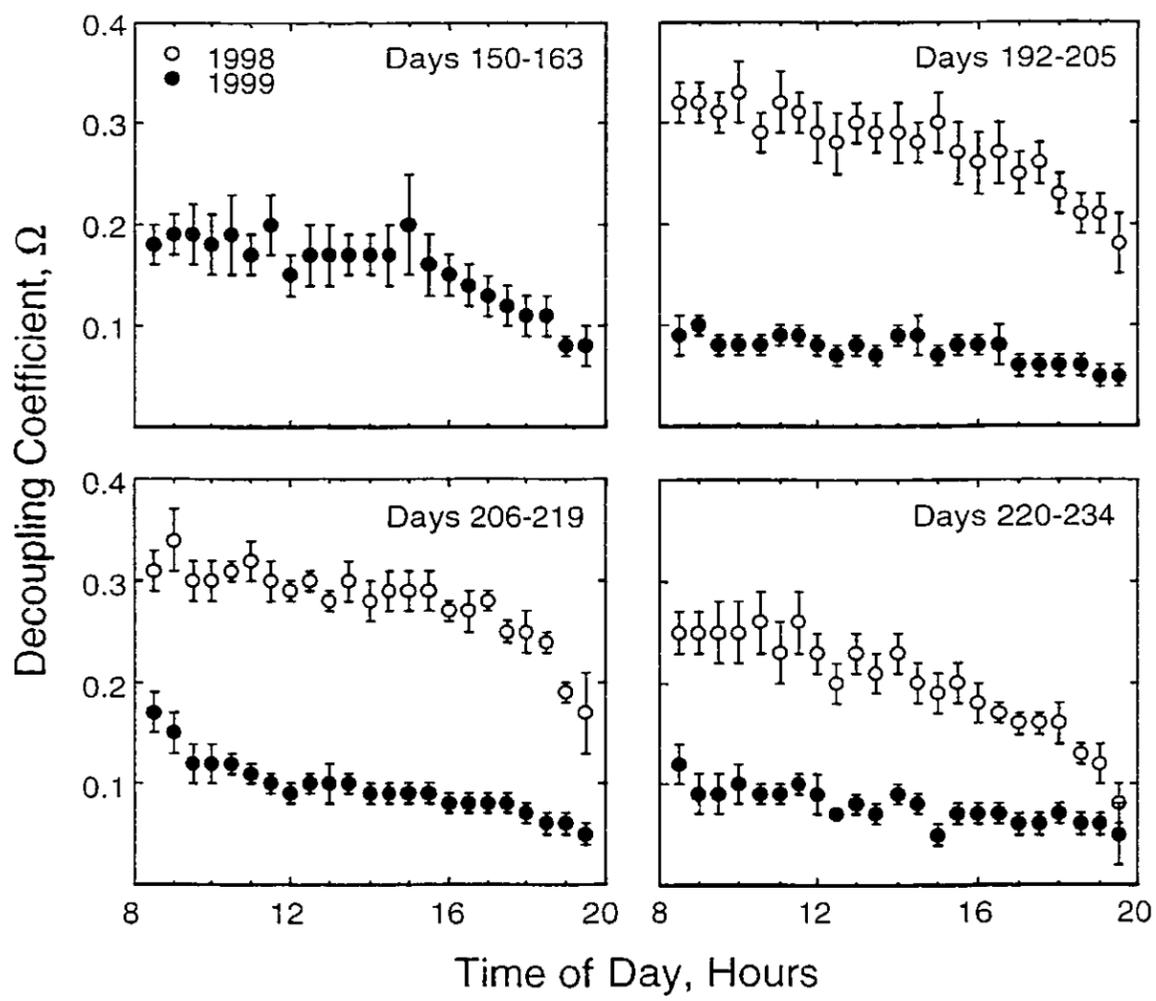


Figure 17. Mean diurnal course of the dimensionless decoupling coefficient,  $\Omega$ , for 1998 (open symbols) and 1999 (closed symbols). Y error bars represent standard error of the mean.

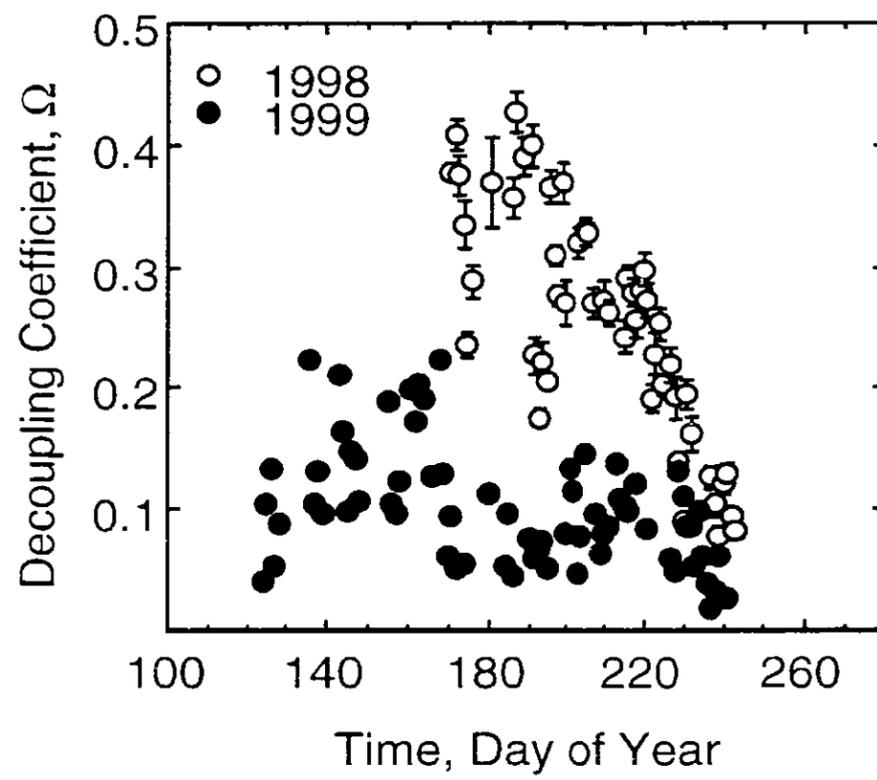


Figure 18. Average daily omega for 1998 (open symbols) and 1999 (closed symbols). Y error bars denote standard error of the mean.

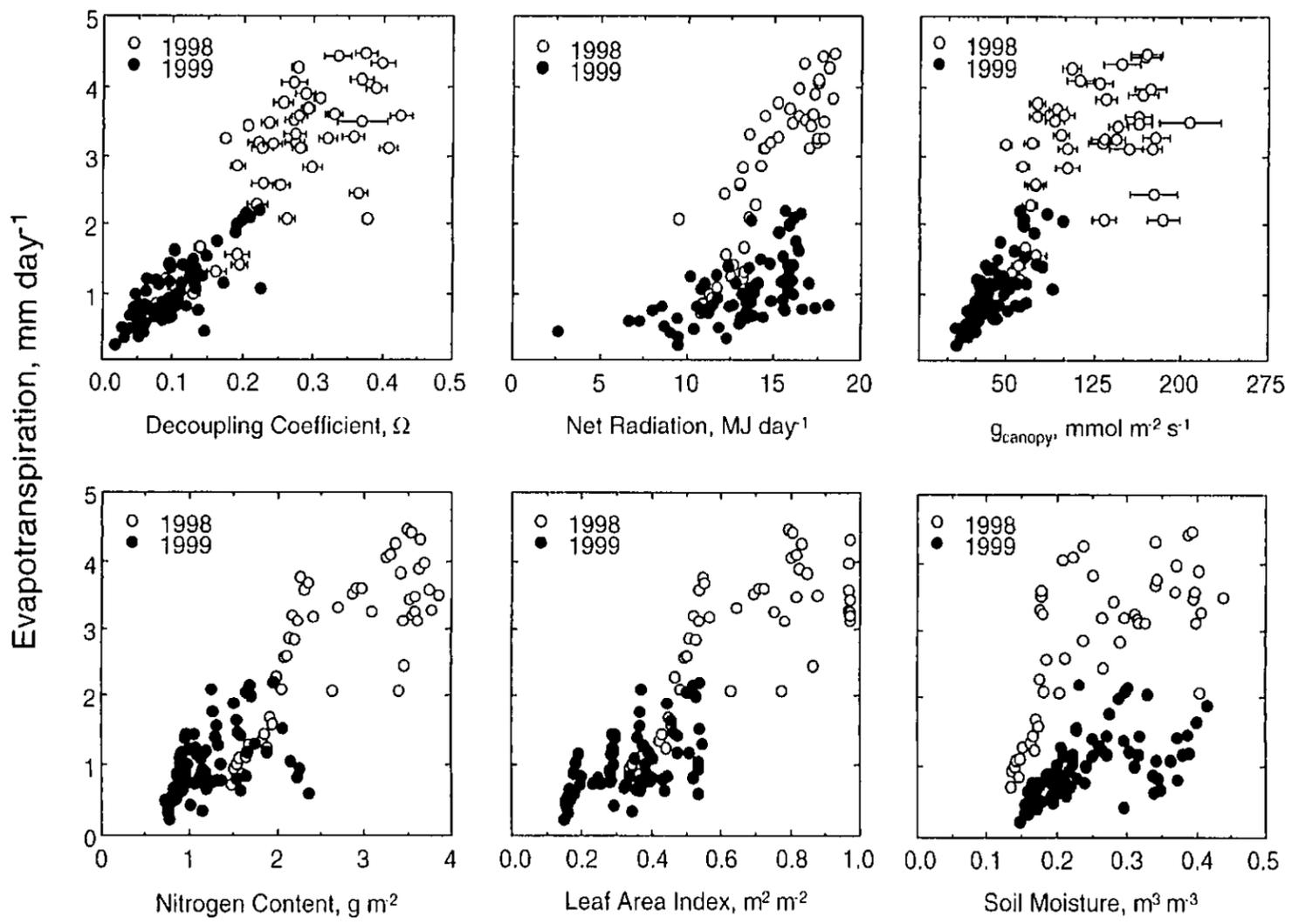


Figure 19. Daily evapotranspiration as a function of mean daily  $\Omega$ , net radiation, mean daily canopy conductance, canopy nitrogen, LAI and soil water availability for 1998 and 1999.

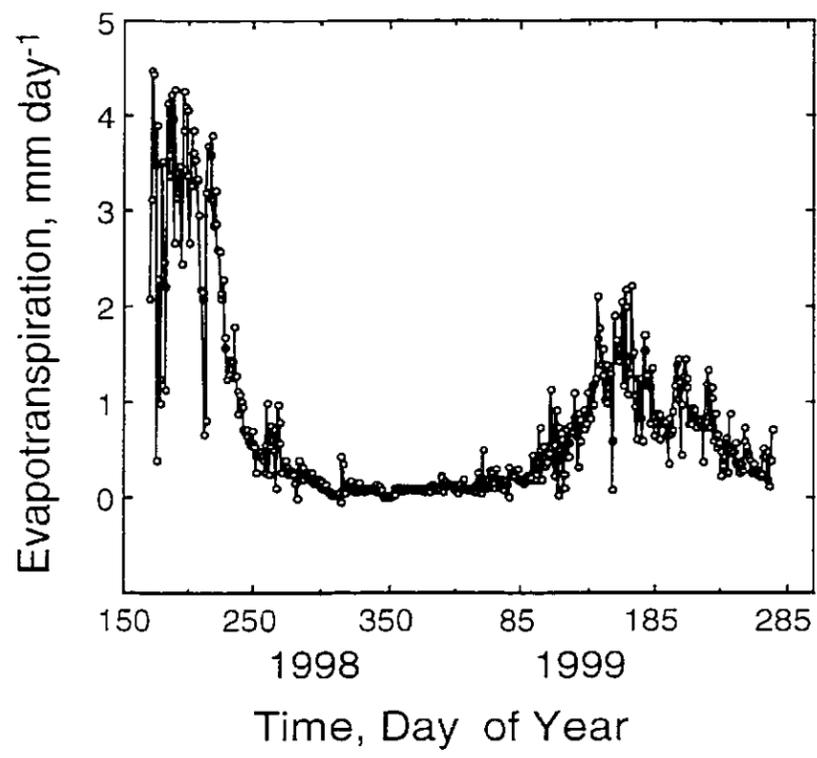


Figure 20. Daily, seasonal and interannual variation of daily total evapotranspiration in a moist temperate grassland located near Lethbridge, Alberta, Canada.

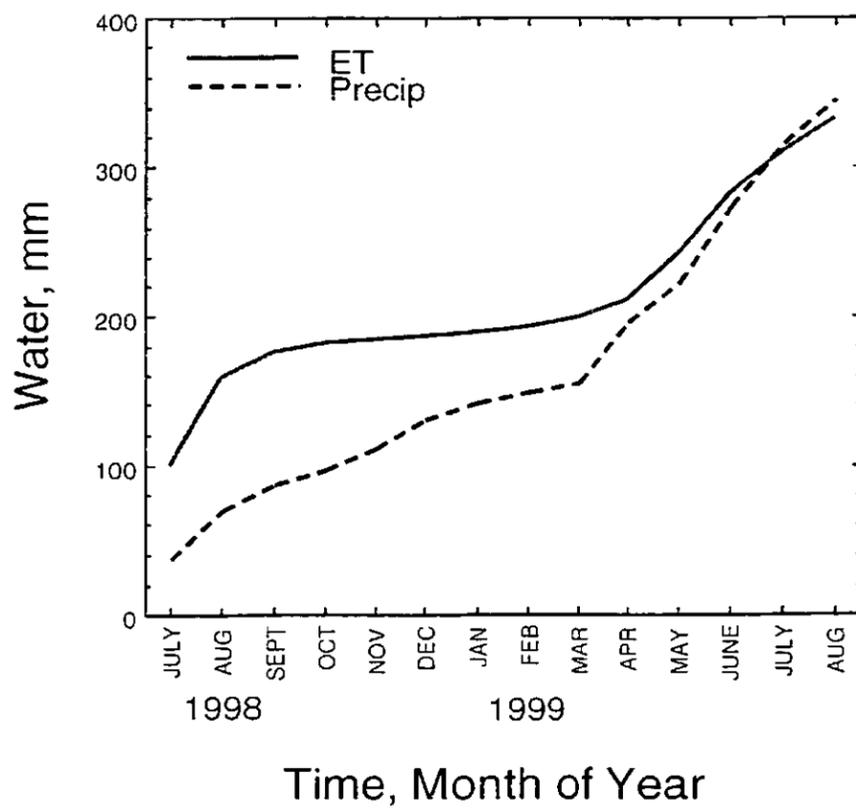


Figure 21. Cumulative evapotranspiration (solid line) and precipitation (dashed line) from July 1998 to August 1999.

#### 4. Discussion

##### *4.1 Seasonal and interannual variation of surface energy balance and evapotranspiration*

In temperate ecosystems one would expect strong seasonal changes in the surface energy balance. Seasonal changes in solar radiation alone would result in changes in the magnitude of sensible and latent heat fluxes. The partitioning of available radiation into sensible and latent heat flux is also strongly influenced by changes in vegetation characteristics. For example, latent heat flux can be influenced by the seasonal variation in leaf area index. In a temperate deciduous forest in Tennessee, there was a dramatic increase in latent heat flux and a decrease in sensible heat flux associated with leaf emergence (Wilson & Baldocchi 2000; Wilson, Hanson & Baldocchi 2000). Furthermore, the decrease in sensible heat flux occurred despite an increase in solar radiation (Wilson & Baldocchi 2000). This occurrence has been documented in other broad-leaved forests (Blanken *et al.* 1997) and in other ecosystem types as well. In a Japanese grassland, a decrease in the Bowen ratio ( $H/\lambda E$ ) corresponded to an increase in LAI (Saigusa, Oikawa & Liu 1998). In a northern boreal fen, the mean Bowen ratio decreased during leaf out and continued to decline as further development of the vegetation proceeded (Lafleur *et al.* 1997). In addition, once leaf senescence was initiated, a switch in the relative magnitude of latent and sensible heat flux occurred (Wilson & Baldocchi 2000; Blanken *et al.* 1997; Saigusa *et al.* 1998; Lafleur *et al.* 1997). For example, in a tallgrass prairie site, latent heat flux utilized approximately 60% of net radiation while sensible heat flux represented less than 20% of net radiation at midday early in the growing season (Verma, Kim & Clement 1992). However, sensible heat flux

became the dominant term in the energy balance once senescence began and green LAI started to decrease (Verma *et al.* 1992). During the autumnal transition in another tallgrass prairie study, Bowen ratio increased from 0.5 to over 4 (Ham & Knapp 1998). In a Californian serpentine grassland, the energy partitioning also shifted from  $\lambda E$  dominated to H dominated (Valentini, Gamon & Field 1995). Latent heat flux increased to a maximum in April representing 62% of the available energy but then declined to 16% of the available energy by mid May. Bowen ratio increased from 0.6 to 5.38 during the same time period (Valentini *et al.* 1995). While the decrease in LAI was attributable to mowing rather than senescence, the Bowen ratio increased accordingly in a Japanese grassland (Saigusa *et al.* 1998). The magnitude of these seasonal variations is likely to depend on how much and how rapidly leaf area index changes.

During the 1998 growing season, a shift in energy partitioning occurred in our moist mixed-grassland. During Days 199-205, sensible and latent heat fluxes were about 150 and 300  $W m^{-2}$  respectively, but by Days 234-240, maximum latent heat flux decreased to 100  $W m^{-2}$  and sensible heat flux increased to 280  $W m^{-2}$ . If there was a switch in the partitioning of energy in 1998, from H-dominated to  $\lambda E$ -dominated coinciding with increasing LAI, it was missed unfortunately as the eddy covariance measurements did not commence until day 170, well after LAI had started to increase. In 1999, however, sensible heat flux dominated the surface energy balance during the growing season, similar to the energy partitioning of a boreal jack pine forest (Baldocchi, Vogel & Hall 1997; McCaughey *et al.* 1997). Latent heat fluxes during the period of maximum evapotranspiration in 1999 were more similar to the fluxes seen during the dry period in 1998.

There were strong seasonal changes in the Bowen ratio observed during both years. Bowen ratio increased six-fold from (0.5 to 3.0) from Days 199-205 to Days 234-240 in 1998. In 1999, mean midday values of Bowen ratio were much higher, 3.5 and 8.5 for Days 199-205 and Days 234-240, respectively. In contrast Bowen ratios calculated for a moist-wet coastal tundra ecosystem changed little during the season (Vourlitis & Oechel 1997). The Bowen ratios for the boreal black spruce forest actually decreased from an average of 1.9 during May 24 to June 16 to an average of 1.3 for July 17 to August 8 (Jarvis *et al.* 1997). During Days 199-205 in 1998, Bowen ratios for this northern temperate grassland were similar to those seen in a broad-leaved temperate deciduous forest (Wilson *et al.* 2000). During Days 234-240 in 1998, Bowen ratios were similar to those observed in a maritime pine stand (Berbigier *et al.* 1996) and in a boreal black spruce forest (Jarvis *et al.* 1997). In contrast, the Bowen ratios calculated for midday periods late in the 1999 growing season approached those seen in desert ecosystems (Oke 1987). Interannual differences in the surface energy budget and energy partitioning can be explained partially by the differences in leaf area index between the two years. Peak LAI in 1998 was almost double that in 1999.

Of course, these interannual differences in the surface energy budget and energy partitioning are also related to interannual differences in evapotranspiration. The peak rate of evapotranspiration in 1998 ( $4.5 \text{ mm day}^{-1}$ ) was double that observed in 1999 ( $2.2 \text{ mm day}^{-1}$ ). In July 1998, a total of approximately 100 mm of water was evapotranspired, compared to a total of only 28 mm in July 1999. This large variation between years can be explained in part by the difference in the amount of precipitation received between the two growing seasons, 295 mm (1998) versus 227 mm (1999).

Wilson & Baldocchi (2000) similarly reported evapotranspiration was lower in a year with low precipitation. Increased precipitation, however, does not always translate into increased evapotranspiration. In a study of moist-wet coastal tundra, it was shown that the seasonal totals of evapotranspiration were relatively unchanged, approximately 120 mm for both years, despite the fact that 1995 received 1.3 times as much precipitation as 1994 (Vourlitis & Oechel 1997).

Seasonal changes in evapotranspiration are also related to variability in the surface energy balance and energy partitioning observed during a growing season. As water becomes limiting and rates of evapotranspiration decrease, more of the available energy is dissipated by sensible heat flux resulting in higher Bowen ratios. In the case of the tallgrass prairie study by Ham & Knapp (1998), the decline in evapotranspiration and the switch in energy partitioning were attributable solely to plant phenological changes. Drought stress was not a factor as soil water content was near field capacity for the duration of the study (Ham & Knapp 1998). In our northern mixed-grass prairie, however, senescence was induced by water stress, and the decrease in leaf area corresponded to a decline in soil moisture content in both 1998 and 1999. Similarly, the decline in evapotranspiration rates corresponded with the start of the dry season in the California grassland (Valentini *et al.* 1995). Clearly, the partitioning of available energy is related to both the biological and environmental factors which influence evapotranspiration.

#### 4.2 Canopy conductance to water vapor

Transpiration is the inevitable cost associated with photosynthetic gas exchange. Plants, however, will close their stomata to prevent excessive water loss. Stomatal conductance is an important physiological property as it quantifies the control of gas exchange exerted by stomata at the leaf level (Kelliher *et al.* 1995). Stomatal conductance is calculated using measurements of VPD and transpiration rate of a single leaf in a ventilated chamber. When studying gas exchange at larger scales, an integrated measure of conductance to water vapor is needed to assess physiological control over water losses (Kelliher *et al.* 1995). Canopy conductance ( $g_{\text{canopy}}$ ) is the counterpart to stomatal conductance. It is determined by measuring evapotranspiration, in addition to various meteorological and turbulence parameters, above the canopy and treating the canopy as one large leaf. If the contribution by soil evaporation is minor, one would expect canopy conductance to mimic the typical responses of stomatal conductance to changes in the environment.

It is well established that stomatal aperture changes with air humidity (Meinzer 1993). In experiments in which leaf temperature, relative humidity and VPD were manipulated, it was determined that VPD at the leaf surface was more appropriate than relative humidity in describing changes in stomatal conductance to humidity (Meinzer 1993 after Aphalo & Jarvis 1991). Stomatal conductance decreases with increasing vapor pressure deficits. This compensatory response of stomatal conductance to increased VPD has been shown in many species (Loustau *et al.* 1996; Berbigier *et al.* 1996; Meinzer *et al.*, 1993; Heath 1998; Bunce 1998). For example, stomatal

conductance of coffee plants and four tropical forest gap species decreased with increased VPD (Gutiérrez, Meinzer & Grantz 1994; Meinzer *et al.* 1995). Similar responses have also been observed for grass species, spring wheat and barley (Bunce 1998). On a larger scale, crown conductance in *Anacardium excelsum*, a lowland tropical forest tree, was also found to decrease with increasing VPD (Meinzer *et al.* 1993).

With the advent of micrometeorological methods of measuring gas exchange, it is now possible to extend analyses initially done at the single leaf to the whole ecosystem. An inverse relationship between total conductance and VPD has been observed in many and varied ecosystems: a forest dominated by *Nothofagus*, (Köstner *et al.* 1992), a boreal aspen forest (Blanken *et al.* 1997), a Central Siberia pine forest (Zimmermann *et al.* 2000), a C<sub>4</sub> pasture and rainforest in Amazonia (Grace *et al.* 1998). Thus it is not surprising that this short-term response of canopy conductance to VPD was also observed in our moist temperate grassland (Figure 14).

Varying levels of irradiance can confound the  $g_{\text{canopy}}$ -VPD relationship. It is imperative to keep in mind that stomata also mediate CO<sub>2</sub> assimilation by the plants. Plants attempt to minimize transpirational losses while maximizing photosynthesis, and photosynthesis is a light dependent process. Until the influence of photosynthetically active radiation (PAR) is taken into consideration, the dependence of conductance (stomatal or canopy) on VPD will not be clearly discernible. For example, once stomatal conductance was normalized by PAR, the physiological response in coffee and four tropical forest species became evident (Gutiérrez *et al.* 1994; Meinzer *et al.* 1995). In a study of large red maple trees, canopy conductance appeared to be actually increasing with increasing VPD, the opposite of what would be expected (Wullschleger, Wilson &

Hanson 2000). Upon closer examination, however, it was evident that PAR was co-varying with VPD, and the low VPD values corresponded to early and late in the day when light was likely to be limiting. At vapor pressure deficits greater than 2 kPa, and at times between 1000 and 1900 hours when light would not be limiting, canopy conductance decreased with increasing VPD (Wullschleger *et al.* 2000). Furthermore, when canopy conductance and VPD were plotted as a function of time of day, it was quite apparent that canopy conductance was decreasing with increasing VPD from 1200 to 1800 hours (Wullschleger *et al.* 2000). Conductance to water vapor was also found to decrease with increasing VPD in a broad-leaved forest of *Nothofagus* when conductance values associated with low photon flux density were excluded from the analysis (Köstner *et al.* 1992). In their study of a boreal aspen forest, Blanken *et al.* (1997) demonstrated that light had a strong influence on the physiological response of stomata to changes in air humidity. As light increased from low to high levels, the response of aspen  $g_{canopy}$  to VPD became more dramatic (Blanken *et al.* 1997). This pattern was also observed in my study (data not shown). The response of  $g_{canopy}$ , in the short term, to changes in VPD explained the diurnal pattern of  $g_{canopy}$ . Canopy conductance tended to be highest early in the morning but then decreased rapidly as air temperature and VPD increased (Figure 12). The same general pattern has also been previously described for other ecosystems (Berbigier *et al.* 1996; Loustau *et al.* 1996; Arneth *et al.* 1998; Hinckley *et al.* 1994; Dang *et al.* 1991). Interestingly, the response of stomata (and consequently canopy conductance) to dry air occurs even when soil water content is not limiting. The exact physiological mechanism by which stomata sense changes in VPD is not yet known. However, it is widely suspected that the plants are reacting to the rate of transpiration

itself and not to VPD *per se* (Meinzer 1993). Though abscisic acid (ABA) has been linked to increased stomatal resistance in droughted plants (Mojayad & Planchon 1994). ABA-deficient and ABA-insensitive mutants of *Arabidopsis* have demonstrated that ABA may not be the chemical signal involved in the short-term responses of stomata. (Assman, Snyder & Lee, 2000).

Stomatal control over water vapor loss becomes even stronger as soil water becomes limiting. It is believed that soil drying stimulates phytohormone production e.g. ABA and results in longer term responses of stomata to water stress (Meinzer 1993). Decreases in canopy conductance related to drought stress are likely to play an important role in ecosystems in which water is frequently limiting. In a maritime pine forest, drought stress resulted in lower stomatal conductance in the morning (Loustau *et al.* 1996). Stomatal conductance was lower overall in a *Pinus radiata* forest experiencing a soil water deficit (Arneth *et al.* 1998). Canopy conductance decreased in a California grassland as the dry season progressed (Valentini *et al.* 1995). Even in a Brazilian rain forest, it was concluded that limitations on water uptake during the dry season resulted in decreased in stomatal conductance (Williams *et al.* 1998). There was a strong seasonal decline in canopy conductance observed in our grassland. Not too surprisingly, soil water limitation was a factor. In both 1998 and 1999 there was a positive relationship between canopy conductance and soil moisture content (Figure 16c). Drought stress, however, is not the sole cause of seasonal variation in canopy conductance. For example, during the autumnal transition, canopy conductance dramatically decreased in the Konza tallgrass prairie even though the soil water content remained high (Ham & Knapp 1998).

Variations in photosynthetic capacity as illustrated by changes in leaf N content and leaf area index, can be quite dramatic and can also be responsible for changes in canopy conductance. For example, in a review of published values of canopy conductance for various ecosystems, Schulze *et al.* (1994) found that maximum values of  $g_{\text{stomatal}}$  and  $g_{\text{canopy}}$  were related to plant nutrition. Conductance to water vapor increased linearly with plant or leaf N content (Schulze *et al.* 1994). Changes in the canopy conductance corresponded to changes in the N content of the grassland canopy (Figure 16a). Daily  $g_{\text{canopy}}$  increased with increasing N content ( $\text{g m}^{-2}$ ). This relationship was very strong during the 1998 growing season. The relationship was more variable in 1999. It should be noted, however, that overcast days were not excluded from this analysis. In addition to explaining the seasonal changes, changes in N content in our grassland also help explain the large interannual variation in canopy conductance observed (Figure 16a). Overall, canopy conductance and N content were much higher in 1998 than in 1999.

Variation in canopy conductance can also be related to changes in leaf area index. LAI relates directly to the size of the transpirational surface and the number of stomata involved. In deciduous forests, canopy conductance increased linearly with increases in leaf area index (Wilson & Baldocchi 2000; Blanken *et al.* 1997). Increased LAI, like N content was also linked to increased  $g_{\text{canopy}}$  in our mixed-grass prairie (Figure 16b) and also explained why  $g_{\text{canopy}}$  values in 1998 were much higher than those in 1999. Decreasing LAI is a likely explanation as to why  $g_{\text{canopy}}$  decreased during senescence in the tallgrass prairie (Ham & Knapp 1998).

As mentioned above, there were large differences in canopy conductance values between the 1998 and 1999 growing seasons. In 1998, average daily conductance was

205 mmol m<sup>-2</sup> s<sup>-1</sup> while average values of  $g_{\text{canopy}}$  did not surpass 100 mmol m<sup>-2</sup> s<sup>-1</sup> in 1999. Peak values of average canopy conductance to water vapor were also observed earlier in 1999 than in 1998. Day 161 vs. Day 176. The seasonal decline was more dramatic in 1998 as this growing season benefited from an extended period of high soil moisture and increased LAI. In 1998, the peak value of  $g_{\text{canopy}}$  was similar to that measured in a Portuguese maritime pine stand (Loustau *et al.* 1996) and another *Agropyron* dominated grassland (Kelliher *et. al* 1993) with a LAI of 1.5. Clearly, the environmental and physiological parameters in 1998 were conducive to higher values of  $g_{\text{canopy}}$ .

#### 4.3 Biological control of evapotranspiration

From the observed changes in canopy conductance, one cannot conclude that plants are exerting complete control over evapotranspiration in this northern grassland. Physiological control is an important determinant of water vapor flux when aerodynamic conductance is large relative to canopy conductance (Meinzer 1993).  $\Omega$  is a means of determining the sensitivity of water vapor flux to a change in canopy conductance (Jarvis 1985; Jarvis & McNaughton 1986). Physiological control of evapotranspiration decreases as  $\Omega$  approaches 1 (Meinzer 1993). Aerodynamically rough canopies (forests) generally have lower values of  $\Omega$  than aerodynamically smooth canopies (crops) (Meinzer 1993).

$\Omega$  has also been found to vary diurnally.  $\Omega$  was found to reach a maximum of 0.38 at 1000 hours while minimum values were recorded towards sunset when light was limiting (Köstner *et al.* 1992). In a hybrid poplar stand  $\Omega$  was 0.82 around midday but then decreased to 0.64 as the day progressed (Hinckley *et al.* 1994).

A similar pattern was also observed in this temperate grassland (Figure 17). Diurnal changes in  $\Omega$  suggested that physiological control of evapotranspiration becomes stronger late in the afternoon. There was also day to day variation related to cloudiness.

The decoupling coefficient also changed on a seasonal basis. In 1998, there was a remarkable decline in  $\Omega$  as water became limiting (Figure 18). The change, however, was not as dramatic as that seen in the California grassland. Omega values approached 1 at the beginning of the growing season but by the end of the season, omega was nearly 0 (Valentini *et al.* 1995). Seasonal declines have also been documented in a lowland tropical forest tree. Omega decreased from 0.84 to 0.32, wet and dry season values respectively (Meinzer *et al.* 1993). During the 1999 growing season, daily average values of  $\Omega$  experienced a slight increase then a decrease (Figure 18). Compared to  $\Omega$  values calculated in a temperate deciduous forest, the seasonal change in omega for the grassland in 1998 and 1999 was very slight. In the broad-leaved Tennessee forest, the seasonal change in  $\Omega$  could be described as parabolic (Wilson & Baldocchi 2000).

In 1999, evapotranspiration was more constrained by canopy conductance than it was in 1998 as suggested by lower values of  $\Omega$ . These interannual differences are related to the fact that 1998 had higher precipitation and soil moisture content than 1999. Peak omega values in 1998 were similar to those observed in deciduous forests (Wilson & Baldocchi 2000; Hinckley *et al.* 1994) while 1999 values closely resembled those recorded in coniferous forests (Blanken *et al.* 1997). Wilson and Baldocchi (2000) have also documented year to year variation in omega. A dry year, 1995, had lower omega values from days 150-280 than what was observed for the same time period in 1996 and 1997 (Wilson & Baldocchi 2000).

Despite the fact that the grassland canopy is partially decoupled from the atmosphere, canopy conductance can play a very important role in regulating water vapor flux on an hourly, daily and yearly basis in moist temperate mixed grasslands. In figure 19, for example, it is clear that evapotranspiration is a function of canopy conductance. Net radiation also plays an important role in determining water vapor flux. When evapotranspiration is plotted as a function of omega, the same conclusions are reached (Figure 19). The calculation of the decoupling coefficient omega was useful when describing the relative importance of biological and environmental (net radiation) controls on evapotranspiration and how these controls vary on a daily, seasonal and yearly basis.

#### *4.4 Water budget*

In our moist temperate grassland, 300 mm of water was evapotranspired on an annual basis (from day 171 in 1998 to day 170 in 1999). This was much less than what has been recorded for other ecosystems. In a boreal aspen forest, annual evapotranspiration totaled over 400 mm (Black *et al.* 1996) and evapotranspiration ranged from 537 to 611 mm in a Tennessee broad-leaved forest (Wilson & Baldocchi 2000). Even during a "drought" year, evapotranspiration in the forest dominated by oak, maple and hickory was almost double that observed in this northern mixed-grass prairie (Wilson & Baldocchi 2000). When expressed on a daily basis the mean rate of evapotranspiration in the grassland was  $0.47 \pm 0.47$  mm day<sup>-1</sup>. Evapotranspirational losses accounted for more than 96% of the precipitation. In contrast, water vapor flux accounted for less than 40% of the precipitation in the Tennessee forest (Wilson & Baldocchi 2000).

#### 4.5 Conclusions

Over the course of the 1998 and 1999 growing season, there was considerable seasonal and interannual variation in the partitioning of available energy in this moist temperate grassland. In 1999, sensible heat flux dominated the surface energy balance during the entire growing season ( $\beta$  ranged from 3.5 to 8.5). In 1998, a wetter than normal year, a switch in the energy balance was observed from  $\lambda E$  dominated ( $\beta = 0.5$ ) in July to H dominated ( $\beta > 2$ ) in August. Overall, Bowen ratios were higher in 1999 owing to lower evapotranspiration rates. Peak evapotranspiration rates in 1998 were double those observed in 1999.

Canopy conductance to water vapor varied on a daily, seasonal and interannual basis. On a daily basis,  $g_{\text{canopy}}$  responded negatively to increases in vapor pressure deficit, a typical physiological response by plants. Average values of canopy conductance were positively correlated with canopy N content, leaf area index and soil moisture content, though 1998 values of  $g_{\text{canopy}}$  were greater than 1999 values. The large interannual differences in LAI and canopy N content explained the large variation in  $g_{\text{canopy}}$  observed between the two growing seasons. Declines in LAI and canopy N corresponded to seasonal decreases in soil water availability. Seasonal changes in  $g_{\text{canopy}}$  were much less pronounced in 1999.

During both 1998 and 1999, evapotranspiration (dry canopy) was limited more by canopy conductance than net radiation. As soil water availability decreased, canopy conductance became even more important as a control on evapotranspiration. Daily rates of evapotranspiration were positively correlated with canopy conductance, leaf area index, canopy N content and omega. Environmental influences were also important

(e.g. net radiation, soil water availability and vapor pressure deficit). The functioning of this moist temperate grassland water was particularly sensitive to the extra precipitation received in June 1998.

Evapotranspiration represented a substantial proportion of the water budget of this moist temperate grassland. Water vapor fluxes accounted for 96% of the precipitation inputs. Annual evapotranspiration was estimated to be about 300 mm.

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