ECOHYDROLOGY OF A RIPARIAN WOODLAND ALONG THE OLDMAN RIVER, ALBERTA

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ABSTRACT

Growth of riparian cottonwoods along regulated rivers can be limited by water availability. In this study we associate seasonal variation of environmental conditions and stream flows with water relations of a natural cottonwood grove located along a regulated river in southern Alberta. To link elements in the river-soil-plant-atmosphere continuum, river and groundwater levels and precipitation were monitored; sap flow was continuously measured with thermal dissipation probes in eight trees and stomatal conductance and leaf water potential were measured monthly; and weather conditions were monitored. From June through August, stomatal conductances at both leaf and canopy levels were increasingly limited by decreasing water availability. Artificially increasing the soil moisture in August resulted in an increase in sap flow and stomatal conductance at leaf and canopy levels. These responses can be attributed to seasonal changes in the water potential difference between soil and leaves or an alteration in hydraulic conductance, or a combination of both.

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TABLE OF CONTENTS

SIGNATURE PAGE ii

ABSTRACT iii

ACKNOWLEDGEMENTS iv

TABLE OF CONTENTS v

LIST OF TABLES viii

LIST OF FIGURES ix

LIST OF ABBREVIATIONS xiv

CHAPTER 1 Introduction 1

1.1 Background 1

1.2 Water Supply 2

1.3 The Soil-Plant-Atmosphere Continuum and Water Potential Differences 3

1.4 Project Objectives and Hypotheses 11

Literature Cited 14

CHAPTER 2 Analyzing Sap Flow with Thermal Dissipation Probes 17

2.1 Introduction 17

2.2 Materials and Methods 19

2.2.1 TDP Installation 19

2.2.2 Sap Flow Calculations 21

2.3 Results 22

2.4 Discussion 28

Literature Cited 32

CHAPTER 3 Seasonal Sap Flow and Ecohydrology of a Riparian Zone Along the Oldman River, Alberta 33
3.1 Introduction 33
3.2 Materials and Methods 37
3.2.1 Study Area 37
3.2.2 Tree Attributes 40
3.2.3 Meteorological Conditions 42
3.2.4 Water Supply 43
3.2.5 Sap Flow and Related Measurements 44
3.2.6 Statistical Analyses 47
3.3 Results 48
3.3.1 Meteorological Conditions 48
3.3.2 Tree Attributes 56
3.3.3 Water Supply 59
3.3.4 Stomatal Conductance and Water Potential Difference 65
3.3.5 Sap Flow 69
3.3.6 Canopy and Leaf Stomatal Conductance 76
3.4 Discussion 86
Literature Cited 99
CHAPTER 4 Is Water Supply Limiting Riparian Cottonwoods? Response to Late Summer Irrigation 104
4.1 Introduction 104
4.2 Materials and Methods 106

4.2.1 Statistical Analyses 108

4.3 Results 109

4.3.1 Meteorological Conditions and Water Supply 109

4.3.2 Sap Flow 110

4.3.3 Mean Canopy Stomatal Conductance 118

4.4 Discussion 122

Literature Cited 126

CHAPTER 5 Conclusions 127

Literature Cited 130

APPENDIX A Statistical Analyses 131

LIST OF TABLES

Table 3.1. Characteristics of the narrowleaf cottonwoods studied at Pearce Corner along the Oldman River 41

Table 3.2. Afternoon (12:00 h to 16:00 h) sap flow (g h^{-1} cm^{-2}) of narrowleaf cottonwoods for groups of days throughout the growing season (n = 6)....71

Table 3.3. Afternoon (12:00 h to 16:00 h) sap flow (g h^{-1} cm^{-2}) for individual trees for 5 groups of days over the growing season 72

Table A1.1. ANCOVA results for M1 132

Table A1.2. Tukey's HSD for the five DOY groups for M1 132

Table A2.1. ANCOVA results for F1 132

Table A2.2. Tukey's HSD for the five DOY groups for F1 132

Table A3.1. ANCOVA results for F2 133

Table A4.1. ANCOVA results for M2 133

Table A5.1. ANCOVA results for M3 133

Table A5.2. Tukey's HSD for the five DOY groups for M3 133

Table A6.1. ANCOVA results for M4 134

Table A7.1. One sample t-test for mean canopy stomatal conductance reference point (G_{Sref} when D = 1 kPa) and slope values comparing the months June, July, and August to a test value of 1 134

Table A7.2. One sample t-test results for mean canopy stomatal conductance reference point (G_{Sref} when D = 1 kPa) and slope values comparing before and after irrigation data for irrigated and control trees 135

LIST OF FIGURES

Figure 1.1. Diagram of the SPAC monitored in a riparian zone for 123 days during one growing season 12

Figure 2.1. Diagram of the TDP system 18

Figure 2.2. Sample of diurnal dT data from three probes within one cottonwood tree (F2) over a three day period from DOY 162 to 165 23

Figure 2.3. Sample of diurnal sap flow variation for three probes at different aspects within one tree (F2) 25

Figure 2.4. Example of inadequate data where unexplained spikes in dT occurred over a three day period from DOY 211 to 213 in all three probes in F4 26

Figure 2.5. Ambient dT of 3 TDPs for tree M2 over three days when power supply was removed from the TDPs 27

Figure 3.1. Map of the Oldman River in southern Alberta showing the study site Pearce Corner 38

Figure 3.2. 1:32,000 aerial photograph of Pearce Corner grove 39

Figure 3.3. Aerial photograph of the location of trees, soil moisture probes, piezometers, and weather station 39

Figure 3.4. Diurnal trends of insolation for clear days in June, July and August in the riparian zone at Pearce Corner grove along the Oldman River 50

Figure 3.5. Hourly insolation values at Pearce Corner from June through September 2006 51

Figure 3.6. Diurnal temperature, relative humidity (RH), and vapor pressure deficit (*D*) at Pearce Corner on 21 August (DOY 233) 52

Figure 3.7. Daily maximum and minimum temperatures at Pearce Corner 54

Figure 3.8. Daily maximum and minimum relative humidity at Pearce Corner.....54

Figure 3.9. Hourly vapor pressure deficit (D) at Pearce Corner from June through October 2006, calculated from temperature and relative humidity (RH) ..55

Figure 3.10. Hourly wind speeds at Pearce Corner for the 2006 season 57

Figure 3.11. Branch length (elongation) of the eight trees from May through mid-July (mean ± S.E., n = 5) 58

Figure 3.12. Relative groundwater table from May through September at the two piezometer locations 60

Figure 3.13. Daily precipitation at Pearce Corner 63

Figure 3.14. Soil moisture (% volume), at groundwater table (GW) 1 and GW 2 at Pearce Corner.....64

Figure 3.15. Diurnal pattern of leaf water potential (Ψ_L) and stomatal conductance measured in one tree on 21 August (DOY 233) (mean ± S.E.) 66

Figure 3.16. Diurnal pattern of Ψ_L of the 8 trees in mid-June, July, and August (mean ± S.E.) 67

Figure 3.17. Predawn and minimum Ψ_L from the 8 trees measured in mid-June, July, and August (mean ± S.E., n = 8).....68

Figure 3.18. Representative sap flow pattern for 20 August (DOY 232) through 22 August (DOY 234) for a narrowleaf cottonwood along the Oldman River.....70

Figure 3.19 A and B. Seasonal pattern of afternoon sap flow (12:00 h to 16:00 h) for M1 (A) and F1 (B) 73

Figure 3.19 C and D. Seasonal pattern of afternoon sap flow (12:00 h to 16:00 h) for F2 (C) and M2 (D) 74

Figure 3.19 E and F. Seasonal pattern of afternoon sap flow (12:00 h to 16:00 h) for M3 (E) and M4 (F) 75

Figure 3.20 A and B. Stomatal conductance on three days, one in each of mid-June, July, and August for a given *D* for M1 (A) and F1 (B) 78

Figure 3.20 C and D. Stomatal conductance on three days, one in each of mid-June, July, and August for a given *D* for F2 (C) and M2 (D) 79

Figure 3.20 E and F. Stomatal conductance on three days, one in each of mid-June, July, and August for a given *D* for M3 (E) and F3 (F) 80

Figure 3.20 G and H. Stomatal conductance on three days, one in each of mid-June, July, and August for a given *D* for M4 (G) and F4 (H) 81

Figure 3.21. Mean canopy stomatal conductance (G_S) data from F2 before the boundary line was calculated 82

Figure 3.22 A and B. Boundary line G_S calculated by using the average hourly sap flow and *D* for each day when insolation was greater than 0.4 kW m^{-2} for M1 (A) and F1 (B) 83

Figure 3.22 C and D. Boundary line G_S calculated by using the average hourly sap flow and *D* for each day when insolation was greater than 0.4 kW m^{-2} for F2 (C) and M2 (D) 84

Figure 3.22 E and F. Boundary line G_S calculated by using the average hourly sap flow and *D* for each day when insolation was greater than 0.4 kW m^{-2} for M3 (E) and M4 (F) 85

Figure 4.1. Soil moistures at 0.5 m, before (n = 7) and after irrigating (n = 6) on 29 August, measured under treated trees (mean ± S.E.).....111

Figure 4.2 A and B. Diurnal patterns of sap flow for irrigated trees M1 (A) and F1 (B) three representative days before irrigating, and three days after irrigating on 29 August (DOY 241).....112

Figure 4.2 C and D. Diurnal patterns of sap flow for irrigated trees F2 (C) and M2 (D) three representative days before irrigating, and three days after irrigating on 29 August (DOY 241).....113

Figure 4.2 E and F. Diurnal patterns of sap flow for control (not irrigated) trees M3 (E) and M4 (F) three representative days before irrigation of other trees, and three days after irrigating on 29 August (DOY 241) 114

Figure 4.3 A and B. Afternoon sap flow (12:00 h to 16:00 h) for irrigated trees M1 (A) and F1 (B) from 19 August (DOY 231) to 3 October (DOY 276).....115

Figure 4.3 C and D. Afternoon sap flow (12:00 h to 16:00 h) for irrigated trees F2 (C) and M2 (D) from 19 August (DOY 231) to 3 October (DOY 276).....116

Figure 4.3 E and F. Afternoon sap flow (12:00 h to 16:00 h) for control (not irrigated) trees M3 (E) and M4 (F) from 19 August (DOY 231) to 3 October (DOY 276) 117

Figure 4.4 A and B. Boundary line G_S calculated by using the average hourly sap flow and D when insolation was greater than 0.4 kW m^{-2}. These data are from the irrigated trees M1 (A) and F1 (B) 119

Figure 4.4 C and D. Boundary line G_S calculated by using the average hourly sap flow and D for each day when insolation was greater than 0.4 kW m^{-2}.

These data are from the irrigated trees F2 (C) and M2 (D) 120

Figure 4.4 E and F. Boundary line G_S calculated by using the average hourly sap flow and D for each day when insolation was greater than 0.4 kW m^{-2}. These data are from the control trees M3 (E) and M4 (F).....121

LIST OF ABBREVIATIONS

AVP actual vapour pressure

cm centimeters

CO_2 carbon dioxide

D leaf-to-air vapor pressure deficit (kPa)

DOY Day of Year/Julian Day

dT difference in temperature measured between upper and lower TDP

dTM maximum difference of temperature (TDP)

G_S mean canopy stomatal conductance

g_S stomatal conductance (mol m^{-2} s^{-1})

m meters

n number of specimens used in a sample

RH relative humidity (%)

SPAC soil-plant-atmosphere continuum

SVP saturation vapour pressure

TDP thermal dissipation probe

Ψ water potential (MPa)

Ψ_L leaf water potential (MPa)

Ψ_S soil water potential (MPa)

CHAPTER 1 Introduction

1.1 Background

Water is essential for plant growth and function. Once soil water is absorbed through the roots and transported through the tree, it is lost to the atmosphere. This process is repeated in a daily pattern; however, if water losses to the atmosphere continuously become greater than the supply, damage to plant processes and decrease in overall plant health occurs (Taiz and Zeiger 2002). The majority of water taken up by the roots is transpired into the atmosphere accompanying the intake of carbon dioxide (CO_2) from the atmosphere for photosynthesis. Thus on a daily basis, terrestrial plants face a dilemma between the loss of water for the gain of CO_2 (Schulze et al. 1987; Hinckley et al. 1991). Riparian trees in southern Alberta are faced with seasonal variability, generally with a decreasing trend in groundwater levels and soil moisture supplies (Rood et al. 2003). This decreasing supply poses a "balance" difficulty for cottonwoods as atmospheric demand increases with higher temperatures and lower relative humidity in July and August. Regulation of water loss at the leaf end of the Soil-Plant- Atmosphere Continuum (SPAC) lies with alterations of the stomatal aperture by guard cells. In this study, we monitor sap flow, stomatal conductance, and leaf water potential to understand how cottonwoods react to the decreasing water supply over one growing season.

1.2 Water Supply

Like all plants, riparian trees such as cottonwoods are dependent on water. Southern Alberta, as defined by the Köppen Climate Classification System, is a semi-arid region (McKnight and Darrel 2000) where potential evapotranspiration exceeds precipitation. In such a region it can be difficult for some plants to maintain a balance between water loss and gain due to the lack of soil moisture. When soil moisture becomes low, riparian trees have the advantage of the additional alluvially fed groundwater source (Rood et al. 2003; Williams and Cooper 2005), which in southern Alberta occurs next to streams. This water source is common to semi-arid regions because of the occurrence of 'losing streams' where river discharge supplies groundwater sources (Rood et al. 2003). Cottonwoods are phreatophytes (Busch et al. 1992; Gazal et al. 2006), tapping their roots into the semi-saturated capillary fringe layer and saturated phreatic layer below the groundwater table while also utilizing soil moisture when available (Heilman et al. 1996; Zhang et al. 1999; Snyder and Williams 2000). The combination of the capillary layer and phreatic layer will be referred to as the groundwater table.

Water supply from stream flows, and hence the groundwater table, is not static. In southern Alberta, fluctuations occur naturally within a season due to weather patterns. High flows are observed during spring snow-melt and low flows occur in the drier, late summer months. Occasionally these annual weather effects can become extreme creating spring flooding or severe summer drought, greatly

varying the amount of water supply throughout the growing season. Natural changes in stream flow can also occur with effects from weather and long term fluctuations of the sea surface temperature which occur during El Nino/ Southern Oscillations and Pacific Decadal Oscillations. For North America, these variations have been reported to influence temperatures and stream flow (Rood et al. 2005). Human alterations, through dam building, reservoir filling, and weir diversions, also modify seasonal and long-term stream flow patterns. Depending on operation of the infrastructure, the withholding and diversion of upstream flows can affect downstream supply. Overall, a combination of natural and anthropogenic influences continuously change groundwater table levels, whether it is within one growing season, between growing seasons, or over decades of time. Over long periods of time, reduced river discharges can harm riparian cottonwoods as evidenced by their decline on many rivers (Rood et al. 2000, Rood et al. 2003, Williams and Cooper 2005).

1.3 The Soil-Plant-Atmosphere Continuum and Water Potential Differences

Once a water supply has been established, there is movement of water from the soil, through trees, and to atmosphere as described by the soil-plant-atmosphere continuum (SPAC) (Taiz and Zeiger 2002). In this interconnected series water movement is influenced by a multitude of factors including the amount of water supply, atmospheric demand, and resistance. These factors work together to determine the rate of flow seen through the SPAC. Once absorbed, more than 95 % of water moves up through the tree without being used for growth and

photosynthesis (Hopkins 1995). Water between the soil and the atmosphere travels upwards against the force of gravity, driven by water potential differences. In general,

$$\text{Flow} = \frac{\text{driving force}}{\text{resistance}} \qquad \text{(Hinckley et al. 1991, Franks 2004)}$$

Hence,

$$\text{Flow} = \text{driving force x conductance}$$

Applying a similar equation to water flow out of the leaves into the atmosphere:

$$E = g_S \text{ x } D \qquad \text{(Jarvis and Davies 1998)}$$

Where

E = transpiration (water flow)

g_S = stomatal conductance

D = vapor pressure deficit

The driving force in this case is the vapor pressure deficit, or the absolute concentration difference of water vapor between the leaf and atmosphere.

At a steady state, transpiration is equal to sap flow (Granier 1987).

Water flow through the tree can be described using the general equation in the form of the Van den Honert equation:

$$J = \frac{(\Psi_S - \Psi_L)}{R_{S-L}} \qquad \text{(Van den Honert 1948)}$$

Where

J = water flow

Ψ_L = leaf water potential

Ψ_S = soil water potential

R_{S-L} = resistance, soil to leaf

Hydraulic conductance represents the efficiency of water supply to the leaves (Meinzer 2002):

$$J = \Delta\Psi \bullet \kappa$$

Where

J = water flow

$\Delta\Psi$ = difference between the Ψ_S and Ψ_L

κ = hydraulic conductance of the soil to leaf pathway

The pathway between roots and leaves can be influenced by the formation of xylem cavitations and changes in extra-xylary pathway tissues (Sperry 2000), but more importantly, there are resistances found throughout the pathway from the roots to the shoots (Meinzer 2002).

The driving force as represented in the Van den Honert equation is the difference in water potential between the soil and leaves.

Soil Water Potential: Soil water potential (Ψ_S) is one end of the water potential difference which drives sap flow. A change in Ψ_S is dependent on soil moisture which relies on inputs from either precipitation or groundwater level which in turn is dependent on stream level. Ψ_S is slow to change with little diurnal fluctuation (Jones 1978; Li et al. 2002) but will vary over the season depending on the relationship between input of moisture and the loss of moisture from root absorption and transpiration, and evaporation.

The relationship between soil moisture and soil water potential is non-linear. Although the relationship is dependent on the soil type, the trend for different soil types is the same with soil water potential becoming more negative with decreasing soil moisture. Development of a decreasing Ψ_S occurs as the soil-water content decreases due to evaporation or plant uptake and transpiration. As moisture is being lost, the air-water surface will be drawn down into capillary spaces found between soil particles. The strong adhesive forces of water will cause it to cling to soil particles, decreasing the radii of the menisci and creating an increasingly negative pressure or tension (Hopkins 1995). Thus, a decrease in soil moisture produces a decrease in the Ψ_S, thereby reducing the water potential difference needed for sap flow.

Ψ_S can be measured directly, with instruments such as a tensiometer, or can be indirectly estimated by the predawn leaf water potential (Ψ_L). In the absence of water flow, generally observed predawn, an equilibrium is reached between the soil and the leaves. Predawn Ψ_L can, thus, be used to indicate the Ψ_S to which the roots are exposed (Ritchie and Hinckley 1975; Tardieu and Simonneau 1998). We did not directly measure Ψ_S, but measured soil moisture and estimated Ψ_S from measurements of predawn Ψ_L.

Leaf Water Potential: Leaf water potential (Ψ_L) creates the other end of the water potential difference which drives sap flow. Unlike Ψ_S, Ψ_L changes diurnally, depending on the balance between the supply of water from the soil and the loss

of water to the atmosphere. As mentioned, the maximum Ψ_L (predawn) will change over the season if there is an alteration in soil moisture (Ψ_S).

The water supply and loss relationship within the leaf determines the Ψ_L which is created in a similar manner as Ψ_S. As described by Sperry et al. (2002), with evaporation of water, Ψ gradients are generated at the air-water interface within a leaf (Taiz and Zeiger 2002) creating capillary tension between leaf mesophyll cells. Since the internal leaf has a higher Ψ than the atmospheric air when there is vapor pressure deficit (*D*), water will evaporate from the leaf surface into the atmosphere. As evaporation occurs, the remaining water surface is drawn further back into the apertures in the cell wall, resulting in a curvature of the air-water surface (Taiz and Zeiger 2002). Due to the cohesive properties of water, the surface tension of the curvatures creates a negative pressure. As water continues to evaporate from the leaf, the smaller the air-water curvature radius and the more negative the Ψ_L will become (Taiz and Zeiger 2002). The driving force for the evaporation of water, *D*, with stomatal resistance will determine the rate and amount of water loss from the leaf. The relationship between loss and supply, the latter dependent on soil moisture and resistances, determines Ψ_L.

Vapor Pressure Deficit (D): *D* difference between the internal leaf vapor pressure, which is assumed to be saturated (RH = 100%), and the ambient vapor pressure. The value of *D* will vary with temperature and relative humidity (Taiz and Zeiger 2002) and is calculated using a combination of

temperature and relative humidity values. Concentration of water vapor in saturated air has a positive, non-linear relationship to air temperature. Warmer air holds an exponentially larger amount of water vapor (Taiz and Zeiger 2002). On an average summer day, the large temperature increase and relative humidity decrease between early morning and late afternoon creates a large decrease in vapor pressures in the ambient air. Within the leaf, the vapor pressure will fluctuate only slightly, remaining near saturation. *D* then increases during the day.

Resistances: Resistances can be found in all steps of the SPAC, from soil water absorption into the roots, and cavitation in the xylem, to stomata and associated boundary layers (Taiz and Zeiger 2002).

Aquaporins: Root permeability varies diurnally (Javot and Maurel 2002) and has been attributed to changes in activity of aquaporins, the water channel proteins found in membranes of cells (Javot and Maurel 2002). Aquaporin effects have also been reported in leaves (Cochard et al. 2007).

Cavitation: Transpiring water at the leaf level can create a large tension causing cavitation to develop. These air bubbles break the continuous stream of water adding a resistance to its upward flow (Tyree and Sperry 1988). To avoid complete cavitation and resulting desiccation of the transpiration stream, there is

coordination with stomatal conductance to not exceed the xylem capacity while maximizing CO_2 uptake (Sperry 2004).

Stomata**:** Stomata play a significant role in the balance of water loss (Hinckley et al. 1991) together with the hydraulic conductance of the water supply from the soil to the leaves (Meinzer 2002). More specifically, it is within the guard cells where turgor pressure is increased and decreased, governing the size of the stomatal aperture (Oke 1987; Taiz and Zeiger 2002; Franks 2004), ultimately regulating the conductance of water and CO_2. The turgor of the guard cells varies in response to environmental factors including radiation intensity, temperature, RH, and intracellular CO_2 concentration, all of which become interpreted as signals for a specific response (Oke 1987; Taiz and Zeiger 2002). For example, radiation is interpreted as an opening signal, triggering successive steps in guard cells which increase turgor and open the stomatal pore (Waggoner and Zelitch 1965; Taiz and Zeiger 2002). Subsequently, with water loss from leaves, turgor is reduced and stomata close, an integral step for preservation of leaf water content. This closure increases the stomatal resistance for water loss and maintains higher leaf water content and Ψ during times of water stress (Oke 1987; Hinckley et al. 1991).

Stomata and Leaf Water Potential: Diurnally, the Ψ_L becomes more negative due to increased *D* driving water out of stomata, and eventually a critical value will be reached where stomata will close, acting as a negative feedback (Matzner and Comstock 2001). This closing of the stomatal aperture will

inherently decrease the rate of water loss. With continuing supply of water to the leaves, the Ψ_L will be maintained or will rise back towards zero and the tension in the xylem will decrease (Ludlow and Bjorkman 1984; Tardieu and Simonneau 1998; Matzner and Comstock 2001). Without guard cell regulation of water loss, the Ψ_L could reach sufficiently low (negative) values to create a large enough tension to cause cavitation development (Tyree et al. 1994; Tardieu and Simonneau 1998). In many species, especially within the *Populus* genus, xylem tension frequently approaches, but does not fall below, critical Ψ_L values known to cause cavitation, thus maximizing stomatal conductance and allowing CO_2 uptake needed for growth (Sperry 2004). In semi-arid regions guard cell control allows the plant to avoid developing water deficits (Schulze et al. 1987).

ABA**:** Hormones such as abscisic acid (ABA) are released under environmental stresses, promoting stomatal closure and decreasing water loss (Taiz and Zeiger 2002).

Laminar Boundary Layer: The final resistance before water enters the atmosphere occurs at the boundary layer. This layer of relatively unstirred air on the leaf's surface reduces the rate of water loss (Taiz and Zeiger 2002).

The SPAC is a series of interlinked, complex, and sometimes unknown relations between the atmosphere, water supply, and the components which make up the vegetation. The water potential difference between soil and leaves fluctuates

daily and throughout the season because of the variability found within the water supply (groundwater table and soil moisture) and *D*. Additional resistances found throughout the SPAC pathway contribute to the variations of water loss rates.

1.4 Project Objectives and Predictions

In this study we investigate the SPAC by monitoring the water flow of 8 cottonwood trees in a riparian zone for 123 days during one growing season. From this we are able to analyze the diurnal patterns and underlying mechanisms that contribute to the overall seasonal fluctuation. Diurnal measurements include whole tree sap flow, stomatal conductance, and leaf water potentials. Seasonal variation was monitored using continuous measurements of supply, demand, and whole tree sap flow. This included monitoring of river stage, groundwater levels, precipitation, and soil moisture (supply); RH, temperature, and *D* (demand); sap flow through the trees using TDPs (Figure 1.1).

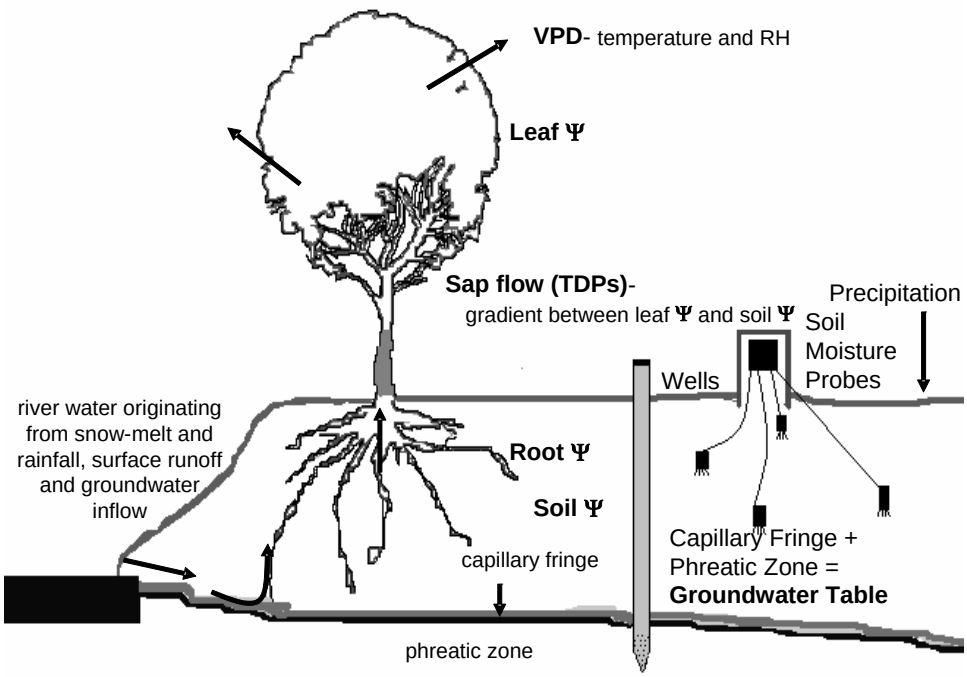

Figure 1.1. Diagram of the SPAC monitored in a riparian zone for 123 days during one growing season.

Prediction: Seasonal decline of river level will result in reduced predawn $\Psi_{L,}$ stomatal conductance, water loss and sap flow in narrowleaf cottonwoods found in a constrained reach along a southern Alberta river. The addition of water through irrigation will increase the water availability and the Ψ_S. *Populus* will respond to the increased availability by increasing sap flow and stomatal conductance.

Overall Objectives:

1. Establish the linkages between the river level, groundwater table, and soil moisture in a native riparian cottonwood grove.
2. Establish the linkages between groundwater table and soil moisture and sap flow by monitoring sap flow and water supply through a summer season.
3. Examine how sap flow changes over the season in relation to water supply and atmospheric demand (*D*).
4. Determine how physiological aspects such as stomatal conductance, mean canopy stomatal conductance, and leaf water potential, change in relation to the sap flow responses and to supply and demand (*D*).
5. Determine how artificially increasing the soil moisture in the late summer will alter sap flow, and mean canopy stomatal conductance, given the results from the above objectives.

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CHAPTER 2 Analyzing Sap Flow with Thermal Dissipation Probes

2.1 Introduction

Thermal dissipation probes (TDPs), also referred to as Granier probes (Lu et al. 2004), indirectly measure sap velocity through a tree trunk. TDPs are useful for estimating whole plant water flow, allowing researchers to gain an understanding of the water flow through trees of differing ages and environments. Recently, TDP use has increased in popularity due to ease of use, accuracy, reliability, and relatively low cost (Lu et al. 2004).

TDPs work by supplying constant heat to the tree. The system consists of two needles, the upper or downstream needle contains a heating element, and the lower or upstream needle has no heating element and acts as a reference (Figure 2.1). Both needles contain a thermocouple to measure temperature, resulting in the measurement of the difference in temperature (dT) between the two probes. dT varies with sap velocity. At times with little sap flow, dT is large as there is no flow to carry heat away from the upper needle. On the other hand, at times with fast sap flow, dT is small as the heat given off by the upper needle is carried away by the upwards flow. From sap velocity and sapwood area, the sap flow (g h^{-1} cm^{-2}) can be estimated.

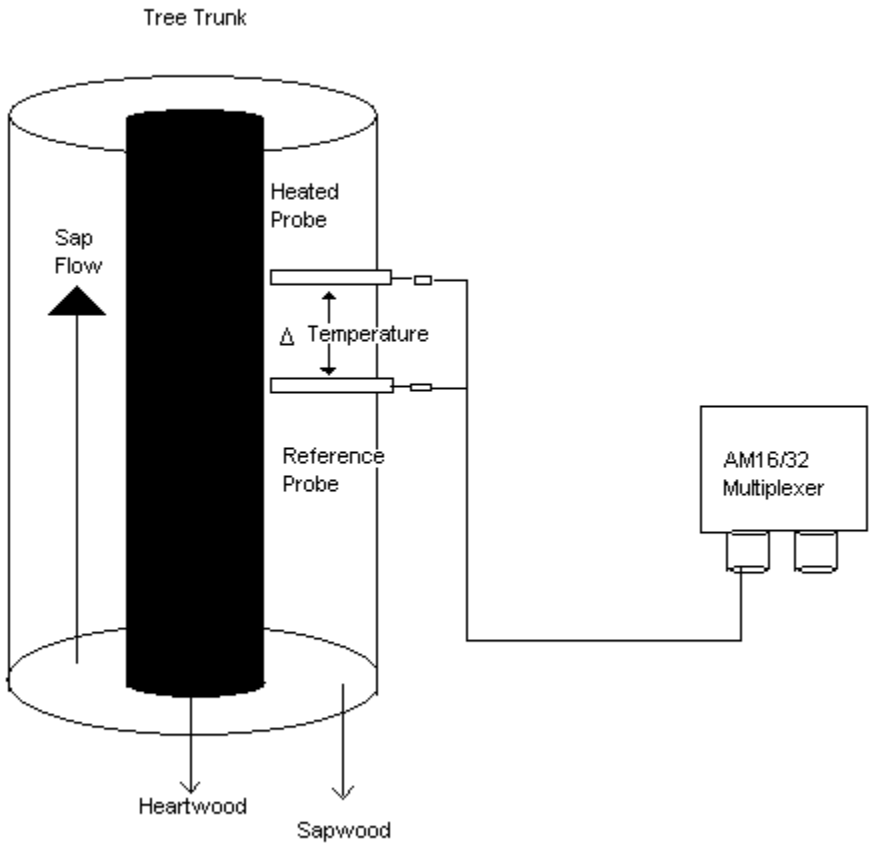

Figure 2.1. Diagram of the TDP system. Modified from Lu et al. (2004).

To understand the TDP system and attempt to continually measure sap flow throughout one growing season, we installed three TDP-30 (30 mm long needles) in each of eight *Populus angustifolia* trees. While we were able to measure sap velocity in many cases we were unable to determine total sap flow due to a number of confounding factors as explained in this chapter.

2.2 Materials and Methods

2.2.1 TDP Installation

In 2006, the probes were installed in cottonwood trees located in a riparian zone at Pearce Corner along the Oldman River (Figures 3.1, 3.2, 3.3). On 30 May (DOY 150), 10 cm x 5 cm areas of bark on the north, southwest, and southeast aspects f the tree trunks were removed at a height of 1.3 m in preparation for TDP installation (Dynamax, Houston, TX, USA). To decrease the influence of ambient gradients on dT, the TDPs were surrounded by three layers of insulation as recommended by Dynamax (1997). This insulation is unable to protect readings from the internal effects of thermal gradients created by cool soil or groundwater rising up through the roots and xylem. For this reason, Dynamax (1997) recommends installing probes at least 1 m above the substrate surface. With such isolated trees of larger diameter, Dynamax (1997) recommended using several probes per tree to obtain an average flow rate. On 1 June (DOY 152), between 5 am and 7 am, one TDP-30 was installed per aspect on each of the eight trees. TDP-30s average temperature over the entire length of the probe. Probes were placed in the tree before sap flow had commenced to reduce the prospect of introducing cavitations. TDPs were installed horizontally within the sapwood

with the pair of needles at 4 cm vertical spacing, as recommended by Dynamax (1997). To provide a waterproof seal, reduce heat loss, and reduce the influence of ambient conditions on TDP readings, each of the probes was surrounded by blue putty (Elmer's Tac 'N Stik, Columbus, Ohio, USA), two Styrofoam quarter-spheres, and reflective insulation. The reflective bubble-wrap insulation was wrapped around the tree from the base to 0.5 m above the probes. The probes were connected to one of two AM16/32 multiplexers (Campbell Scientific Inc., Logan, UT, USA) using extension cables when necessary, ranging in length from 8 m to 30 m. If extension cables were used, the same length was used for the three probes within one tree. Both AM16/32 multiplexers were connected to a CR10x datalogger (Campbell Scientific Inc., Logan, UT, USA) which stored the collected TDP outputs. Using a voltage regulator within each of the AM16/32 multiplexers, power supply to the probes was set for a constant nominal voltage of 3.0 V. The measured voltages ranged between 2.9 V to 3.3 V over the course of the season. Three MSX 60 solar panels (Atlantic Solar Products, Inc., Baltimore, Maryland, USA) charged three 12 V deep cycle batteries (P31DC, Battery Direct Inc. Lethbridge, AB, Canada), which provided power for the TDPs.

Measurements of the difference in temperature (dT) between the heated upper needle and the unheated lower needle were acquired in 30 second intervals and averaged every half hour. Readings were taken from 2 June (DOY 153) through 3 October (DOY 276), with short periods where measurements were not taken primarily due to lack of power supply to the probes. Between 14 and 18 August

(DOY 226 to 230) the power supply to the TDPs was shut off to observe ambient gradients.

2.2.2 Sap Flow Calculations

Sap flow was obtained from a three step calculation derived by Granier (1987) as supplied to us by Dynamax (1997):

$$(1) K = \frac{(dTM - dT)}{dT}$$

where

K is a dimensionless parameter

dT is the difference in temperature measured between the upper heated and lower reference needles

dTM is the value of dT when there was zero sap flow.

A new dTM was calculated every 24 hours and was usually an average value that occurred between 03:00 and 06:00 h.

(2) $V = 0.0119 \times K^{1.231}$ (Granier 1987)

where

V is average flow velocity in cm s^{-1}

The relationship between V and K has been established empirically by Granier (1987).

Finally sap flow, F_S (cm^3 h^{-1}), is the product of sapwood area and sap velocity (Edwards et al. 1996).

(3) $F_S = A_S \times V \times 3600$ (seconds $hour^{-1}$)

where

A_S is the cross-sectional area of the conducting tissues (cm^2)

3600 is the number of seconds in one hour

We did not estimate sapwood area, for reasons described later, and so for purposes of this study, A_s was given the value of 1 cm^2, yielding relative flow rates or velocities within trees, rather than estimates of absolute sap flow based on the area of conducting sapwood.

On 15 November 2006 three cores per tree were extracted, one from each of the north, south-west, and south-east aspects, using a 0.5 cm increment borer at a tree height of 1.3 m. Annual radial increments (RI) were measured to 0.002 mm precision with a dissecting microscope, a Velmex stage and Acu-Rite encoder (Velmex Inc., Bloomfield, NY, USA); and MeasureJ2X software (VoorTech Consulting, Holderness, NH, USA). These cores provided a visual representation of the sapwood area and depth in which the TDP were situated, aiding in the assessment of the sapwood depth in relation to the length of the probes.

2.3 Results

dT followed the expected diurnal pattern with low dT during the day, indicating faster flows, and high dT during the night, indicating slower flows (Figure 2.2).

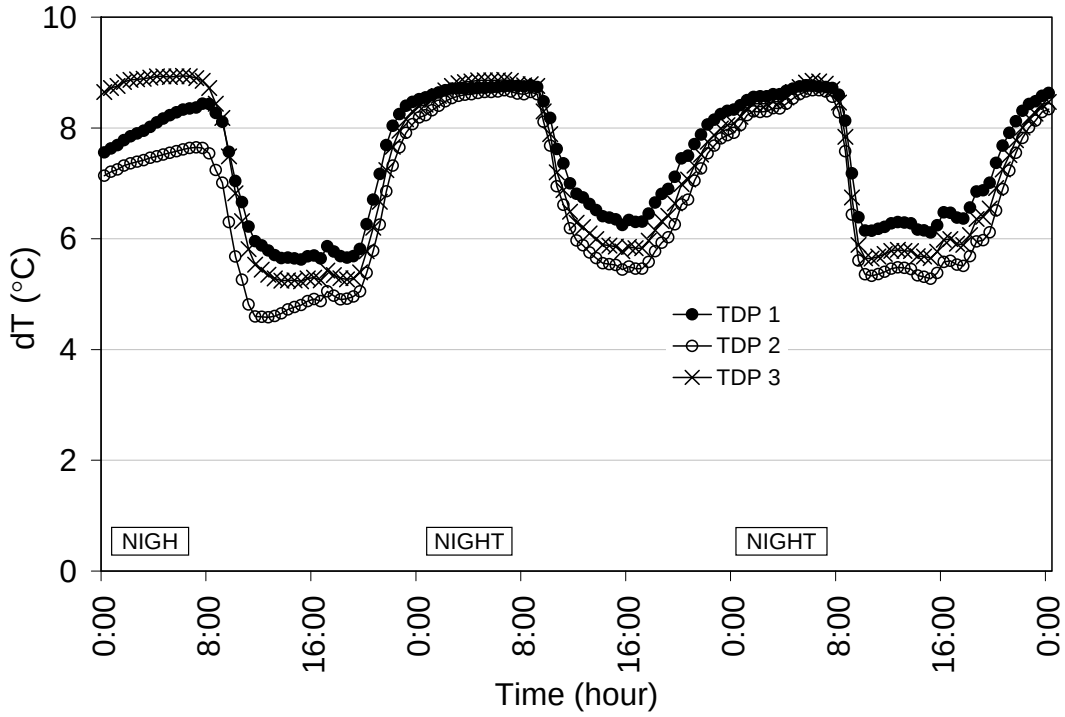

Figure 2.2. Sample of diurnal dT data from three probes within one cottonwood tree (F2) over a three day period from DOY 162 to 165.

Diurnal Variation in Sap Flow: Diurnal variations in dT correspond to variations in sap flow after calculation (Figure 2.3).

Comparison Between Probes: The three probes demonstrate a consistent diurnal pattern, but show variation in sap flow around the circumference of the tree (Figure 2.3).

Inadequate Data: For some TDPs the diurnal pattern of dT included fluctuations (Figure 2.4). The cause of these fluctuations is uncertain as they were not consistently associated with changes in ambient atmospheric conditions such as temperature, *D*, RH, or precipitation.

Ambient Gradients: When the power supply was shut off to observe ambient gradients between 14 and 18 August (DOY 226 to 230) the natural variations for TDP 2 were large ranging from 0.79 to -0.92 dT (°C) and others were small ranging from 0.35 to -0.05 for TDPs 1 and 3, despite the three layers of insulation (Figure 2.5).

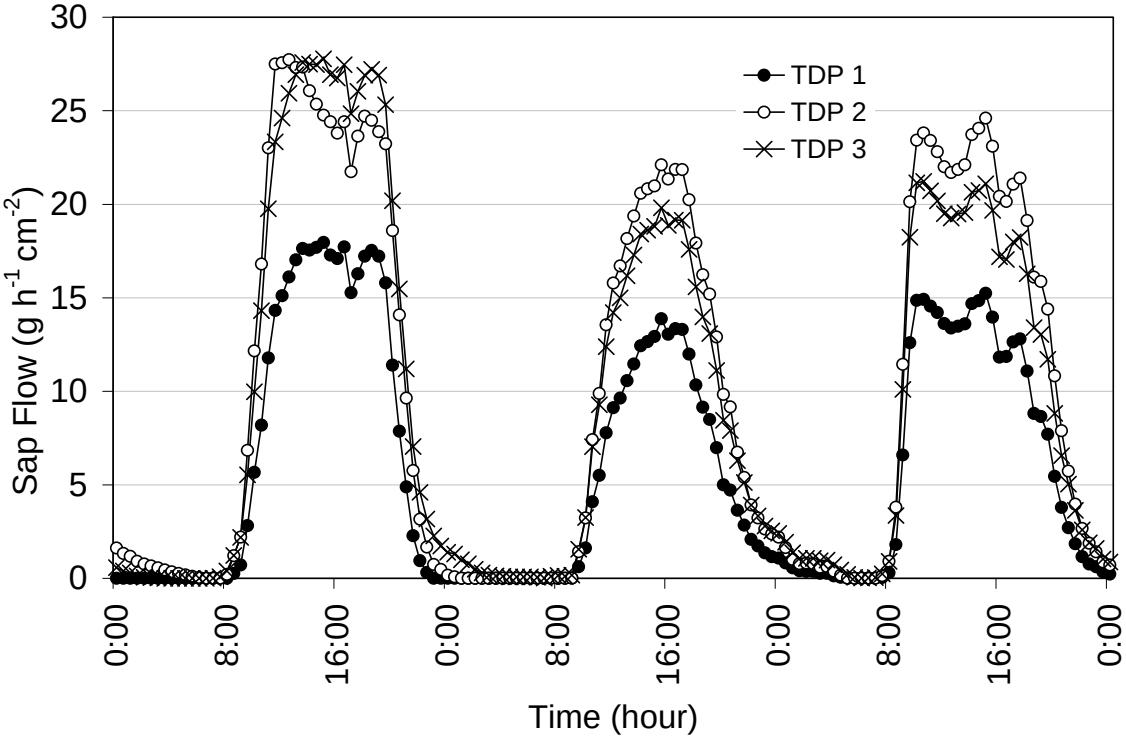

Figure 2.3. Sample of diurnal sap flow variation for three probes at different aspects within one tree (F2). These measurements are from the dT shown in Figure 2.2.

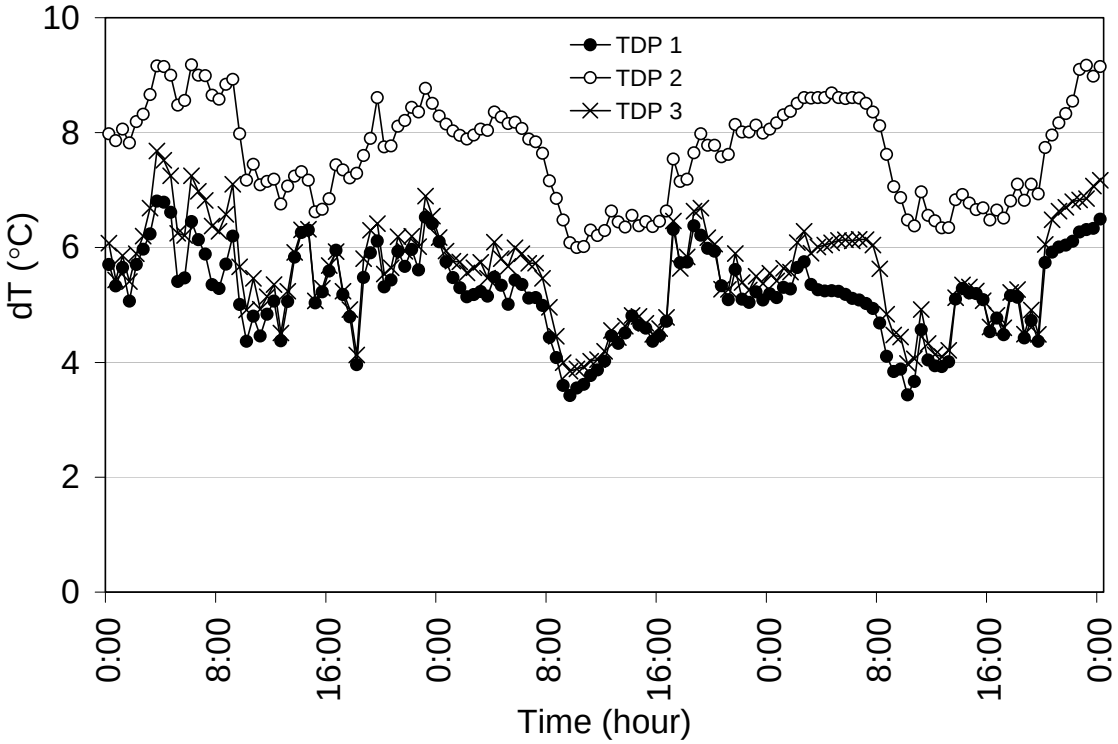

Figure 2.4. Example of inadequate data where unexplained spikes in dT occurred over a three day period from DOY 211 to 213 in all three probes in tree F4.

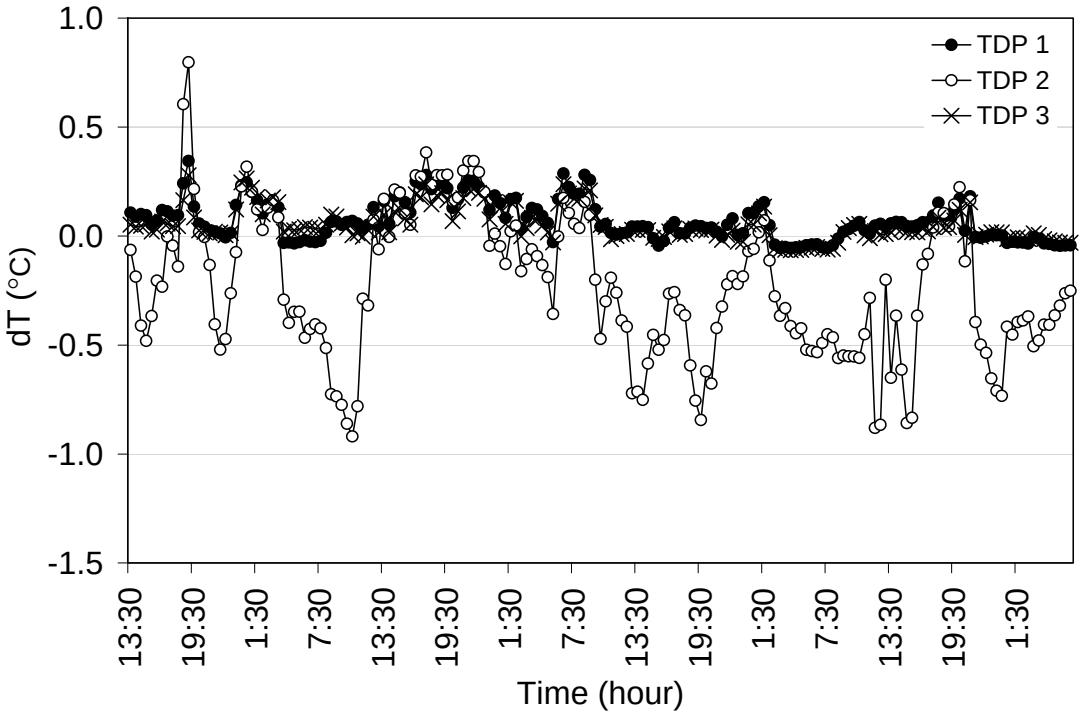

Figure 2.5. Ambient dT of three TDPs for tree M2 over three days in August when power supply was removed from the TDPs.

Estimation of Sapwood Area: The most recent three growth rings of the tree cores (growth from 2004 to 2006) were between 7 and 15 mm total in radial width (data not shown).

2.4 Discussion

Consistent and smooth diurnal dT for some TDPs in some trees gave sap flow data for much of the time between 6 June and 1 October (DOY 157 and 274). At other times, within this time period, the unexplained fluctuations in dT precluded further analysis. This resulted in the elimination of all data from two trees in the study as all three probes within these trees failed to yield smooth diurnal patterns.

As evident from the variation between probes, functional xylem area is heterogeneous throughout the sapwood. Features such as knots have an effect on the velocity found on both downstream and upstream sap flow. The variation among probes is not unusual as it was previously reported to occur in mature Norway spruce and oak trees (Cermák et al. 1992), and among shelterbelt poplar trees (Kort 2005). Because of sap flow around the circumference of the tree is variable due to sapwood area abnormalities, we determined relative sap flow would be best represented using the same TDP(s) throughout the season.

Maximum Temperature Difference: The determination of the maximum temperature difference (dTM) between probes is a crucial component to the calculation of flow from dT. Generally, dTM occurs early morning when there is no sap flow. However, there are conditions in which zero sap flow may not occur,

such as *D* not reaching zero or restoration of storage water. When night time flow occurs, the dTM will be underestimated, leading to an underestimation of flows for that day (Lu et al. 2004). For each probe, the dTM should be calculated separately as they are independently influenced by their local conditions (Lu et al. 2004). Over the season, drifts in dTM can occur as contact between the probes and the sapwood is lost, resulting in decreased thermal conductivity (Lu et al. 2004). Drift of dTM has also been demonstrated with changes in soil moisture (Lu et al. 2004). All of these effects were observed in our experiments, and were accounted for in the estimation of dTM during the course of the season.

Ambient Conditions: Possibly adding to the influence of ambient conditions on the dT readings, the trunk above the insulation would heat up earlier than the trunk beneath the insulation, potentially causing heat transfer in a downward direction toward the probes. In those probes where ambient dT (the dT resulting from ambient conditions when there was no power supply to probes) was small, it was typically quite small in the predawn hours, when dTM was estimated, giving confidence that dTM was not influenced much by effects of ambient dT. Noisy dT signals, at times before and after ambient dT was measured, occurred in probes where there were large fluctuations in ambient dT. While the magnitude of variation in dT differed among probes, fluctuations in ambient dT among probes were mostly synchronous, within and among trees. This suggests that despite the layers of insulation, probes are still influenced by meteorological conditions.

Calculating Sapwood Area: To calculate sap flow for the entire tree as g h^{-1} cm^{-2}, sap velocity estimated from measurements of dT made by the TDP must be multiplied by the sapwood area. Determining an accurate sapwood area is then another essential step in the estimation of sap flow. Increment borers can be used to take tree cores at probe locations for an estimation of in situ sapwood area. However it is difficult to determine the functional xylem area by visually examining the heartwood (darker area) and sapwood (lighter area) as was done in previous studies with *Populus* using TDPs (Pataki et al. 2000; Pataki et al. 2005; Gazal et al. 2006). To successfully determine the exact sapwood area surrounding TDPs, destructive actions must be undertaken. For example, by removing a section of a *Populus* trunk, Sperry et al. (1994) used dye perfusion experiments to show that two rings of functional xylem were contained within the outer sapwood. Cutting down each of the trees used was not an option in our study. However, given this report by Sperry et al. (1994), and results from dye perfusion experiments with one tree from Pearce Corner (D.W. Pearce, C.A. Phelan and S.B. Rood unpublished) and findings from our own tree cores, we established that the 30 mm probes used in our experiment would have extended past the two to three rings of active sapwood. This would have resulted in an underestimation of flow velocity, as TDP method assumes temperature and flow to be integrated over the entire probe length and the relationship between dT and velocity is asymptotic (Lu 1997; Clearwater et al. 1999). This effect was demonstrated in a trial with a tree from the grove at Pearce Corner (D.W. Pearce, C.A. Phelan and S.B. Rood unpublished).

Conclusion: The complexities and variability of using TDPs allowed us to calculate relative sap flow from one or two TDP(s) per tree for six *P. angustifolia* trees. We were unable to calculate estimates of absolute sap flow.

Future Work: When using TDPs the dT output of the TDP probes should be checked regularly for smoothness and consistency, and problems should be resolved in order to decrease the amount of eliminated data. Trees must always be well insulated to help decrease dT variability by diminishing the influence of ambient conditions and achieve a more accurate sap flow. Further, when measuring sap flow in cottonwoods (*Populus*), using short TDPs, such as the TDP-10 (1 cm needles), will measure flow in the active sapwood found in the outer two to three rings. This would help to decrease underestimation errors of calculated flow (Clearwater et al. 1999; Lu et al. 2004).

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CHAPTER 3 Seasonal Sap Flow and Ecohydrology of a Riparian Zone along the Oldman River, Alberta

3.1 Introduction

Cottonwoods in southern Alberta are an integral component of riparian woodlands (Rood and Mahoney 1990). Riparian zones provide rich habitats for wildlife, benefit water quality, enable water storage, and create areas for recreation, especially in semi-arid southern Alberta (Knopf et al. 1998; Horton et al. 2001a). Cottonwoods are classified as phreatophytes (Busch et al. 1992; Gazal et al. 2006), but can utilize both soil moisture and water associated with the groundwater table (Heilman et al. 1996; Zhang et al. 1999; Snyder and Williams 2000). Cottonwoods are the primary and often the only trees in semi-arid regions such as southern Alberta (McKnight and Darrel 2000), where low precipitation and high potential evapotranspiration create low soil moistures and riparian trees and shrubs depend on the riparian groundwater.

In southern Alberta, the riparian groundwater table is variable both seasonally and over the longer term, due particularly to stream flow fluctuations (Rood et al. 2003). Each year, snow-melt and rainfall increase stream flows in the spring. During the later summer months, precipitation is usually limited and there is a decrease in flow. Long term weather phenomena including El Nino Southern Oscillation and Pacific Decadal Oscillation influence the amount of precipitation in southern Alberta (Rood et al. 2005). At the study site at Pearce Corner, a prominent alteration in the long term stream flows occurs due to an upstream dam

and weir. The dam and weir act to alter the naturally dynamic flow regime through their storage and diversion of river water (Rood et al. 2003; Willms et al. 2006).

For cottonwoods, the long term consequences downstream from dams and diversions include, but are not limited to, drought stress created by lower water availability (Rood et al. 2003). Observed impacts are short term physiological responses and their long term accumulation leading to overall population decline (Rood and Mahoney 1990; Stromberg et al. 1996; Rood et al. 2003).

As reviewed by Rood et al. (2003), the short term responses of modified flows can range in duration from minutes to weeks. Initially, with lower water supply it will take a shorter amount of time to reach a critical midday xylem water potential, and once this point is reached, turgor pressure will be reduced promoting stomatal closure to maintain the water potential above the cavitation threshold (Tyree et al. 1994; Tardieu and Simonneau 1998; Horton et al. 2001b; Matzner and Comstock 2001). Stomatal closure causes a decline of CO_2 acquisition which affects the growth of the tree as reported by Stromberg and Patten (1990) who found a strong positive relationship between stream flow and cottonwood trunk expansion and by Scott et al. (1999) who found a decrease in branch growth increments. As discussed in Chapter 1, the reduced soil moisture results in a reduced soil water potential and a decline of the water potential difference between roots and leaves. In adjusting to a decline in the water

potential difference, several morphologic changes were observed including reduced shoot elongation and total leaf area (Rood et al. 2003). Another change included crown die-back or branch sacrifice (Rood et al. 2003). This reduced leaf area possibly compounding the decreased CO_2 acquisition.

While researchers have emphasized the water relations following damming, diversion, and groundwater extraction, there have been few studies where the relationship between normal seasonal variation and stream flow are related to consequences on water relations in a natural population of *Populus* (Hogg and Hurdle 1997; Pataki et al. 2000; Pataki et al. 2005; Gazal et al. 2006). Consequentially, in this study we analyzed water relations in a natural, and fairly healthy, *Populus* grove.

Predictions:

1. Seasonal decline in river level will lead to a decline of the groundwater table and soil moisture.
2. The decrease in soil moisture will result in a decline in Ψ_S over the season.
3. The minimum Ψ_L will remain fairly constant through the season due to the isohydric nature of *Populus*.
4. The reduction of Ψ_S but maintenance of Ψ_L will reduce the difference in soil water potential between the soil and leaves (Ψ_S-Ψ_L).
5. The rate of sap flow will decline with the decreased water potential difference (Van den Honert equation), assuming resistance or alternatively conductance between soil and leaves remains constant.

6. Given the same atmospheric demand (*D*), stomatal conductance will decline over the season to maintain $\Psi_{L.}$

For testing these predictions, river, precipitation, groundwater table, and sap flow along with environmental conditions were continuously measured. We monitored the sap flow, an approach that has recently increased in popularity among tree physiologists who use it to compare water relations between the environment and woody vegetation (Kort 2005). Leaf level physiology was also monitored in June, July, and August through stomatal conductance and leaf water potential measurements. Further, when the tree is at a steady state, sap flow is equal to transpiration (Chapter 1) thus sap flow combined with vapor pressure deficit (*D)* data allows for canopy conductance to be estimated. The data were evaluated to understand what occurs in a natural population of cottonwood trees as the river and groundwater table fall, and as soil water supply is depleted.

3.2 Materials and Methods

3.2.1 Study Area

The study area, Pearce Corner, is located along a constrained reach of the Oldman River (49°51' N, 113°15' W), approximately 30 km northwest of Lethbridge Alberta, Canada (Figure 3.1). Upstream from this point the river changes from a sinuous, alluvial, open valley reach to a straight, narrow, and confined reach (Willms et al. 2006) (Figure 3.2). Pearce Corner is located downstream from two flow- regulating structures: the Lethbridge Northern Irrigation District (LNID) weir and the Oldman Dam. The LNID weir, approximately 40 km upstream of Pearce Corner, was built in 1922 and is used to divert stream flows into the LNID canal to provide water for irrigation. High irrigation demands resulted in low downstream summer flows and unfavorable conditions for riparian areas (Rood and Mahoney 1991). The Oldman Dam, approximately 75 km upstream, began operations in 1992. It was built to provide a reservoir to trap water during spring runoff, storing it for release in the late summer months when stream flows are low and irrigation demands are high (Rood and Mahoney 1991).

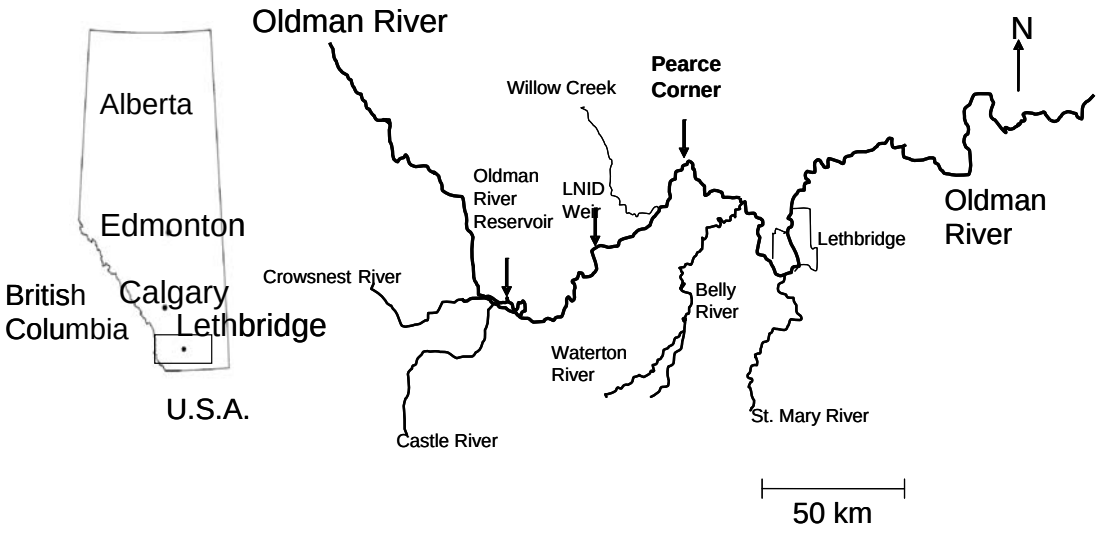


Figure 3.1. Map of the Oldman River in southern Alberta showing the study site at Pearce Corner. LNID = Lethbridge Northern Irrigation District.

Figure 3.2. 1:32,000 aerial photograph of Pearce Corner cottonwood grove (surrounded by the black box) (Obtained from Alberta Sustainable Resource Development. Picture dated March 1970).

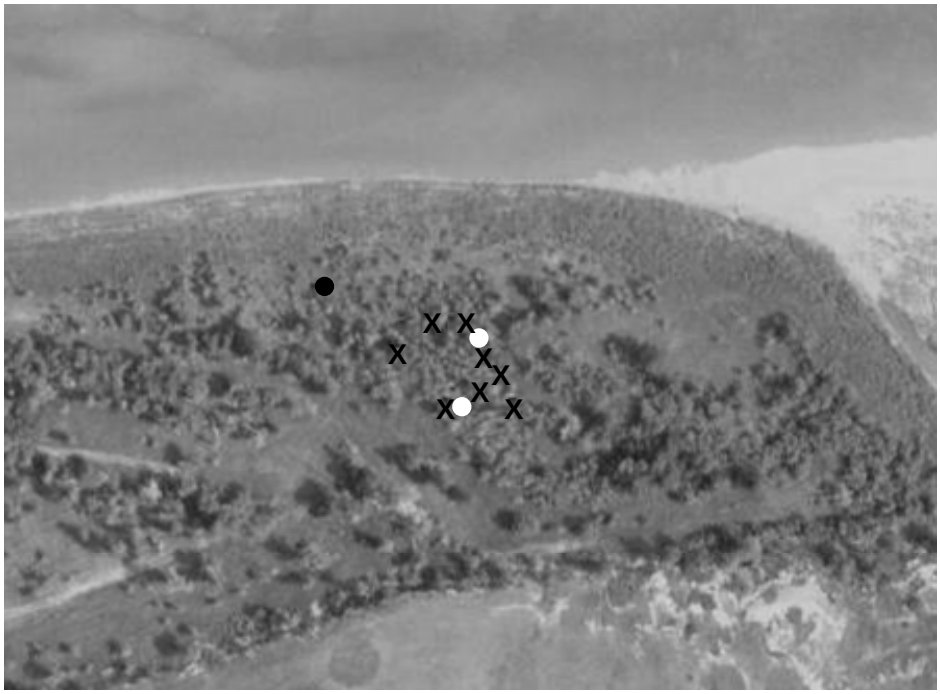


Figure 3.3. Aerial photo of location of trees (**X**), the two sets of THLOG soil moisture probes and piezometers (white dots), and the weather station (black dot) (Obtained from Alberta Sustainable Resource Development. Picture dated 1997).

3.2.2 Tree Attributes

Trees: At Pearce Corner the trees are predominately narrowleaf cottonwoods, *Populus angustifolia* James, with some hybridization and introgression from black cottonwoods, *P. balsamifera* L. There are also a few *P. balsamifera* L., subspecies trichocarpa, and some hybrids with *P. deltoides* Bartr. Ex Marsh (Rood et al. 1986). To ensure that clones were not chosen as study trees, stages of vegetative and reproductive bud flush in potential subjects were recorded on 10 and 15 May (DOY 130 and 135) (Gom and Rood 1999). Leaves were also collected between 19 and 25 June (DOY 170 to 176) and were photocopied for the species analysis which considered petiole, leaf and blade shape (Rood et al. 1986). Eight trees were selected based on their proximity for instrumentation, species, clonal identity, height, diameter, canopy accessibility, sex, and overall health (Table 3.1, Figure 3.3). The trees were surveyed using a transit and staff to determine the level of the base of trunks in relation to groundwater table depth and river level.

Branch Elongation: To monitor growth, rate of canopy expansion, and for age determination, branch increments were measured and increment cores were extracted and analyzed, following the methodology described by Willms et al. (1998). Once weekly, new shoot length was measured on five branches per tree that were located at a mid-canopy height of approximately 3.7 m. If accessible, branches were chosen to encompass the tree. Measurements commenced on 19 May (DOY 139) and ended on 17 July (DOY 198) after 2006 branch elongation was complete.

Table 3.1. Characteristics of narrowleaf cottonwoods studied at Pearce Corner along the Oldman River. Height was estimated using a clinometer. DBH is diameter at breast height (1.3 m). Age was estimated from ring counts on increment cores.

Tree Name	Tree	Sex	Age	Height (m)	DBH (cm)
Carlos	M1	M	34	10.5	24.5
Rico	M2	M	38	12.3	24.5
Pedro	M3	M	39	8.0	21.0
Juan	M4	M	41	12.0	24.8
Maria	F1	F	29	8.6	17.5
Rosa	F2	F	33	12.2	27.1
Bertha	F3	F	43	12.1	30.2
El Chup	F4	F	33	12.9	28.9

3.2.3 Meteorological Conditions

A Dynamet weather station (Campbell Scientific Inc. Logan, Utah, USA), positioned in a clear area approximately 60 m from the study trees, was used to measure and record meteorological conditions at Pearce Corner from 12 April (DOY 102) through 3 October (DOY 276) (Figure 3.3). A temperature and relative humidity probe (CS500, Campbell Scientific, Inc.) was set at 1.2 m and enclosed by a Gill Radiation Shield. These were used to calculate *D*. A tipping bucket rain gage (TE525, Campbell Scientific Inc.) was used to measure precipitation. A silicon radiation sensor (LI-200SZ Pyranometer Sensor, LI-COR Biosciences, Lincoln, Nebraska, USA) was set at 1.2 m to monitor changing day length and diurnal variation of insolation. A cup anemometer (03101-5 Anemometer, Campbell Scientific) measured wind speeds.

Vapor Pressure Deficit (D): The *D* was calculated from temperature and RH according Buck (1981):

$$\text{Saturated Vapour Pressure (SVP)} = 0.611 \times e^{\left(\frac{17.502 \times T}{T + 240.97}\right)}$$

$$\text{Actual Vapour Pressure (AVP)} = \frac{RH \times SVP}{100}$$

$$D = \text{SVP} - \text{AVP (kPa)}$$

Where

e = normal log base 2.718282

T= temperature in °C

RH = % relative humidity

D = vapor pressure deficit, defined as the difference between the internal leaf vapor pressure, which is assumed to be saturated (RH = 100%), and the ambient vapor pressure.

The weather station was powered by a 12 V battery, recharged by an MSX 10 solar panel, and data was acquired and stored under the control of a CR 10X datalogger (Campbell Scientific Inc.). Measurements were made every 10 seconds by the instruments and values from the previous hour were averaged for hourly outputs.

The closest weather station (Monarch, AB) was 18 km downstream and is in an upland setting (Environment Canada 2007). However, this location would not give an accurate representation of the environmental conditions at Pearce Corner because of the unique microclimate of this valley site.

3.2.4 Water Supply

River level was measured through the season by measuring the distance from a fixed point to the water edge. The river level at each of these times was determined from an elevational profile that was surveyed with a transit and staff gauge (± 0.5 cm) and related to an arbitrary zero level.

Groundwater Table: A stainless steel drive well point (model 615N, Solinst Canada Ltd., Georgetown, Ontario) attached to 4 m of steel tubing was driven down approximately 3.8 m into the ground for groundwater table measurement at

two locations among the trees (Figure 3.3). These two piezometers were installed on 29 May and 31 May (DOY 149 and 151) and after installation, groundwater level was regularly measured with a water level meter (Solinst Canada Ltd.).

Soil Moisture: Soil moisture was measured with Theta Probe ML2x soil moisture sensors and recorded with a THLOG-4 data logger (Dynamax, Houston TX, USA). Calibration values were programmed into the soil moisture loggers using BoxCar software version 3.7 (Dynamax, Houston TX, USA). A logger was set up at each of two locations, next to the groundwater table wells (Figure 3.3). At each location four probes were placed at different depths ranging from 22 cm to 140 cm to measure moisture percent by volume. Measurements were made every four hours from 1 June (DOY 152) through 30 September (DOY 273), except for the period between 5 June (DOY 156) and 4 July (DOY 185) when the power supply failed.

3.2.5 Sap Flow and Related Measurements

Thermal dissipation probes (TDPs) were installed and operated to measure sap flow as discussed in Chapter 2. Diurnal courses of sap flow were established, and in order to compare sap flows over the season, for each day half hourly sap flow values were used to calculate the average "afternoon sap flow" in the period between 12:00 h and 16:00 h, two hours on either side of solar noon (Figure 3.4). During this time the insolation level was above the stomatal conductance light saturation point 0.4 kW m^{-2} estimated from our data and also determined in a similar study with poplars (Zhang 1997) (Figure 3.4). Below 0.4 kW m^{-2}

conductance was found to increase with increasing insolation and *D*. This time period was chosen as at this time removes the influences on sap flow estimates of changing day length, possible overnight flow and stem water recharge. Further this time period removes influential factors such as temperature, RH, and *D* were usually not changing sharply (Figure 3.6), and Ψ_L and sap flow tended to be relatively stable (Figures 3.17 and 3.20). For each tree sap flow data gaps occurred due to inadequate data.

Stomatal Conductance: On four days during each of mid-to-late-June,-July, and -August (DOY 170, 173, 174, 176, 202, 206-208, 229, 230, 233, 234) the stomatal conductance (g_S) and leaf water potential (Ψ_L) were measured on fully developed leaves, with two trees measured per day. An LI-1600 steady state porometer (LI-COR, Lincoln, Nebraska, USA) was used to measure g_S on the abaxial side of the leaf. Measurements were taken between a height of 4.0 m to 5.0 m in the outer canopy for one leaf on each of the first five short shoots on one branch. Leaves on three branches, one at each N, SE, SW aspect, were measured per tree, for a total of 15 leaves measured at every sample interval. To represent the leaf level aspect of transpiration, we graphed g_S against *D*, enabling a comparison between June, July, and August water loss for a given *D*.

Mean Canopy Stomatal Conductance: A related measurement of (relative) mean canopy stomatal conductance (G_S) was calculated for each tree. Whole- tree transpiration (g H_2O/ m^2 leaf/ second) is equivalent to sap flow (g H_2O/ second)

divided by leaf area, provided that there is no lag time between transpiration and sap flow. In this study, sapwood area was not measured, and an area of 1 cm^2 arbitrarily assigned. Leaf area was not measured and an area of 1 m^2 has been arbitrarily assigned. Values of whole-tree transpiration calculated on this basis are then not absolute, and can thus be compared only in relative terms. For the purpose of comparison within individual trees during the course of the season it has been assumed that sapwood and leaf area were constant. G_S for a tree canopy can be calculated from whole-tree transpiration and D as

$$G_S = \frac{(G_V T_a \rho E_L)}{D} \quad \text{(Schafer et al. 2000)}$$

Where

G_V is the universal gas constant adjusted for water vapor

T_a is the air temperature (K)

ρ is the density of water

E_L is transpiration per leaf unit area

D is vapor pressure deficit (kPa)

It is assumed that D can be used as the driving variable for G_S, a common assumption if trees are well-coupled with the atmosphere, for example if leaf boundary layers are small. However it is important to mention that variation in leaf temperature does occur and may not be the same as the ambient temperature. This difference is notable as it will influence the internal leaf vapor pressure and subsequent transpiration (Tyree and Wilmot 1990). To represent seasonal G_S, sap flow data above the stomatal light saturation level of 0.4 kW m^{-2} were divided up into periods for June (DOY 157-174), July (DOY 194-207), and August (DOY

231-240). For each group the data were fit with a logarithmic trend line which then provided slope and a reference point of the relative G_S when D was 1 kPa for June, July, and August (Schafer et al. 2000).

Leaf Water Potential (Ψ_L): A PMS Model 1000 Pressure Chamber (PMS Instrument Company, Corvallis, Oregon, USA) was used to measure Ψ_L. For each tree, two leaves for each of the three aspects were removed from outer canopy branches at similar heights and were measured within five minutes of removal. When weather conditions permitted, measurement times occurred from 6 am through 8 pm for June and July, and from 7 am to 8 pm during August, with two trees being measured each day. Hourly measurements were made from 6 am until noon, then in the afternoon every 1.5 to 2 hours.

3.2.6 Statistical Analyses

To test for differences in sap flow among different groups of DOY, an analysis of covariance (ANCOVA) was used with D as a covariate using JMP version 6.0.0 (2005 SAS Institute Inc.). Sap flows were divided up into five groups (when sap flow was not interrupted by power losses) ranging from 6 June – 21 June (DOY 157-172); 3 July – 13 July (DOY 184-194); 14 July – 26 July (DOY 195-207); 30 July – 13 August (DOY 211-225); 19 August – 28 August (DOY 231-240). When significant results were found between groups, a Tukey's HSD post hoc test was used to determine which groups were significantly different.

Using SPSS version 13.0 Ψ_S, g_S and G_S values were analyzed. Predawn Ψ_L values which represented Ψ_S were compared using an ANOVA. g_S values were interpolated during the morning values to find values that corresponded to a D = 1. These g_S values were then analyzed using a paired t- test. G_S values were analyzed using a one-sample t-test. For all trees, values of reference canopy stomatal conductance (G_{Sref} when D = 1) and slope for June, July, and August were taken and divided by one another (July/June; August/June; August/July) to create a ratio which could then be compared to a reference ratio of 1. A value of 1 represented the ratio where reference stomatal conductance or slopes were the same.

3.3 Results

3.3.1 Meteorological Conditions

Insolation: Between June and August day length decreased due to the later rising and earlier setting of the sun in August (Figure 3.4). Although the diurnal maximum insolation decreased, the time of the maximum remained constant, occurring between 13:00 h and 15:00 h. There was a gradual decline in maxima from 17 June (DOY 168) where at 14:00 h insolation peaked at 0.98 kW m^{-2} through to 1 September (DOY 244) where the 14:00 h insolation peak reached only 0.78 kW m^{-2} (Figure 3.5).

Temperature: Diurnally, as insolation increased, the temperature rose (Figure 3.6). Lagging behind the insolation pattern, peak temperature occurred between 15:00 h and 18:00 h. Average daily maximum temperatures were 23°C for June,

30°C for July, and 28°C for August (Figure 3.7). The maximum riparian zone temperatures found at Pearce Corner were 2 to 4°C higher than those measured at a nearby upland weather station. For example, in 2006 the Monarch weather station (18 km downstream) had average maximum temperature for June, July, and August of 21°C, 27°C, and 24°C (Environment Canada 2007). For Pearce Corner, average daily minimum temperatures were 8°C for June, 10°C for July, and 6°C for August with the minimum temperatures remaining above 0°C until 1 September (DOY 244). These higher temperatures in July and August decrease the vapor pressure of the atmosphere and hence increase *D*.

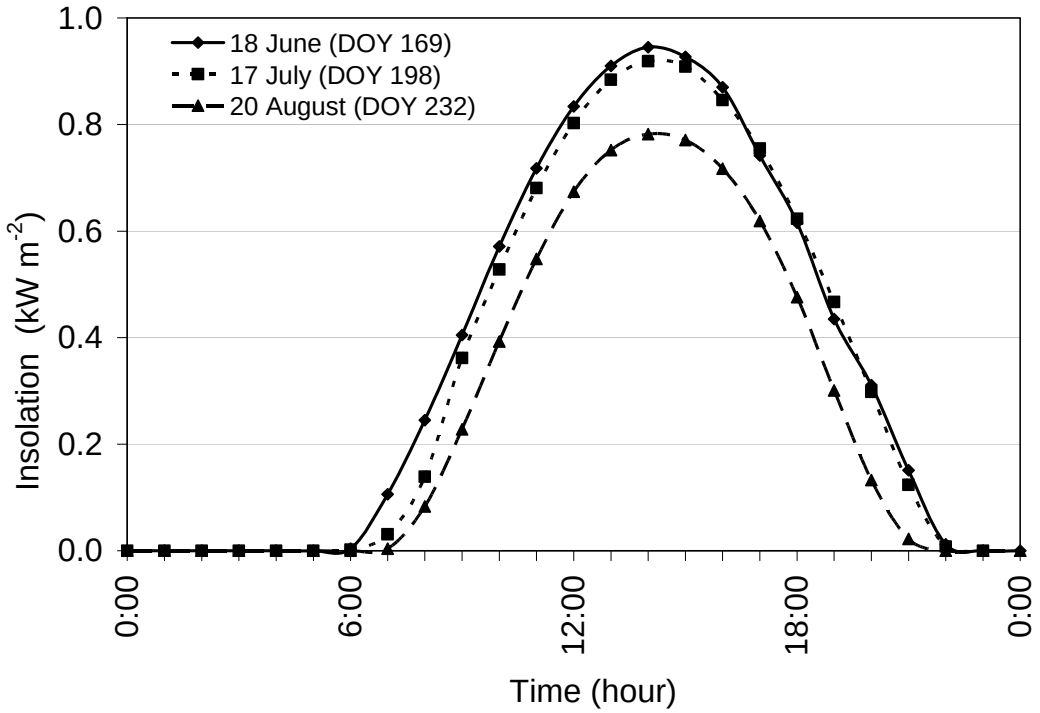


Figure 3.4. Diurnal trends of insolation for clear days in June, July, and August in the riparian zone at Pearce Corner cottonwood grove along the Oldman River. Time is Mountain Standard Time.

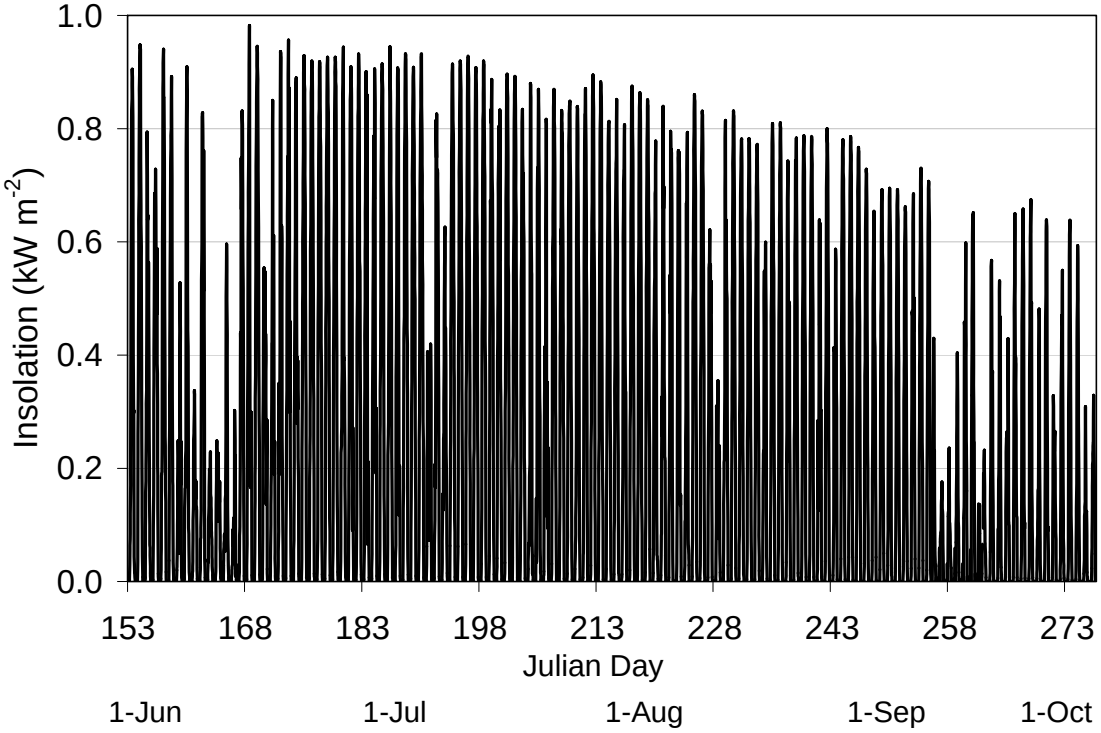


Figure 3.5. Hourly insolation values at Pearce Corner from June through September 2006.

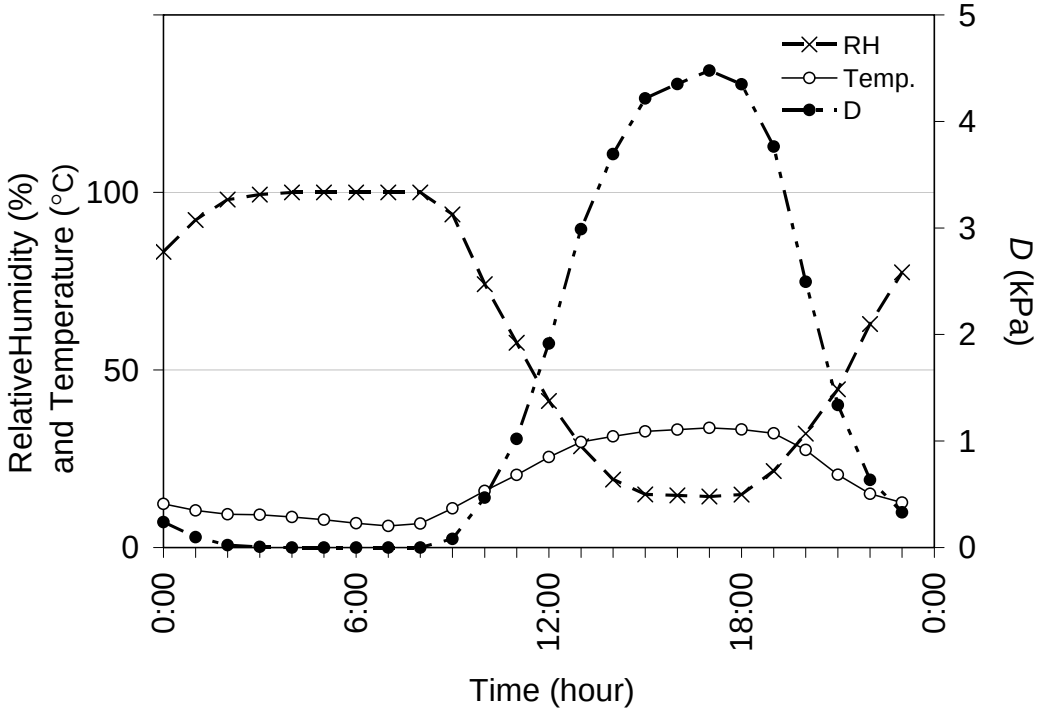


Figure 3.6. Diurnal temperature, relative humidity (RH), and vapor pressure deficit (*D*) at Pearce Corner on 21 August (DOY 233). These results are typical of a clear, sunny day.

Relative Humidity: During early morning hours, relative humidity (RH) reached 100 % 111 of the 128 days plotted (Figure 3.6). With increasing insolation and temperatures, RH decreased daily to an average minimum of about 40 % in June, 30 % in July, and 25 % in August (Figure 3.6 and 3.8). Daily minimum RH was generally reached around 14:00 h in June, and 15:00 h in July and August. On hot and dry days in July and August, RH values fell as low as 15 %.

Vapor Pressure Deficit(D): The combination of high temperature and low RH resulted in *D* peaking between 15:00 h and 18:00 h, with the highest values measured at 17:00 h (Figure 3.6). The average daily maximum *D* in June, July, and August was 1.55 kPa, 2.64 kPa, and 2.79 kPa, respectively (Figure 3.9). The highest *D* was reached on 7 August (DOY 219) at 4.8 kPa.

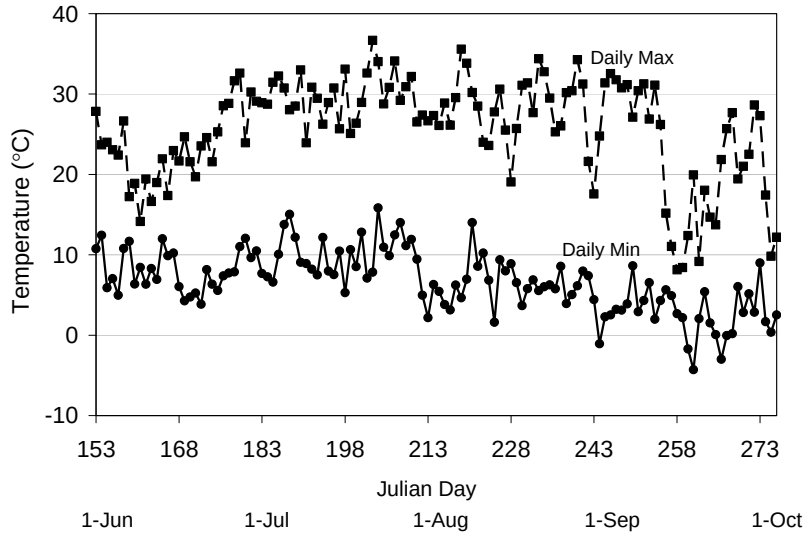


Figure 3.7. Daily maximum and minimum temperatures at Pearce Corner.

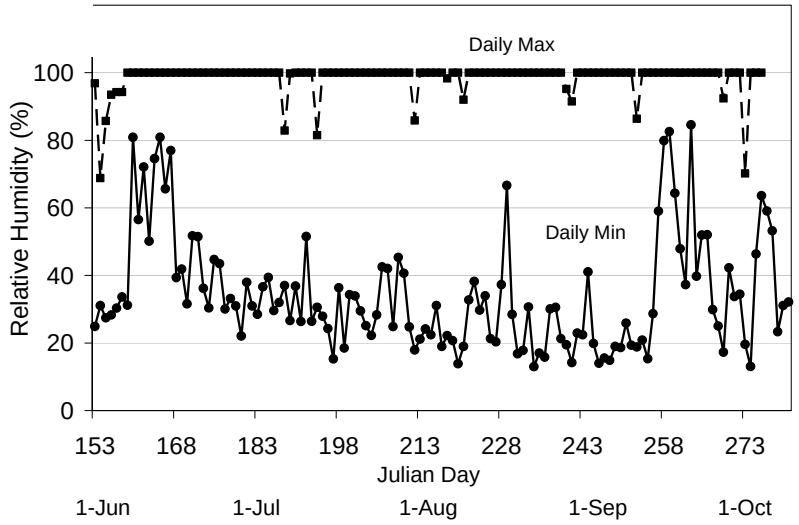


Figure 3.8. Daily maximum and minimum relative humidity at Pearce Corner.

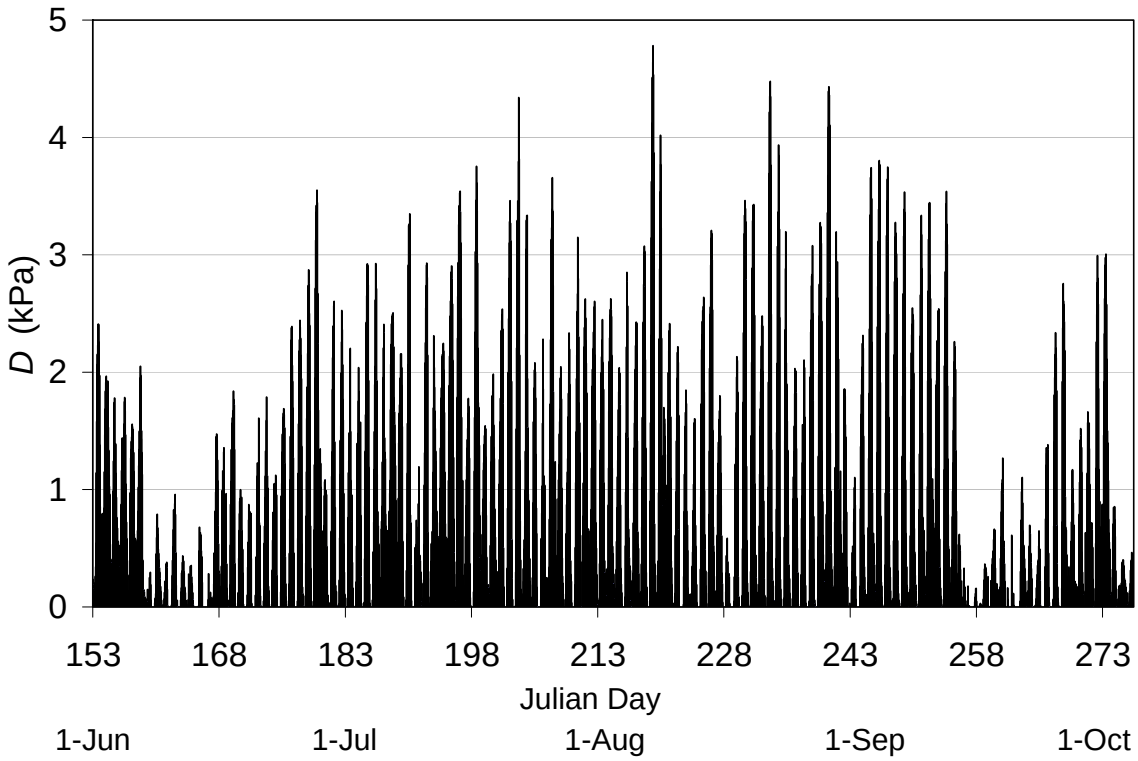


Figure 3.9. Hourly vapor pressure deficit (*D*) at Pearce Corner from June through October 2006, calculated from air temperature and relative humidity (RH).

Seasonal Wind Speeds: The majority of wind speeds at Pearce Corner were less than 6 km h^{-1} (Figure 3.10). The exceptions are on 9 July (DOY 190) at 20:00 h and 13 September (DOY 256) at 19:00 h where winds reached speeds of 14 km h^{-1} and 9 km h^{-1}, respectively. When winds were present, they were typically light through night and early morning hours but became stronger in the late morning and afternoon.

3.3.2 Tree Attributes

Branch elongation was measured weekly from 19 May (DOY 139) to 17 July (DOY 198) (Figure 3.11). Maximum current season length was reached between 4 July (DOY 185) and 17 July (DOY 191). The branches were at low to mid-canopy height and may not be representative of the whole tree as higher branches might have continued to elongate. The diameter at DBH was similar for all eight trees on which sap flow was measured (Table 3.1).

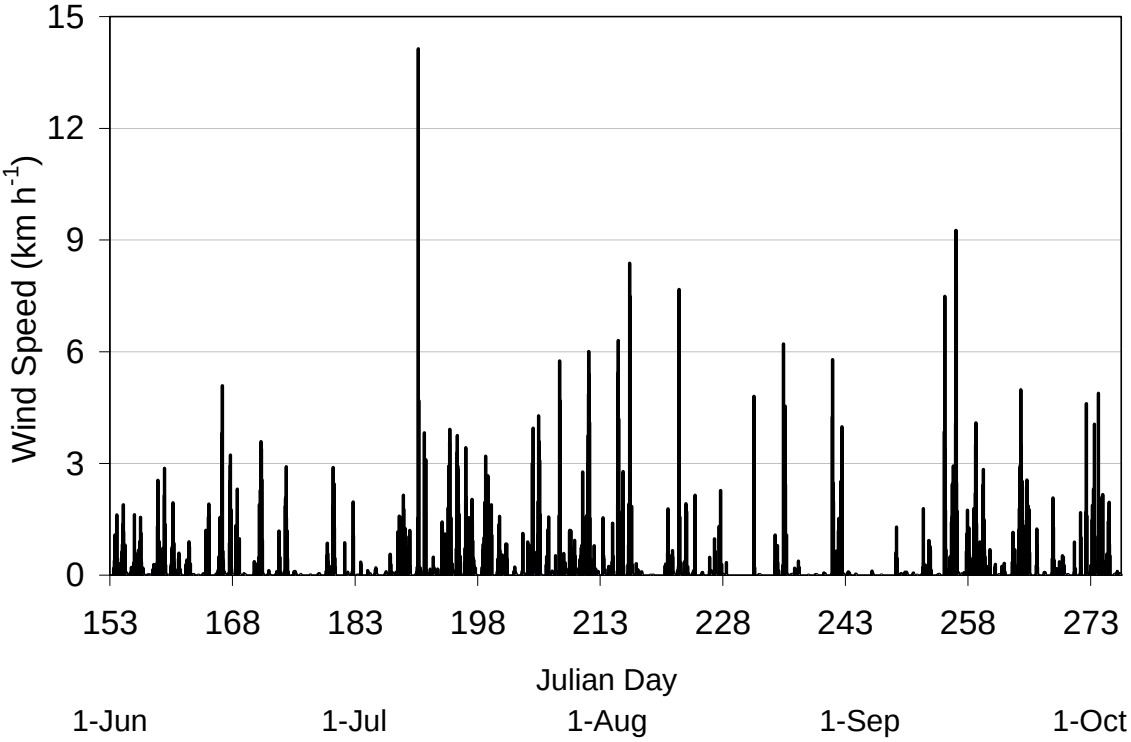


Figure 3.10. Hourly wind speeds at Pearce Corner for the 2006 season.

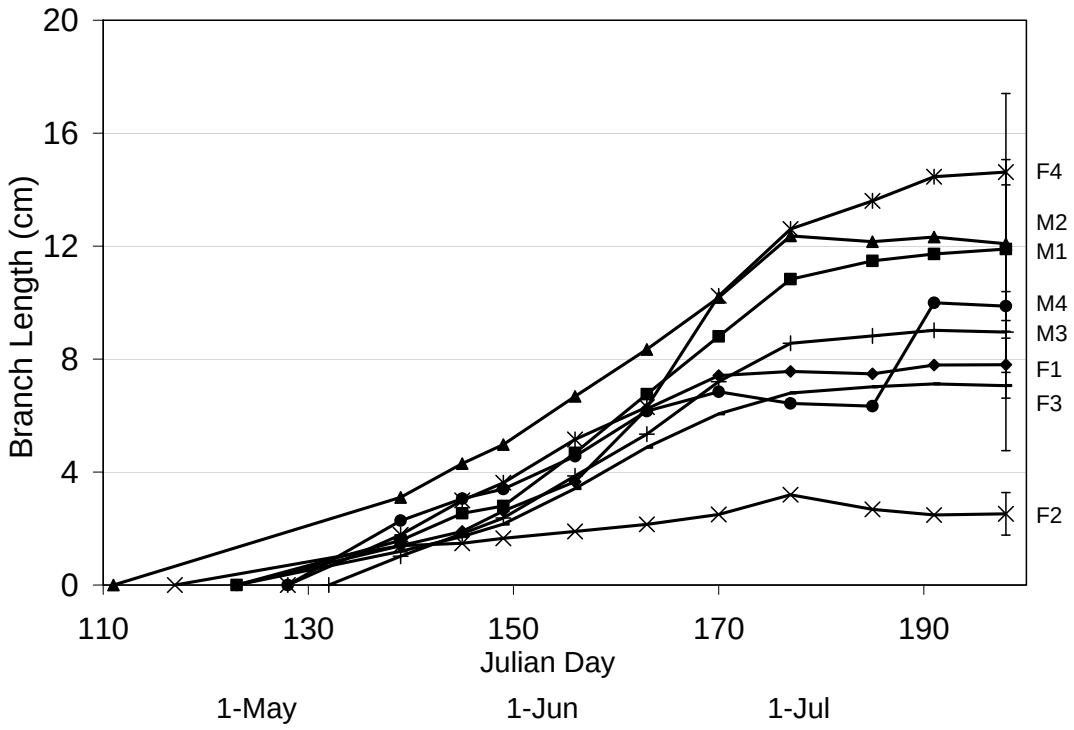


Figure 3.11. Branch length (elongation) of the eight trees from May through mid-July (mean ± S.E., n = 5). The mean of five branches within the lower canopy are shown with S.E. on the last point, typical of S.E. at other measurements.

3.3.3 Water Supply

River: River level increased between 19 May (DOY 139) and 25 May (DOY 145) following snow-melt in the headwaters, and increased again on 16 June (DOY 167) after heavy rainfall in the watershed (Figure 3.12). After this peak, the river level decreased by 187 cm in late August. Compared to historical data from the Lethbridge gauging station (35 km downstream), the 2006 stream flows were low to average. May, June, July, August, and September average discharge ranked 60th, 45th, 65th, 51st, and 47th respectively, out of the 88 years on record (Environment Canada 2007).

Groundwater Table: Maximum groundwater table levels lagged three days behind the peak river level (DOY 170 and 167) and were lower by 37 cm (Figure 3.12). Resembling river flows, there was a decline of the groundwater table levels by approximately 160 cm from the high levels measured in June. Through surveying it was found that the elevation of the bases of the trees was comparable, varying only by 50 cm in relative elevation (Figure 3.12). At the peak groundwater table levels, trees were found to be within 25 cm (for the lowest tree), and 75 cm (for the highest tree) of the saturated zone.

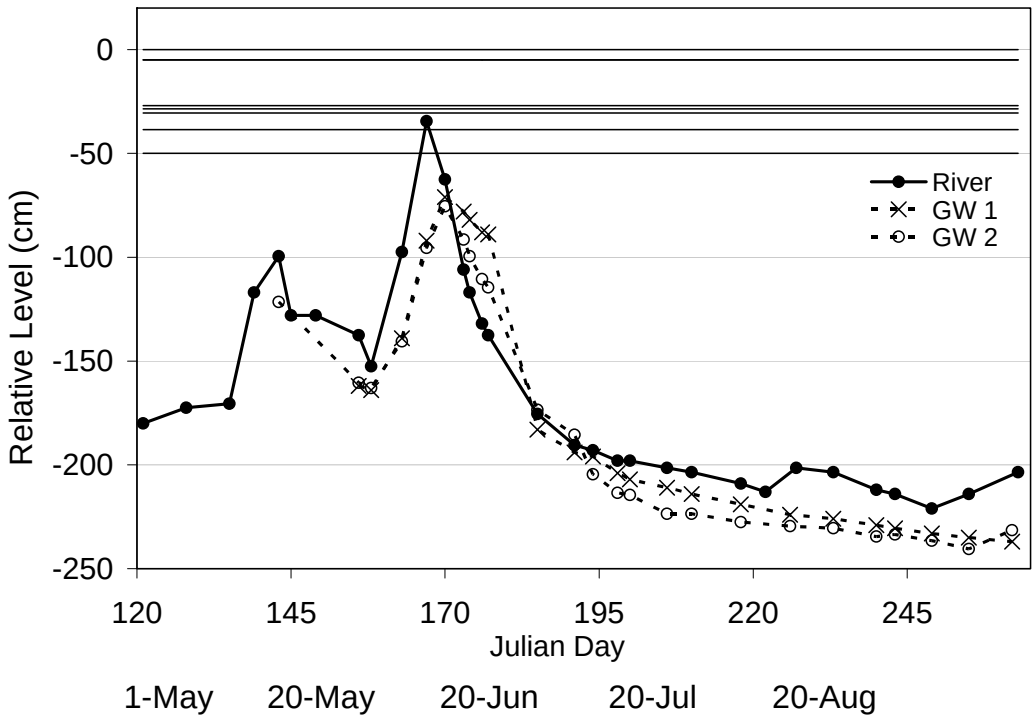


Figure 3.12. Relative groundwater table from May through September at the two piezometer locations (GW 1 and GW 2). GW 1 and GW 2 were approximately 85 m and 100 m, respectively, from the river. The relative level of the river is included for comparison. Horizontal lines between 0 and - 50 cm are the relative elevations of the bases of the trunks of the eight trees measured.

Rainfall: A total of 20.0 cm of rain fell from 1 May (DOY 121) to 1 October (DOY 274) (Figure 3.13). One-third of this rain fell on 15 June (DOY 166) which received 6.6 cm of rain. Total rainfall for June was 11.4 cm, 0.4 cm for July, and 3.5 cm for August. To put 2006 rainfall into a historical perspective, total rainfall data from the Monarch weather station (18 km downstream) was compared to find May, June, July, and August ranked 15th, 8th, 25th, and 13th respectively, out of 26 years on record (Environment Canada 2007). It is possible that moisture carryover may have occurred into the early 2006 growing season, due to flooding in June 2005.

Soil Moisture: At all depths, soil moisture increased between 5 June (DOY 156) and 19 June (DOY 170), during the period when the groundwater table increased, and when heavy rain fell on 14 and 15 June (DOY 165 and 166) (Figures 3.12, 3.13 and 3.14). Peak moisture was measured on 19 June and 20 June (DOY 170 and 171) during which the 84 cm, 92 cm, and 140 cm probes would have been under the high groundwater table. The measurements taken while submerged in the groundwater table indicate the maximum moisture content for this soil, which ranged between 36 % to 41 % by volume. Following peak moisture, soil moisture at 0.5 m declined to 12 % (1st set of probes, GW1) or 17 % (2nd set of probes, GW2) by 31 July (DOY 212), during a time when there was little precipitation and the groundwater table had declined (Figures 3.12, 3.13 and 3.14). At both locations, the deepest probes (84 cm and 140 cm) did not record the highest moisture %. This could be due to the soil composition as it became sandier with

less clay as depth increased, indicating it could not retain water as well as the upper layers.

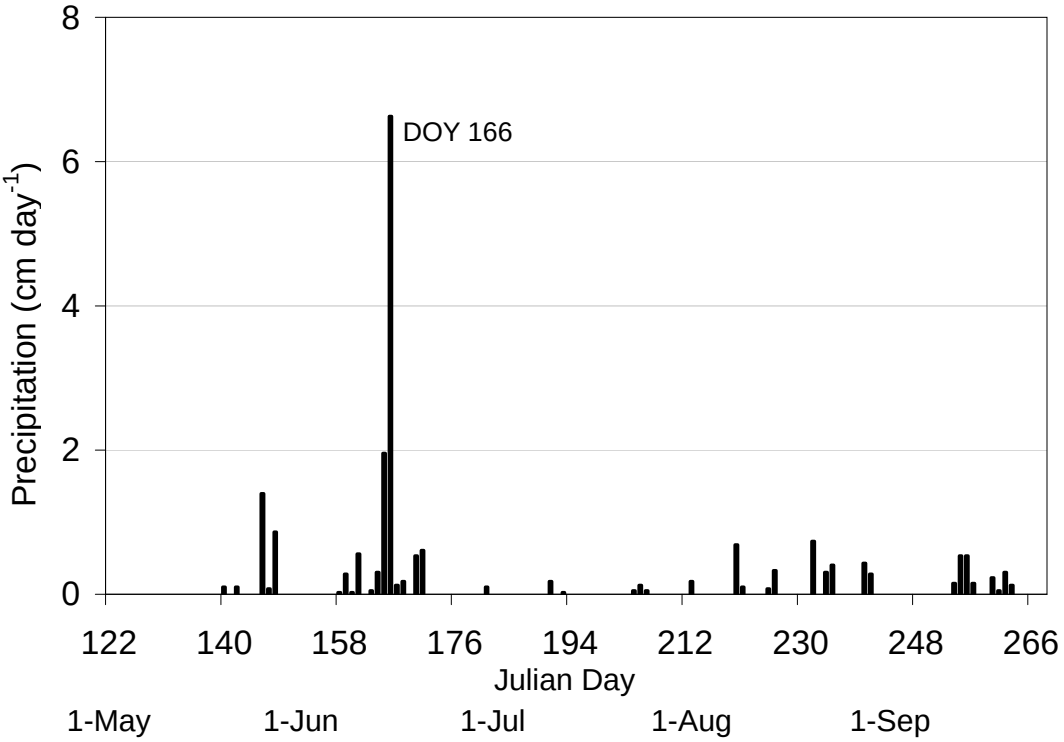


Figure 3.13. Daily precipitation at Pearce Corner.

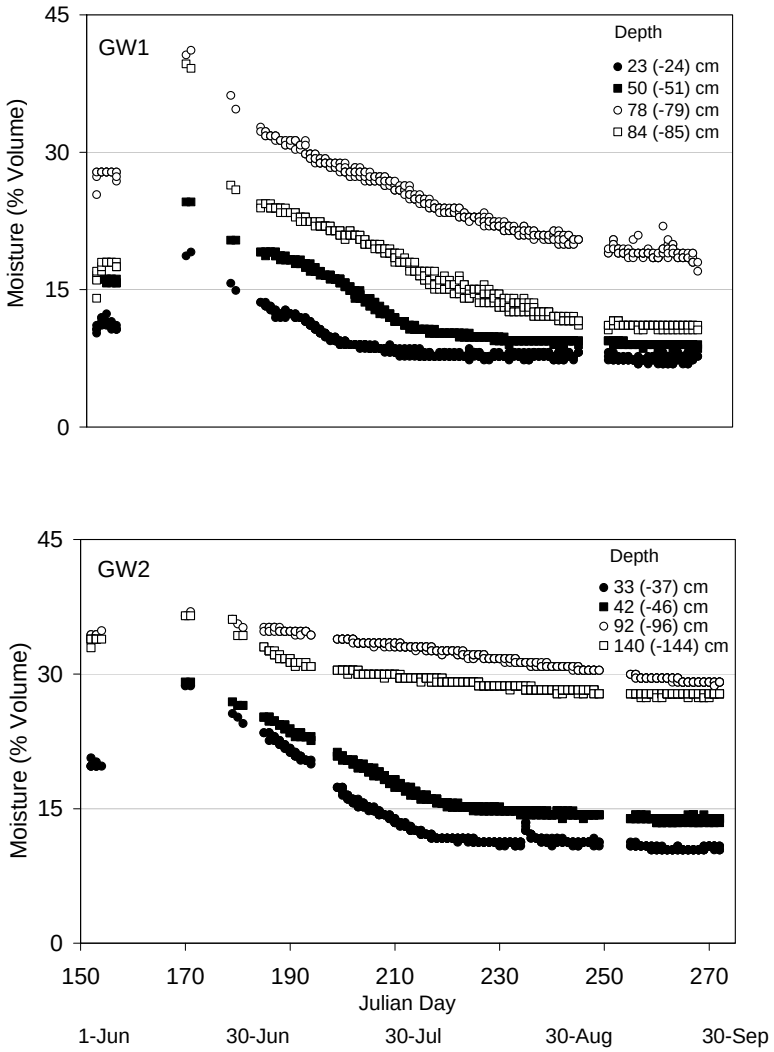


Figure 3.14. Soil moistures (% volume), at groundwater table (GW) 1 (top) and GW 2 (bottom) at Pearce Corner. Probes for each soil moisture set were placed at different depths below the soil surface (see legend). The bracketed numbers in the legend show the depths of each of the probes in relation to the arbitrary fixed zero point found in Figure 3.12. Measurements were interrupted during 5 June (DOY 156) to 4 July (DOY 185) when the power supply failed.

3.3.4. Stomatal Conductance and Water Potential Difference

Soil Water Potential: Ψ_S was not directly measured; however, it can be represented by the average predawn Ψ_L for June, July, and August (Figure 3.17). Ψ_S decreased ($F_{2,19} = 8.617$, $p = 0.002$) as soil moisture declined from 19 June (DOY 170) to 22 August (DOY 234) where the for June was larger than July and August ($p = 0.056$ and 0.002 respectively) and July was not significantly larger than August ($p = 0.198$).

Stomatal Conductance and Leaf Water Potential: Diurnally, stomatal conductance (g_S) rose sharply to a peak around 10:00 h (Figure 3.15). Accompanying this increase, Ψ_L declined, reaching its most negative value at about noon (Figure 3.15). After peaking, g_S declined and the Ψ_L was maintained until 17:00 h when it began to increase (Figure 3.15). On this day, the g_S began to increase again at 17:00 h, however this was atypical.

Leaf Water Potential Differences: Diurnally, in June, July, and August, Ψ_L showed similar patterns of change with a decrease towards a consistent midday Ψ_L value, then maintenance of this value, followed by an increase (Figure 3.16). This is further demonstrated in average of midday Ψ_L where values from June through August were maintained at about -2.1 MPa (Figure 3.16). June predawn Ψ_L was less negative than August ($F_{2,19} = 8.617$, $p = 0.002$), but there was no difference between June and July ($p = 0.056$) and July and August ($p = 0.198$). By subtracting the midday Ψ_L from the predawn Ψ_L the difference changed from 1.9 MPa in June, to 1.8 MPa in July, and to 1.6 MPa in August.

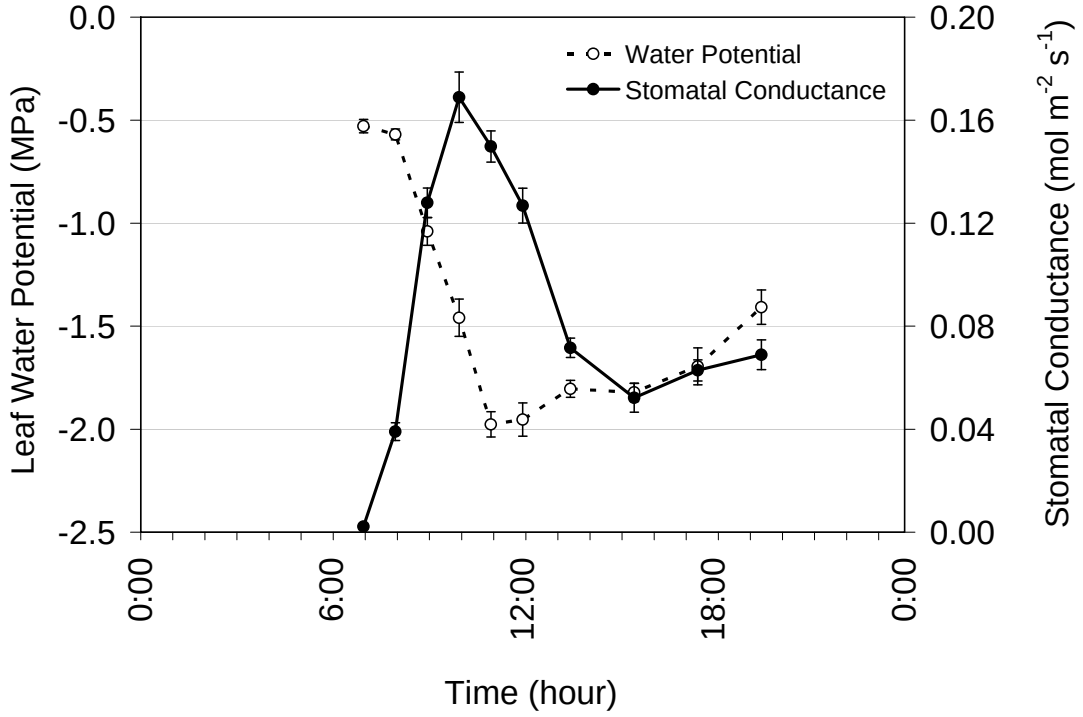


Figure 3.15. Diurnal pattern of leaf water potential (Ψ_L) and stomatal conductance measured in one tree on 21 August (DOY 233) (mean ± S.E.). For Ψ_L, six leaves were measured at each time; for stomatal conductance, 15 leaves were measured at each time.

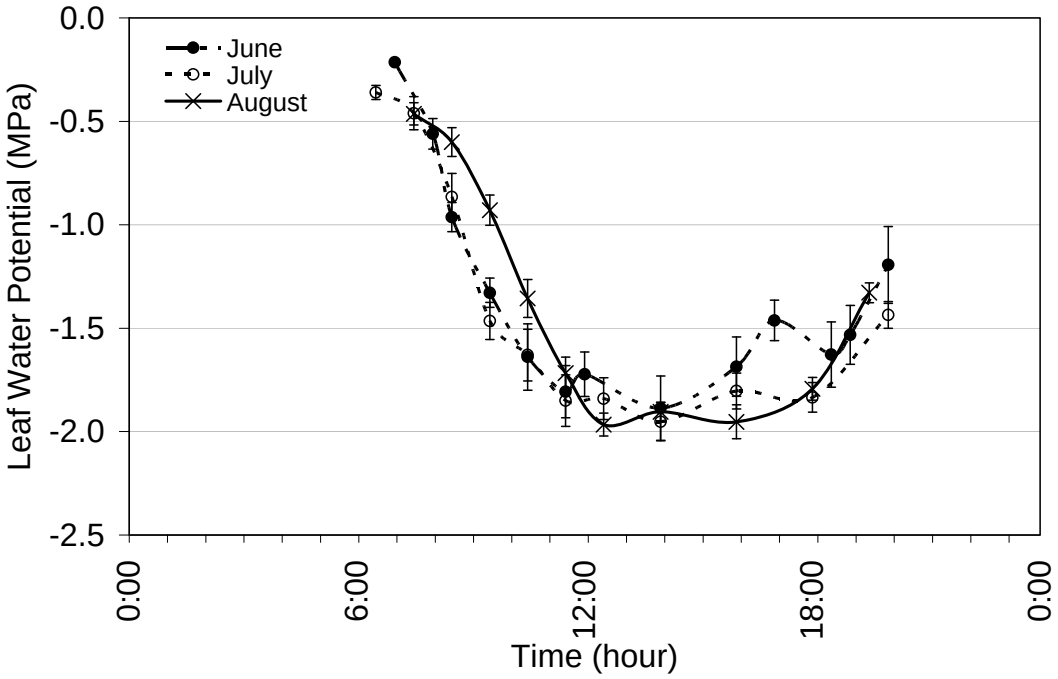


Figure 3.16. Diurnal pattern of Ψ_L of the 8 trees in mid-June, July, and August (mean ± S.E.).

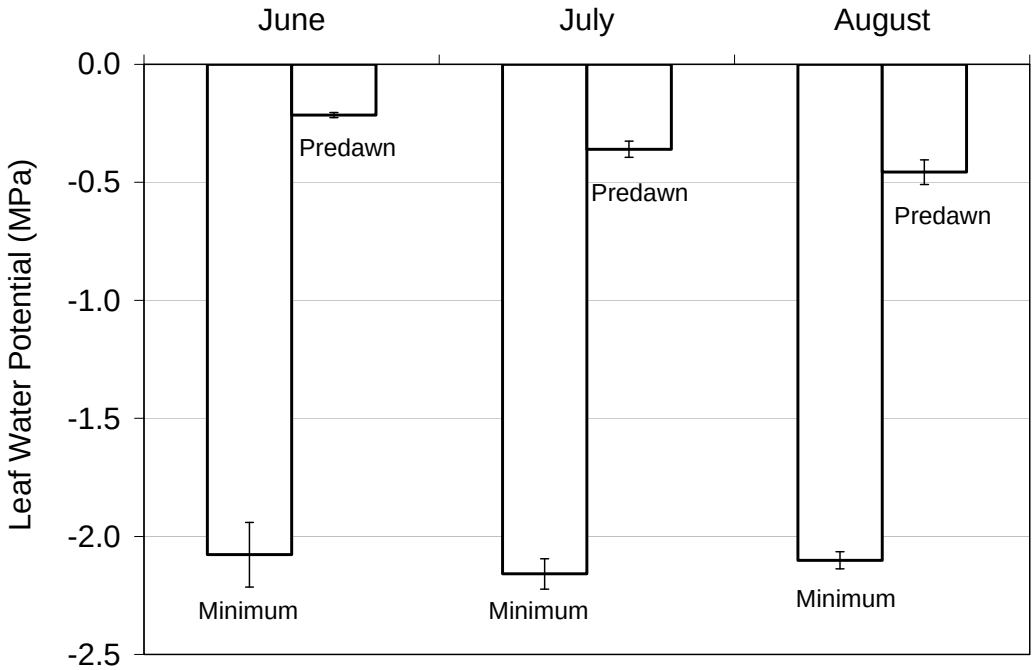


Figure 3.17. Predawn and minimum Ψ_L from the 8 trees measured in mid-June, July, and August (mean ± S.E., n = 8). Maximum values were measured as predawn Ψ_L, while the minimum values occurred between noon and early afternoon.

3.3.5 Sap Flow

Diurnal Sap Flow: Sap flow, dependent on the water potential difference between Ψ_S and Ψ_L, commenced shortly after stomatal opening between 8:00 h to 8:30 h (Figure 3.18). Flow rose in the morning to plateau from 11:00 h to 12:00 h before declining gradually to near zero overnight.

Seasonal Sap Flow: For the trees as a group, there was no significant difference in relative afternoon sap flow (12:00 h to 16:00 h daily average) among the different periods of the season from 6 June (DOY 157) through 28 August (DOY 240) ($F = 0.2521$, $p = 0.6197$) (Table 3.2) (after which four of the trees were irrigated (Chapter 4)). However, individual trees showed variable seasonal patterns (Table 3.3, Figure 3.19 A to Figure 3.21 F). Both M1 (Figure 3.19 A) and M2 (Figure 3.19 D) had higher sap flow within the first DOY group, while F1 (Figure 3.19 B) and M4 (Figure 3.19 F) increased sap flow over the season (Table 3.3). The remaining two trees, F2 (Figure 3.19 C) and M3 (Figure 3.19 E) had no change in sap flow over the season. Following a cold period from 13 to 23 September (DOY 256 to 266) senescence resulted in lower sap flows. Results of the statistical analyses are represented in Appendix A.

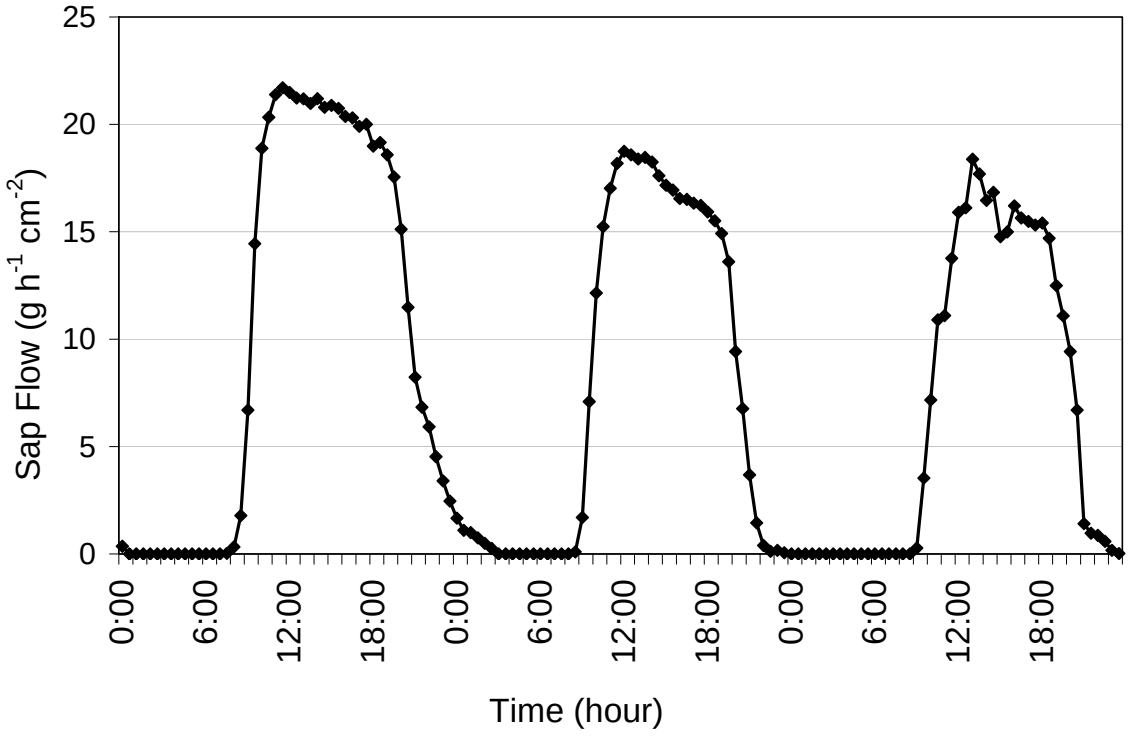


Figure 3.18. Representative sap flow pattern, for 20 August (DOY 232) through 22 August (DOY 234) for a narrowleaf cottonwood along the Oldman River. Stomatal conductance and Ψ_L were measured on 21 August (DOY 233) in this tree (Figure 3.15).

Table 3.2. Afternoon (12:00 h to 16:00 h) sap flow (g h^{-1} cm^{-2}) of narrowleaf cottonwoods, for groups of days throughout the season.

Date	DOY	Mean Sap Flow* (g h^{-1} cm^{-2}) ± S.E.
6 June - 21 June	157 - 172	22.9 ± 1.50
3 July - 13 July	184 - 194	19.3 ± 1.33
14 July - 26 July	195 - 207	20.3 ± 1.15
30 July - 13 August	211 - 225	20.6 ± 1.20
19 August - 28 August	231 - 240	23.4 ± 1.99

* means do not differ ($p = 0.05$; $n = 6$)

Table 3.3. Afternoon (12:00 h to 16:00 h) sap flow (g h^{-1} cm^{-2}) for individual trees for 5 groups of days over the growing season. DOY 157-172, 195-207, and 233-240 are similar date ranges as those used in stomatal conductance measurements and canopy stomatal conductance comparisons.

Tree	DOY: 157-172	184-194	195-206	214-225	233-240
M1 [a, b]	23.7 [c]	17	18.6	19.7	18.6
F1 [a]	21.1	18.5	19.3	20.8	26.4 [c]
F2	27.6	25.4	25.7	25.1	25.9
M2	24.2 [d]	18.5	20.9	18.2	19.2
M3 [b]	16.7	16.4	18.8	19.3	19.6
M4	23.9	20.1	18.3	N/A	30.4 [c]

a = sap flow increased with D ($p = 0.05$)

b = DOY Group – D interaction ($p = 0.05$)

c = within rows, differs from other values ($p \leq 0.05$)

d = within rows, differs from other values ($p = 0.10$)

N/A = sap flow data not available

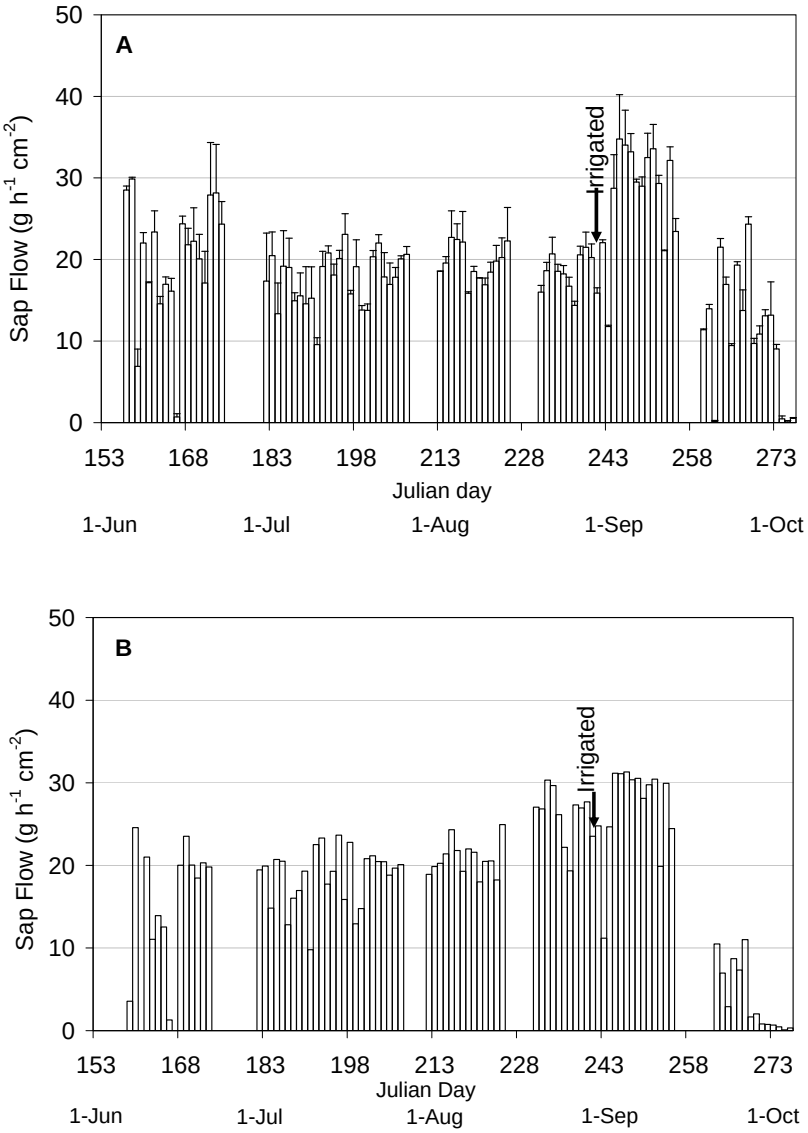


Figure 3.19 A and B. Seasonal pattern of afternoon sap flow (12:00 h to 16:00 h) for M1(A) and F1 (B). Mean sap flow was calculated from two TDPs, ± S.E. for (A) and from one TDP for (B). Both trees were irrigated on 29 August (DOY 241) (Chapter 4). Where no flow is shown, data were missing or inadequate.

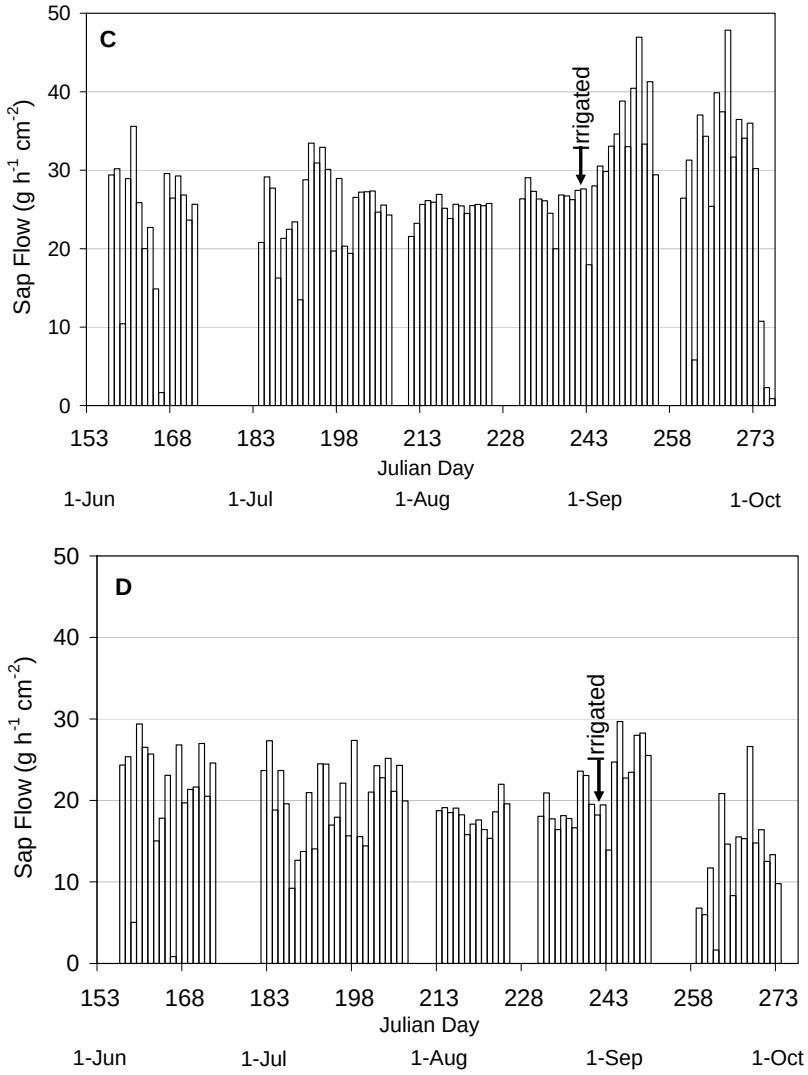


Figure 3.19 C and D. Seasonal pattern of afternoon sap flow (12:00 h to 16:00 h) for F2 (C) and M2 (D). Mean sap flow was calculated from one TDP for both trees. Both trees were irrigated on 29 August (DOY 241) (Chapter 4). Where no flow is shown, data were missing or inadequate.

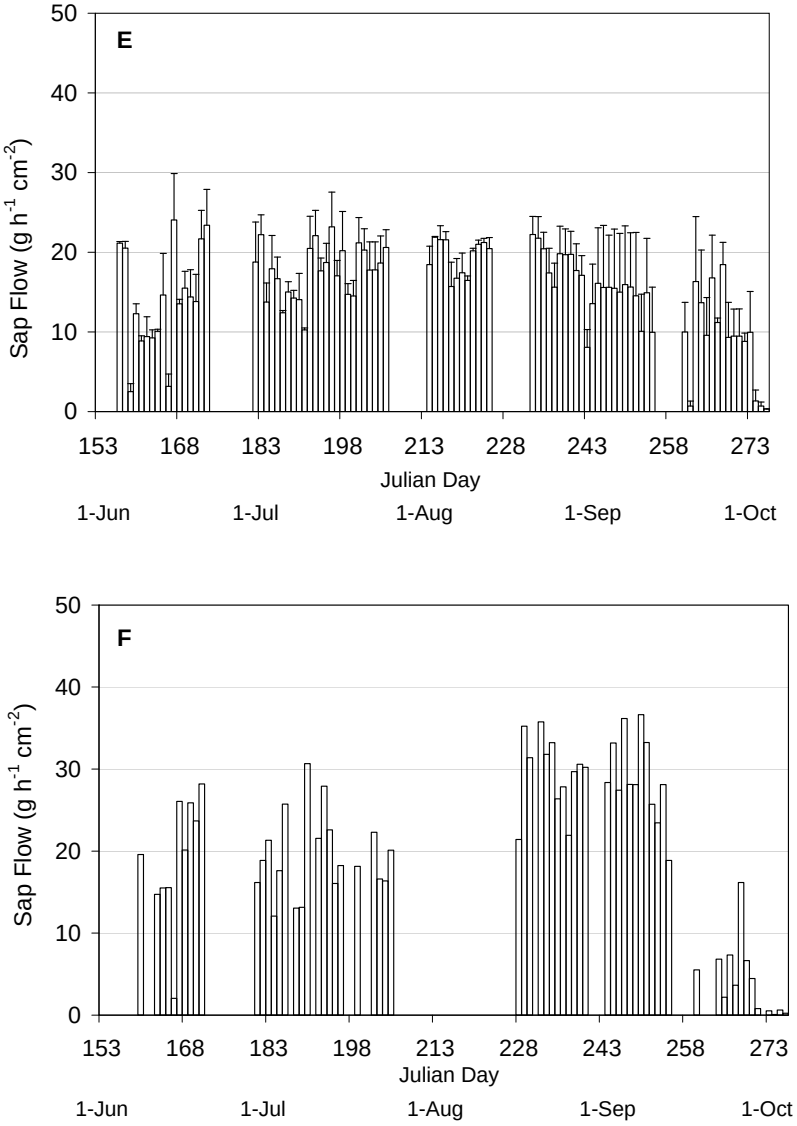


Figure 3.19 E and F. Seasonal pattern of afternoon sap flow (12:00 h to 16:00 h) for M3 (E) and M4 (F). Mean sap flow was calculated from one TDP. These trees were not irrigated on 29 August (DOY 241) (Chapter 4). Where no flow is shown, data were missing or inadequate.

3.3.6 Canopy and Leaf Level Stomatal Conductance

Stomatal Conductance and Vapor Pressure Deficit (D): On days that were clear and warm, particularly in July and August, stomatal conductance (g_S) decreased with increasing *D* during the course of the day (Figure 3.20 C and D for July and August). Specifically at 1 kPa, July g_S was significantly higher than August ($t_{(7)}$ = 5.720, p = 0.001). In June especially, cloudy or variably cloudy days with higher RH yielded g_S that could not easily be compared with measurements in ideal conditions. In 7 out of 8 trees hourly g_S values starting at 11:00 h declined from July to August for a particular *D* (Figures 3.20 A through H).

Mean Canopy Stomatal Conductance: Mean canopy stomatal conductances (G_S) were calculated for 6 of the 8 study trees. The other two trees were omitted from this analysis because of missing sap flow data. G_S for tree canopies estimated from sap flow and *D* in the three periods during the season declined with increasing *D* (Figures 3.21, 3.22 A to F). This decline was linear with lnD (Figures 3.22 A to F) and could be described by

$$G_S = G_{Sref} - m \times \ln D \qquad \text{(Schafer et al. 2000)}$$

where

G_{Sref} is the intercept (value of G_S at D = 1 kPa in a log-linear relationship)

m is the slope of the regression fit, representing stomatal sensitivity to *D*

With the exception of one tree, the boundary line of relative G_S demonstrates a decrease in the reference G_S from June through August (Figures 3.22 A to F). As a whole group, the six trees had higher G_S at G_{Sref} in June compared to July (p =

0.044), and August (p = 0.012) (Appendix A). Further, relative G_S at G_{Sref} was higher in July compared to August (p = 0.036). The six trees together had significantly higher stomatal sensitivity (slope) to *D* in June compared to July (p = 0.000) and August (p = 0.001), and July had higher values that August (p = 0.016) with the exception of M4 which had an increase in stomatal sensitivity in August (Figure 3.22 F) (Appendix A).

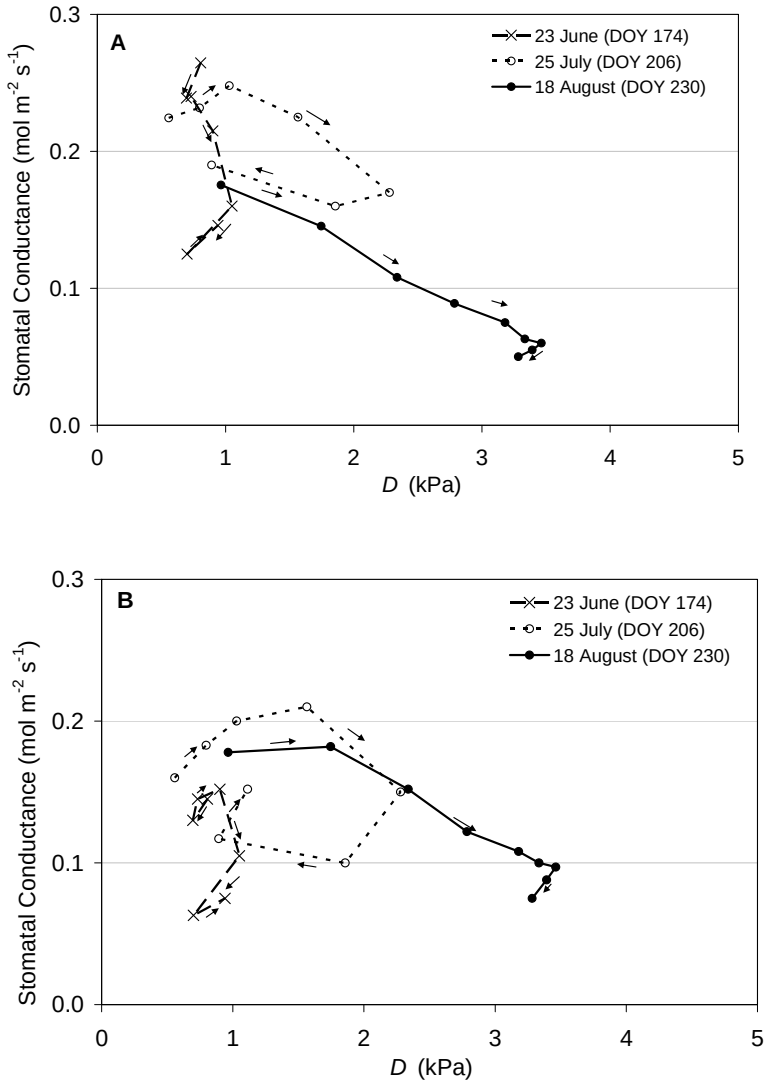


Figure 3.20 A and B. Stomatal conductance on three days, one in each of mid-June, July, and August for a given *D* for M1 (A) and F1 (B). Arrows indicate the time course of the measurements, beginning from 11:00 h. Fifteen leaves were measured at each time. To match hourly *D*, values of stomatal conductance were interpolated to fall on the hour. Minimum and maximum S.E. ranged from 0.003 to 0.01 June through August for (A) and from 0.003 to 0.02 for (B).

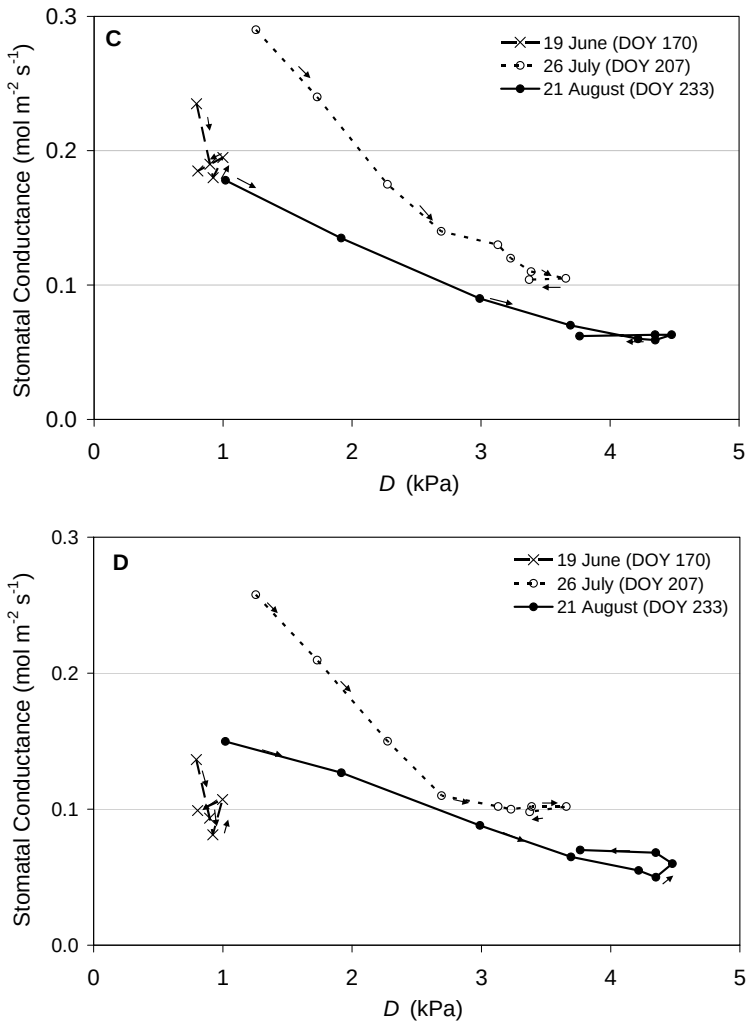


Figure 3.20 C and D. Stomatal conductance on three days, one in each of mid-June, July, and August for a given *D* for F2 (C) and M2 (D). Arrows indicate the time course of the measurements, beginning from 11:00 h. Fifteen leaves were measured at each time. To match hourly *D*, values of stomatal conductance were interpolated to fall on the hour. Minimum and maximum S.E. ranged from 0.0008 to 0.018 June through August for (C) and from 0.002 to 0.017 for (D).

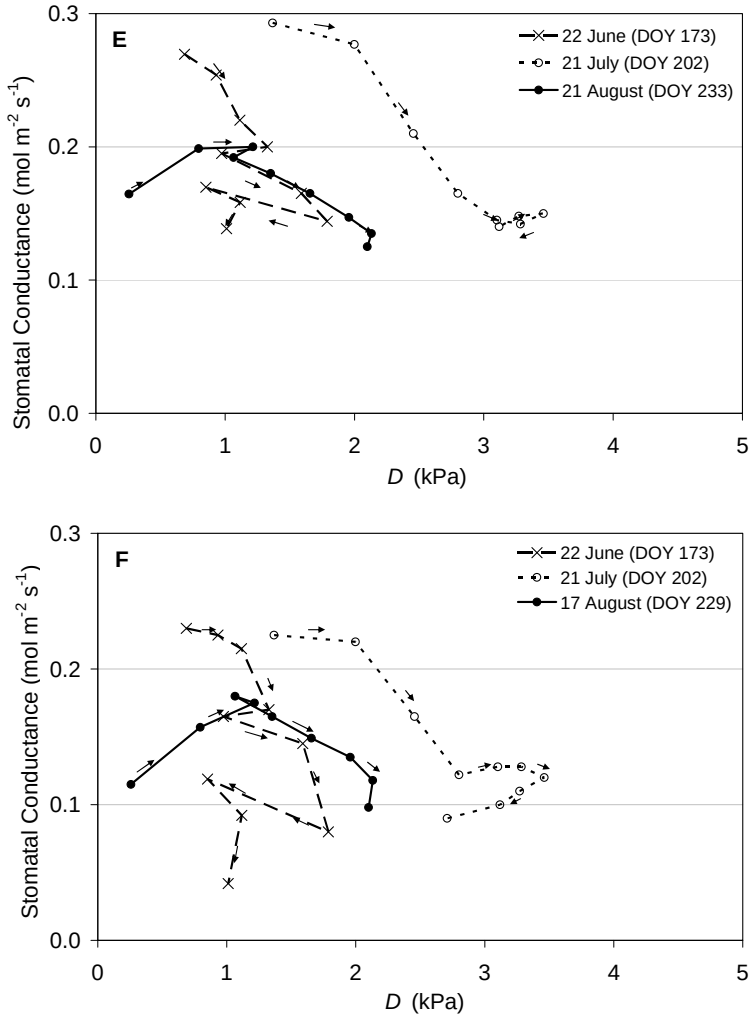


Figure 3.20 E and F. Stomatal conductance on three days, one in each of mid-June, July, and August for a given *D* for M3 (E) and F3 (F). Arrows indicate the time course of the measurements, beginning from 11:00 h. Fifteen leaves were measured at each time. To match hourly *D*, values of stomatal conductance were interpolated to fall on the hour. Minimum and maximum S.E. ranged from 0.007 to 0.02 June through August for (E) and from 0.002 to 0.02 for (F).

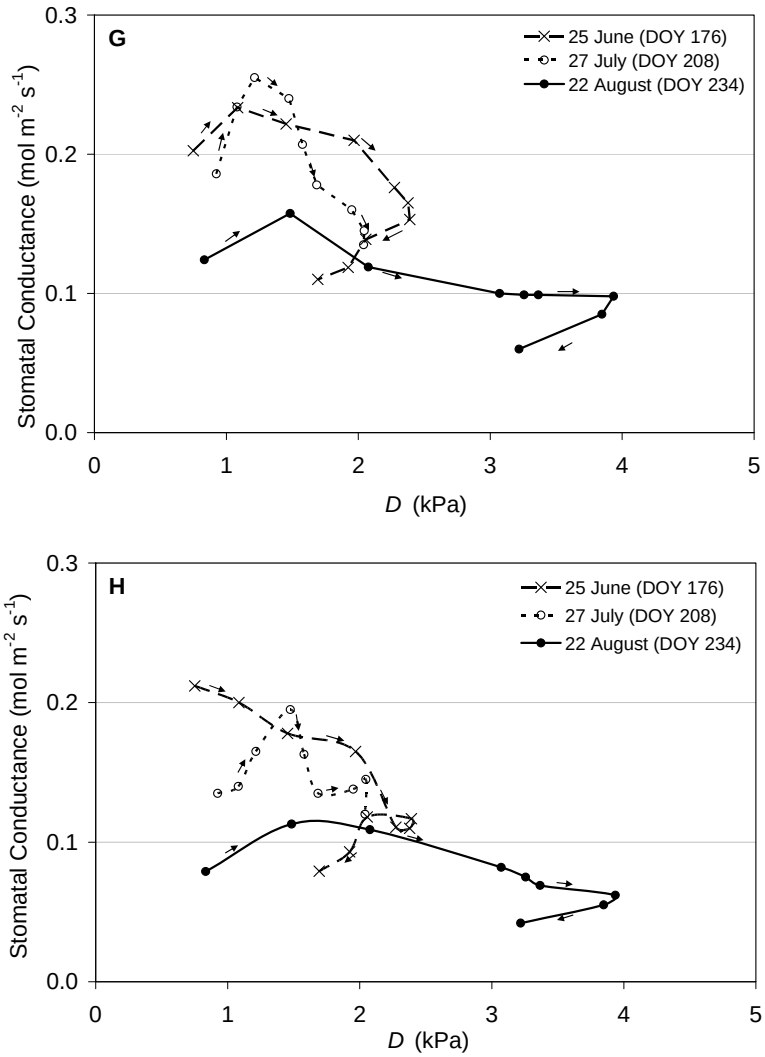


Figure 3.20 G and H. Stomatal conductance on three days, one in each of mid-June, July, and August for a given *D* for two trees in which sap flow was not measured M4 (G) and F4 (H). Arrows indicate the time course of the measurements, beginning from 11:00 h. Fifteen leaves were measured at each time. To match hourly *D*, values of stomatal conductance were interpolated to fall on the hour. Minimum and maximum S.E. ranged from 0.005 to 0.016 June through August for (G) and from 0.003 to 0.027 for (H).

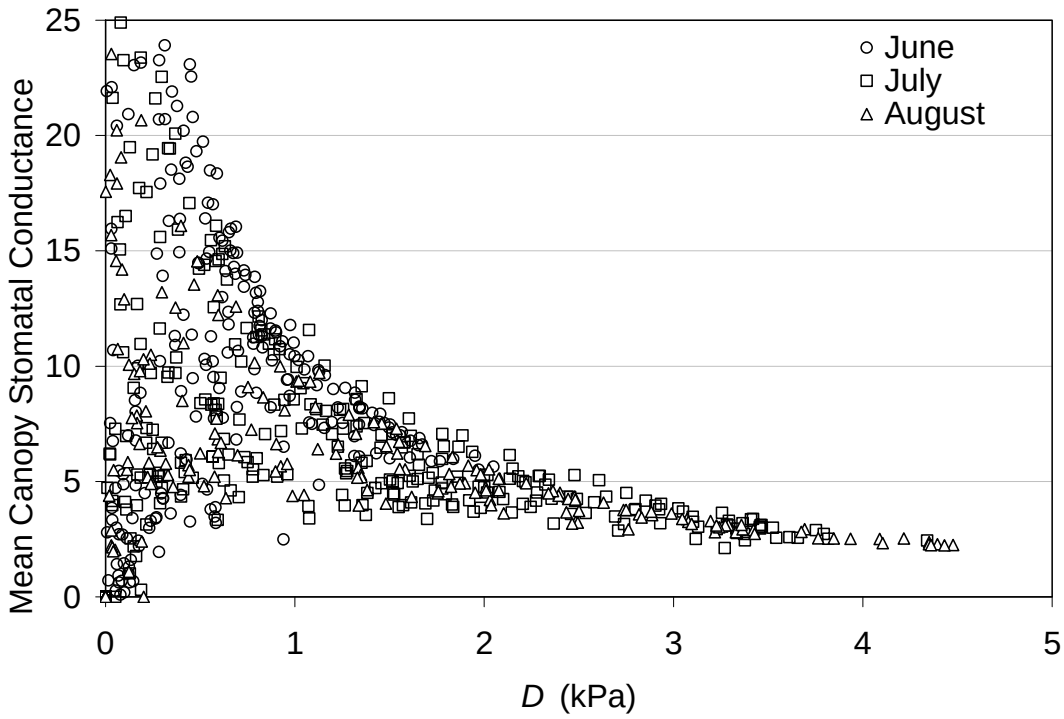


Figure 3.21. Mean canopy stomatal conductance (G_S) data from F2 before the boundary line was calculated.

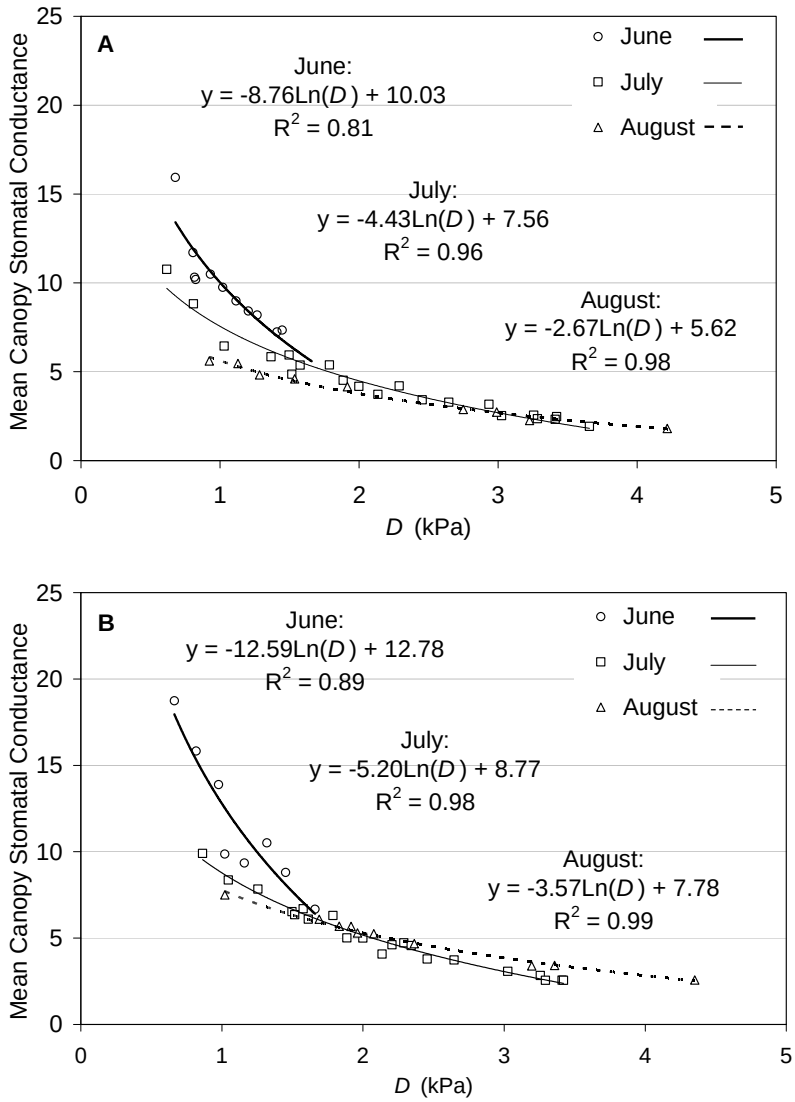


Figure 3.202 A and B. Boundary line values of mean canopy stomatal conductance (G_S) calculated by using the average hourly sap flow and D for each day when insolation was above 0.4 kW m^{-2}. These data are from M1 (A) and F1 (B). Data were divided up to represent the season. June dates ranged from DOY 157-174, July from 194-207, and August from 231-240. Logarithmic trend lines were fitted to each group and the resulting slope and G_{Sref} (at D = 1) are shown.

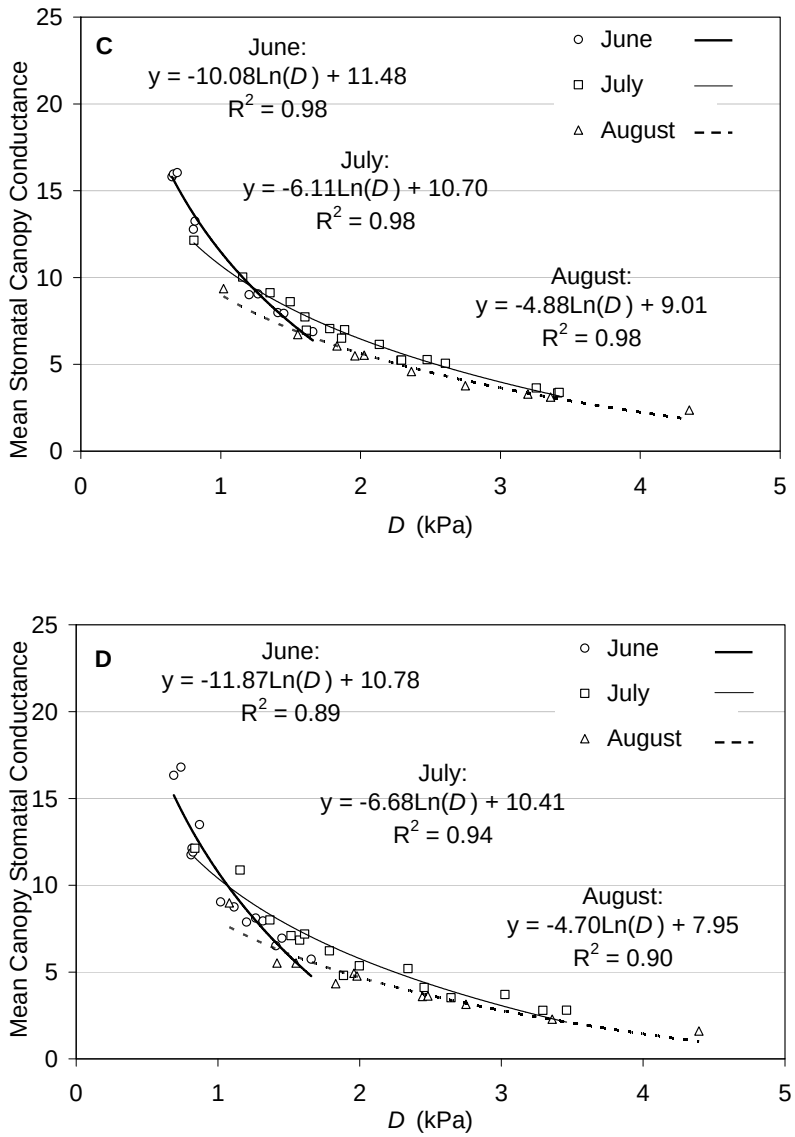
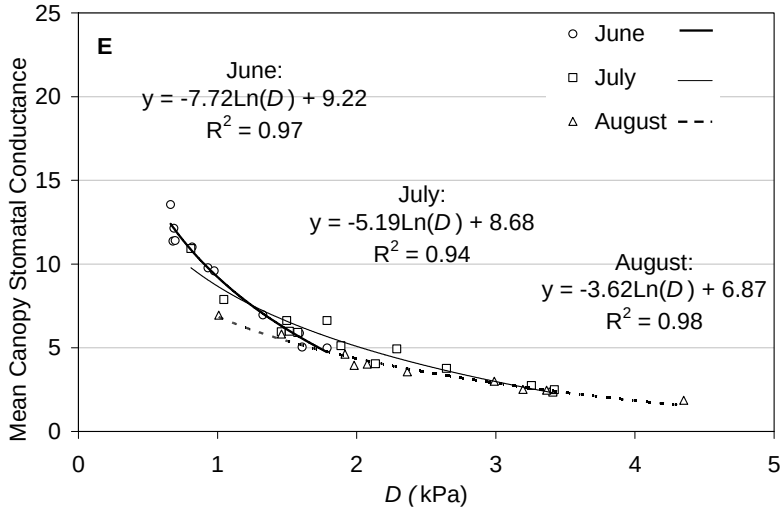


Figure 3.22 C and D. Boundary line values of mean canopy stomatal conductance (G_S) calculated by using the average hourly sap flow and D for each day when insolation was above 0.4 kW m^{-2}. These data are from F2 (C) and M2 (D). Data were divided up to represent the season. June dates ranged from DOY 157-174, July from 194-207, and August from 231-240. Logarithmic trend lines were fitted to each group and the resulting slope and G_{Sref} (at D = 1) are shown.



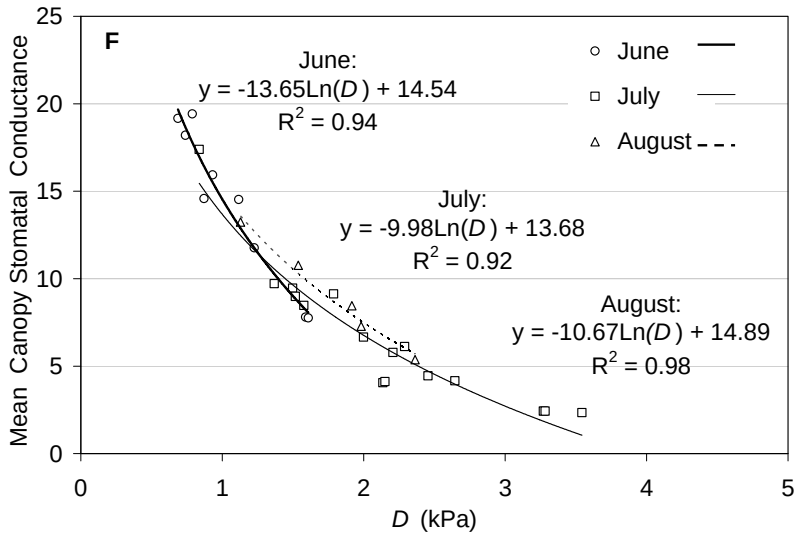


Figure 3.22 E and F. Boundary line values of mean canopy stomatal conductance (G_S) calculated by using the average hourly sap flow and D for each day when insolation was above 0.4 kW m^{-2}. These data are from M3 (E) and M4 (F). Data were divided up to represent the season. June dates ranged from DOY 157-174, July from 194-207, and August from 231-240. Logarithmic trend lines were fitted to each group and the resulting slope and G_{Sref} (at D = 1) are shown.

3.4 Discussion

In southern Alberta, there is natural variation in stream flows over each year and among years. The influence of this variation in water supply for riparian trees has yet to be related to aspects of water relations including sap flow, stomatal conductance, and canopy stomatal conductance of a natural *Populus* grove. In this study we suggest a link between river levels, groundwater levels, and soil moisture, and further relate this to sap flow, water potential difference, and stomatal conductance. We discovered a close association between river water, the groundwater table, and soil moisture confirming that river discharge provides a crucial water source that determines the water available for cottonwood use (Figures 3.12, 3.14). Soil water potential, Ψ_S, estimated as equivalent to predawn Ψ_L, declined from June through August (Figure 3.17). Given the isohydric behavior of the trees as seen in the consistent midday value of minimum Ψ_L, the water potential difference that drives sap flow, Ψ_S - Ψ_L, decreased from June to August (Figure 3.17). This decrease in water potential difference was accompanied by differing relative sap flow trends in different trees from June through August (Figures 3.19 A to F, Table 3.3). Using our relative sap flow data, we were able to estimate mean canopy stomatal conductance for June, July, and August which indicated for the majority of trees a decrease in stomatal sensitivity to *D*, and a decline in reference canopy stomatal conductance over the season (Figures 3.22 A to F). These findings are consistent with our direct individual leaf stomatal conductance measurements (Figures 3.20 A through H). Our overall results demonstrate that both sap flow, and stomatal conductance, at

the leaf and canopy levels, were increasingly limited by water availability during the growing season at Pearce Corner along the Oldman River.

With respect to water supply, close associations were found between river stage (level), the groundwater table depth and soil moisture. Melting snow in the mountain headwaters and rain within the basin and locally at the study site increased soil moisture in late May and early June by raising the river level and subsequently the groundwater table (Figure 3.12). The high groundwater table recharged both upper and lower soil layers and their moisture amounts increased (Figures 3.12, 3.14). Water supply decreased after this as river and groundwater table levels declined and soil moisture decreased due to limited precipitation and groundwater recharge throughout the summer. Comparison of the river level to the groundwater table over the season shows that the Oldman River at Pearce Corner was generally, but not always, a "losing stream", one that loses water to the adjacent groundwater table during most of the season. For a 15 day period, following a large rain event in June, the Oldman was a gaining stream when the decline in the groundwater table after the peak was slower than that of the river and the river thus gained water from the groundwater table (Rood et al. 2003) (Figure 3.12). However, part of this would have included discharge of the groundwater table that had previously infiltrated from the river.

Understanding the effects of the seasonal decline in soil moisture supply on cottonwood water use was assisted by first examining the diurnal patterns of

stomatal conductance, leaf water potential, and sap flow (Figures 3.15, 3.18). With an assumption of minimal diurnal variation in Ψ_S, the water potential difference between Ψ_S and Ψ_L increases with the presence of sunshine and subsequent stomatal opening (Figures 3.6, 3.15). As atmospheric demand increased, stomatal regulation allowed Ψ_L to stabilize near -2.1 MPa. Subsequently, as demand decreased in the late afternoon, Ψ_L became less negative so that an equilibrium was re-established overnight between the water potential of leaves and roots. Comparison of these diurnal trends from June through August indicated declining Ψ_S (-0.2 MPa to -0.5 MPa) and consistent minimum Ψ_L to yield an overall decrease of about 0.3 MPa in the driving water potential difference (Ψ_S - Ψ_L) from June to August (Van den Honert equation) (Figure 3.17). The declining Ψ_S is consistent with the established relationship between soil moisture and Ψ_S where a decline in soil moisture results in a more negative Ψ_S (Hopkins 1995). The physiological consequence of the decline in Ψ_S suggests that the trees were obtaining water partially from the upper soil levels which dried during the season (Figure 3.14). Horton et al. (2001) reported similar findings with *P. fremontii* predawn water potentials significantly decreasing with large (9 m) declines of the groundwater table depth. The constant average minimum Ψ_L values in June, July, and August provide further evidence of the isohydric nature of the *Populus* genus (Tardieu and Simonneau 1998; Johnson et al. 2002) (Figures 3.16, 3.17).

Diurnally, the formation of the difference of water potential between the soil and leaves drives sap flow (Figures 3.15, 3.18, and Van den Honert equation). In a typical day, the water potential difference is formed, maintained, and then decreases, with sap flow following the same pattern (Figures 3.15, 3.18). The cavitational threshold establishes a maximum rate of sap flow that can be observed, which is also influenced by the hydraulic conductance of the pathway (Tyree et al. 1994; Hogg and Hurdle 1997; Horton et al. 2001a). Cavitation vulnerability curves were determined for branches from the trees in this study (D.W. Pearce, C. Franks, C.A. Phelan, M.T. Tyree and S.B. Rood unpublished) and the 50 % loss conductivity (PLC) was found to occur at -1.90 to -2.39 MPa in the eight different trees. The pressure bomb measurements of minimum Ψ_L were consistent with these findings, ranging from -1.3 to -2.31 MPa. These values measured were more negative than those found by Tyree et al. (1994) who found the PLC at 50 % for both *P. balsamifera* and *P. angustifolia* trees to occur around -1.7 MPa.

A variety of differences in sap flow were found over the season (Table 3.3). Two trees demonstrated little change, two trees increased sap flow later in the season, by 35 % (F1) and 59 % (M4), and two trees decreased sap flow from June through August, by 28 % (M1) and 27 % (M2). Sap flow is dependent on the water potential difference (Ψ_S - Ψ_L) and hydraulic conductance of this pathway. From the pressure bomb measurements, the water potential difference decreased over the season. Consequently, for sap flow to remain constant, the hydraulic

conductance should increase. For sap flow to increase the conductance would increase and for sap flow to decrease, the conductance would either remain constant or decrease. The decrease in sap flow, indicated by two of the six trees is consistent with sap flow being limited by water availability. Hydraulic conductance was not measured directly, and it can be altered through adjustments made in factors such as the extent of cavitated xylem vessels, root aquaporin function, and through the effective root area taking up water. For comparison, few studies of sap flow have been carried out over one season. An extensive seasonal study carried out by Pataki et al. (2000) on quaking aspen, *P. tremuloides,* in a western subalpine forest found results similar to the two decreasing sap flow trees in my study. Pataki et al. (2000) attributed the decrease to the decline in soil moisture found. Nagler et al. (2007) measured the sap flow of *P. fremontii* trees on the lower Colorado River in the western U.S.A. for 30 days from DOY 210 (29 July) to DOY 245 (28 August) and found no change in sap flow over this time with a decline of soil moistures in the top 30 cm of soil. Lambs and Muller (2002) found that riparian black poplar, *P. nigra*, were sensitive to groundwater table fluctuations with sap flow decreasing with reduced groundwater table. Overall, the two comprehensive studies found a decrease in sap flow with declines in water availability.

Early in the season, sap flow variations are dependent on the phenology of leaf, root, and xylem development, as well as water availability and weather conditions. Leaf formation and shoot expansion at Pearce Corner began in mid-

May and was completed by mid-July as indicated by the course of branch elongation (Figure 3.11). During this period it is expected that sap flow would increase (Tyree et al. 1978; Pataki et al. 2000) with high soil moisture and decreasing Ψ_L. Our first measurements of sap flow were in mid-June, just before canopy expansion was complete and when soil moistures were high, possibly representing the maximum flow rates during the season. Further, *Populus* net photosynthetic rates reach a maximum just before leaf expansion is complete, requiring a high CO_2 intake, increasing stomatal conductance, and thus the larger need for water supply to the leaves for stomata to remain open (Tyree et al. 1978).

Similar DBH and functional sapwood across the six trees used is an important factor when comparing sap flows and conductances among trees, however we suspect that the trees will be more or less similar in terms of hydraulic properties. Larger DBH could represent a larger sapwood area supplying the leaves with more water. The incorporation of DBH would be more important if we were concerned with making estimates of water loss based on the total sapwood area. However within our study the sap flow for all trees was based on a 1 cm^2 sapwood area. Further complicating matters is the relationship between DBH and leaf specific conductance (conductance/leaf area) where smaller and larger stems have large differences in leaf specific conductance in maple (Yang and Tyree 1993) and consequently Ψ_L and g_S. However, since our DBH were all similar for trees for which sap flow data were calculated (0.18 m to 0.27 m; Table 3.1) we expect only slight difference in leaf specific conductance, Ψ_L and g_S.

Hydraulic conductance from the soil to leaves varies within trees, between trees, diurnally and within each season (Sperry 2000; Tyree and Zimmermann 2002). Conductance within the stem can decrease due to cavitation within the xylem (Sperry 2000), although it was found that hydraulic resistance in the non-vascular tissues of roots and shoots is greater than what would occur from cavitations (Tyree and Zimmermann 2002). An influential variable on hydraulic conductance is soil drought where drought induces a loss of hydraulic conductance due to xylem cavitation or inhibition of aquaporins (Addington et al. 2004). Once water is within the roots, resistance varies depending on the path of water, whether it is apoplastic or transcellular, and resistance is greater in small diameter roots (Tyree and Zimmermann 2002; Cochard 2006). Within the leaves, resistances are found at junctions such as the joining of the petiole to the branch and larger leaves can be more conductive than smaller leaves (Tyree and Zimmermann 2002). Over the duration of our study, hydraulic conductance could have been altered throughout the pathway from the soil to the leaves. As the soil dries, its conductance declines, cavitations could develop in the xylem vessels, and the leaf size was altered during the expansion phase in June.

During the season, in some trees in particular (Figure 3.22A) G_S decreased at any particular *D*. This was particularly marked at low D, and is seen in the decrease in the G_{Sref} value from June to July to August. This reflects sap flow decreasing during the season due to the combination of hydraulic conductance and water potential difference decreasing. The second consequence of a decrease in

hydraulic conductance and water potential difference will be a decrease in stomatal sensitivity to an increase in D, which would be shown as a decrease in the slope of the relationship between G_S and D. Such a pattern has been generally observed (Oren et al. 1999). Over the season, the reduction in stomatal conductance at a particular D (G_{Sref}) can be related to the need to maintain Ψ_L above the critical threshold value which is influenced by the water potential difference between soil and leaves, or hydraulic conductance, or a combination of both factors (Addington et al. 2004). These findings by Addington et al. (2004) were from data collected on *Pinus palustris*, and are also supported by our riparian cottonwood data (Figures 3.22 A to F). Addington et al. (2004) attributed the decrease of stomatal sensitivity to the decrease in hydraulic conductance which was created by drought conditions and lack of soil moisture availability. However, without direct evidence from our trees we are only able to speculate on possible changes in hydraulic conductance over the season. Gradual stomatal closure occurs at high D within one month and within the season from June through August at both leaf levels and canopy levels, supporting findings by Hogg and Hurdle (1997) who studied upland *P. tremuloides* and by Addington et al. (2004) for *Pinus palustris*.

A number of assumptions were used in the calculation of G_S. One assumption is that the measured atmospheric conditions, most importantly D, represents leaf to air vapor pressure deficit at all canopy levels (Ewers and Oren 2000; Schafer et al. 2000). Our meteorological values are weather station measurements and these do

not necessarily reflect what actually occurs at leaf levels. For example, temperature, RH, and thus *D* may be different at the leaves due to surface reflectance, cooling from transpiration, and the variation in boundary layer depth. Fortunately, Meinzer (1993) reported that temperate trees such as *Populus* have a low decoupling coefficient, indicating the vapor pressure at the leaf's outer surface is generally similar to the ambient vapor pressure. This coupling arises when leaves are well-spaced and small, which acts to create a smaller boundary layer (Meinzer 1993), reducing the difference between the measured *D* and the leaf level *D*. Other assumptions include the maintenance of leaf area and sapwood area through the season. We estimated that growth in leaf area was complete in early-to mid- July (Figure 3.11) and can predict that if a sufficient driving gradient and conducting pathway was available, G_S in June would be larger than overall values presented due to the smaller leaf area in June. The sapwood area would also have increased slightly over the season. Finally, in these G_S calculations there is assumed to be no lag time between sap flow and transpiration. Measurements of our own transpiration compared to sap flow failed to reveal a trend between lag times, whether sap flow preceded or followed transpiration, or if they started at the same time (data not shown). The G_S calculations made for the season are less valid for comparing across trees but are appropriate for comparing June through August rates within each tree. A known leaf area, sapwood conducting area, and true estimates of sap flow would allow us to incorporate these values into the calculations relative to total water flow and thus allow for comparisons between trees.

Consistent with the G_S analysis, 7 of 8 trees demonstrated declines in stomatal conductance (g_S) for a given *D* from July to August (Figures 3.20 A to H). We thus conclude that the majority of trees responded to diminishing water supply by decreasing leaf water loss for a given *D*. June *D* levels on the days of measurement often did not reach the high values seen in July and August and thus the g_S for a given *D* in June are difficult to compare with July and August. Similar to sap flow data, each tree acts as an individual as the extent of decline for a given *D* was tree-dependent. Comparable results have been reported by Hogg and Hurdle (1997) and Gazal et al. (2006) who saw evidence of stomatal closure at high *D*. Horton et al. (2001a) found there were also significant decreases in *P. fremontii* mid-morning and mid-afternoon g_S with increasing groundwater depth, implying stomatal closure and consequentially a reduced CO_2 gain. Differences between g_S and G_S are seen in the magnitude of decrease between July and August. This deviation could be related to sampling techniques used for stomatal conductance where only the outer canopy within a small height range was incorporated into the measurements. Further, the differences in environmental factors such as insolation, temperature, and RH will also have influence specific g_S values.

Many water relation studies have been carried out on other tree species which incorporate the relationships between the soil to leaf pathway, hydraulic conductance, stomatal and canopy conductance (Saliendra et al. 1995; Sperry et

al. 1998; Sperry et al. 2002; Sperry et al. 2003). Other studies have focused directly on hybrid poplars to demonstrate the importance between water balance of water source and atmospheric demand, cavitations, and plant growth (Tyree and Ewers 1991; Braatne et al. 1992; Hinckley et al. 1994). In our study, associations were found between the Oldman River and cottonwood water relations, confirming that these riparian trees are reliant on water supply from groundwater sources. Variation of poplar water source have also been documented in other studies. Zhang et al. (1999), Snyder and Williams (2000) and Horton et al. (2001b) found riparian poplar trees took anywhere between 15 to 100 % of water transpired from groundwater sources, with the proportion increasing as soil moisture declined. Isotopic water analysis from Pataki et al. (2005) and the ecophysiological measures reviewed by Rood et al. (2003) support the association between trunk water and the groundwater table. Due to this association and the SPAC, the declining soil water supply and constant minimum Ψ_L created a decrease in the soil-leaf water potential difference (Ψ_S - Ψ_L). In response, there were a variety of sap flow patterns but all of these showed a clear decrease in mean canopy and leaf level conductances from June through August for a given *D*.

These findings have important implications for the regulation of rivers since a decrease in river flow will reduce groundwater levels and riparian soil moisture recharge, creating a smaller supply for root uptake. A reduced water supply will decrease stomatal conductance as a whole and reduce the amount of CO_2 uptake,

negatively influencing tree health over the long-term. As described by Rood et al. (2000) prolonged water loss can induce branch dieback, improving the water supply for leaves on the remaining branches. Although this permits higher stomatal conductance and CO_2 uptake rate per leaf, the reduced leaf area may lead to a decrease in overall tree growth.

Management Strategies: Although precipitation and atmospheric demand are uncontrollable, upstream dams and weirs can be managed to control river levels and hence water supplies. Infrastructure could be operated to maintain the natural flow regime (Poff and Hart 2002) of high flows in the spring followed by a decline in river flows while maintaining the crucial groundwater table within access by cottonwood roots. This flow regime is demonstrated by the Oldman Dam operation (Rood et al. 1998). However, the decline of soil water potential and of stomatal conductance at equivalent *D*, in July and August provides evidence that water supply was limiting gas exchange in the trees at Pearce Corner in 2006. This allows us to predict that higher river flows in these months would maintain the groundwater table and increase soil moisture and so improve gas exchange and tree productivity. This is especially crucial when there is minimal precipitation to recharge moisture in the upper soil levels, as occurred in 2006.

Future Work: To fully appreciate the SPAC at Pearce corner, gaining a better understanding of the root distribution within the soil layers through excavations

would be beneficial. Further, directly measuring the Ψ_S at different levels throughout the day while continuing to estimate Ψ_S from predawn Ψ_L values, would give accurate numbers to calculate the water potential difference between Ψ_S and Ψ_L diurnally and seasonally. As also as mentioned in Chapter 2, measurements of sap flow with shorter TDPs (i.e. TDP 10, Dynamax, Houston, TX) might provide additional information to estimate sap flows, allowing for a comparison between trees. Finally, interannual measurements of additional trees would provide further information about the water relations of the riparian cottonwood population at Pearce Corner along the Oldman River.

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CHAPTER 4 Is Water Supply Limiting Riparian Cottonwoods? Response to Late Summer Irrigation

4.1 Introduction

Within the riparian zone at Pearce Corner, cottonwood reliance on groundwater and soil moisture was demonstrated in Chapter 3. This chapter explores how increasing the soil moisture through irrigation changes the sap flow and provides a direct test of the conclusion that water supply was limiting by late summer for the riparian cottonwoods.

As discussed, water flow from the soil to the leaves is dependent on the water potential (Ψ) difference created between the roots and the leaves (Van den Honert equation) and the conductance of the pathway. The addition of water to the soil layers above the groundwater table will increase the soil Ψ, thus increasing water availability. The leaf water potential (Ψ_L) varies diurnally, depending on the balance between water supply and water loss from the leaves (Chapter 3). The raising of the soil water potential (Ψ_S) combined with the diurnal changing of the Ψ_L will create a larger difference in water potential for sap flow during the late morning and afternoon hours, potentially enhancing sap flow assuming that Ψ_L remains the same following irrigation. Increasing water availability will further induce stomatal opening, facilitating carbon acquisition and aiding in growth and overall health of the tree (Taiz and Zeiger 2002).

Following from this sequence, it is predicted that increasing soil moisture through irrigation would promote sap flow and cottonwood growth. Other researchers have undertaken irrigation experiments on *Populus* to test this association, but have reported differing responses. Cox et al. (2005) found that an increase in soil water content through irrigation did not significantly increase mean daily transpiration rates of *P. angustifolia* and *P. fremontii* riparian tree cuttings grown along the Weber River in Utah. After irrigating a former floodplain along a regulated river, Williams and Cooper (2005) found no significant change in stomatal conductance for irrigated riparian *P. fremontii* along the Green River in Colorado. Williams et al. (2006) contrasted *P. fremontii* growing next to an intermittent stream (limited groundwater access) to trees growing next to a perennial stream (groundwater was not limiting) along the Upper San Pedro River in Arizona. Following monsoonal rains, trees growing next to the intermittent stream had an increase in stomatal conductance, transpiration, and sap flow. However the trees next to the perennial stream had no response to the increased water availability (Williams et al. 2006). Kort (2005) added water to shelterbelt poplars (no access to groundwater), and observed an increase in sap flow and relative canopy conductance when compared to controls. Two separate studies of coppiced poplars in plantations (*P. tristis* x *P. balsamifera* and *P. deltoides*) in Michigan and Washington found non-irrigated cottonwoods to have lower stomatal conductance rates than cottonwoods that were irrigated (Roden et al. 1990; Dickmann et al. 1996).

Few studies have been published on the sap flow alteration of a natural *Populus* population in their native floodplain habitat following an increase of water availability. In Chapter 3 it was shown that *Populus* trees decreased stomatal conductance at the same vapor pressure deficit (*D*) with seasonally decreasing water availability. In late August we irrigated four of six narrowleaf cottonwoods at Pearce Corner. Using thermal dissipation probes (TDPs), sap flow was continuously measured to determine if there was a change in sap flow and stomatal conductance of these riparian trees.

Prediction: From the findings in Chapter 3 and with the trees using both soil water and groundwater, the increase in soil moisture will result in an increase in sap flow and stomatal conductance of the irrigated trees when compared to the control trees.

4.2 Materials and Methods

Study Site: This study was undertaken at the Pearce Corner riparian zone along the Oldman River, Alberta (Figures 3.2, 3.3).

Environmental Conditions: Weather was monitored using the Dynamax weather station (Chapter 3). Hourly averages of precipitation, temperature, RH, and radiation were made using data collected from the hour before (Chapter 3). Using temperature and RH data, *D* was calculated (Chapter 3).

River Level: Continual river level measurements were made from a fixed point to the river's edge (Chapter 3). The cross-sectional bank elevational profile was surveyed to determine the river stages at each measurement.

Groundwater Table: The level of the groundwater table was monitored with wells, using a water level meter (Solinst, Georgetown, ON, Canada) (Chapter 3).

Soil Moisture: Theta Probe ML2x soil moisture sensors measured and recorded soil moisture with a THLOG-4 data logger (Dynamax, Houston, TX, USA) every six hours within the non-irrigated area (Chapter 3). Soil samples surrounding irrigated trees were taken at 0.5 m depth before and after irrigation. Soil samples were weighed then oven-dried at 105°C for 24 hours, and re-weighed to determine the percent moisture by weight.

Trees: The same six trees selected in Chapter 3 were used for this experiment (Table 3.1). Two pairs of adjacent trees were irrigated while the other two acted as controls (Chapter 3, Figure 3.3, Table 3.1). Comparisons were made between the irrigated and control trees, and also of individual trees before and after irrigation.

Sap Flow: Half hourly averages of sap flow were continuously collected using Granier-type TDPs (TDP-30, Dynamax Inc. Houston, Texas) on all six trees according to the methods outlined by Dynamax (1997) (Chapter 2). For each tree,

one probe was placed in each of the north, south-east, and south-west aspects. Probes were installed on 1 June (DOY 152) and measurements were made until 3 October (DOY 276) 2006. From probe readings the relative sap flow was calculated using the Granier equation (Chapter 2). For each tree a 1 cm^2 sapwood area was used to allow for a relative comparison between trees.

Irrigation: On 29 August (DOY 241) trees were irrigated by pumping water with a 4 horsepower Honda pump from the river through fire hoses to the bases of the trees, for approximately 2 hours per tree. Calibration of flow rate from the fire hoses was found to be about 410 L $minute^{-1}$. Using this rate and the time irrigated, each tree received between 40,700 L and 49,000 L that spread out horizontally over about a 12 m^2 oval area and down vertically approximately 3 m to the groundwater table depth at that time.

Mean Canopy Stomatal Conductance: Mean canopy stomatal conductance (G_S) was calculated following the same procedures as described in Chapter 3, and as outlined by Schafer et al. 2000.

4.2.1 Statistical Analyses

JMP version 6.0.0 (2005 SAS Institute Inc.) was used to conduct an analysis of covariance (ANCOVA) on the sap flow before and after irrigation, with *D* as a covariate, and a regression analysis on sap flow versus DOY. For the analyses, all data were divided into two groups, representing before versus after irrigation sap flows. The before treatments included 19 August (DOY 231) to 28 August

(DOY 240) while the after data were from 30 August (DOY 242) to 9 September (DOY 252).

Using SPSS version 13.0 both soil moistures and G_{Sref} values were analyzed. Soil moistures measured before and the first day following irrigation as % weight were analyzed using a paired t-test. For all trees, values of G_{Sref} (when $D = 1$) and slope for before- and after-irrigation were taken and divided by one another to create a ratio which could then be compared using a one-sample t-test. A value of 1 represented the ratio where reference stomatal conductances or slopes were the constant.

4.3 Results

4.3.1 Meteorological Conditions and Water Supply

Environmental: Environmental conditions were similar from 18 August (DOY 230) through 9 September (DOY 252), before and after irrigation with the exception of 0.7 cm rain on 24 and 25 August (DOY 236 and 237) before irrigation, and 0.7 cm after irrigation on 30 and 31 August (DOY 242 and 243). In the grove at 1.2 m, wind speeds remained under 6 km h^{-1}. River level, groundwater table elevation, and soil moistures outside of the irrigated zones were stable through the study interval (Chapter 3, Figures 3.12, 3.13 and 3.15).

Soil Moisture: Soil samples taken at 0.5 m beneath irrigated trees demonstrate a 59 % increase in soil moisture by weight the day following irrigation relative to the measurement taken before irrigation occurred ($t_{(5)} = -5.449$, $p = 0.003$) (Figure

4.1). These soil moistures (% weight) cannot be related directly to soil moisture from the soil moisture probes (% volume).

4.3.2 Sap Flow

Sap flow increased somewhat differently in the irrigated trees. The increase occurred in the period between about 11:00 h to 19:00 h each day (Figure 4.2 A to D). Mean afternoon sap flows (12:00 h to 16:00 h) in the ten day period after irrigation increased between 10 % and 60 % relative to sap flow measured 10 days before irrigation (Figure 4.3 A to D). In the two control trees sap flow either remained stable or decreased in the same interval (Figures 4.2 E and F, 4.3 E and F). The control trees also differed with later sap flow start in the morning and an earlier decline in the early evening hours.

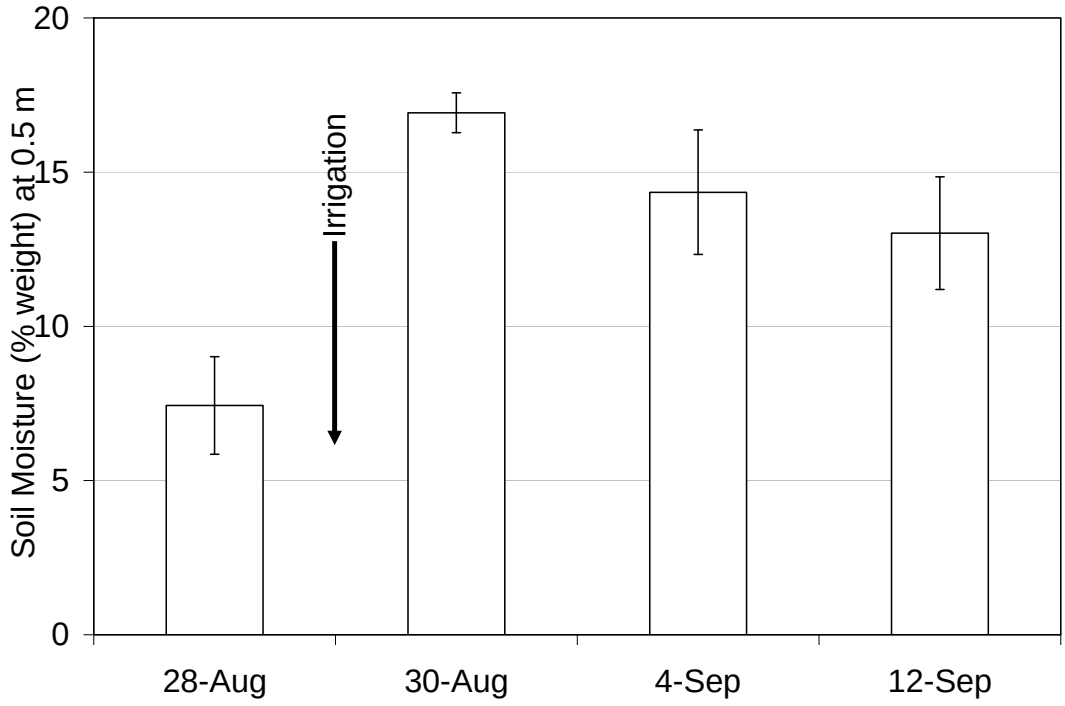

Figure 4.1. Soil moisture at 0.5 m, before (n = 7) and after irrigation (n = 6), measured around irrigated trees (mean ± S.E.). Note that moisture units (% weight) differ from those measured by soil moisture probes (% volume).

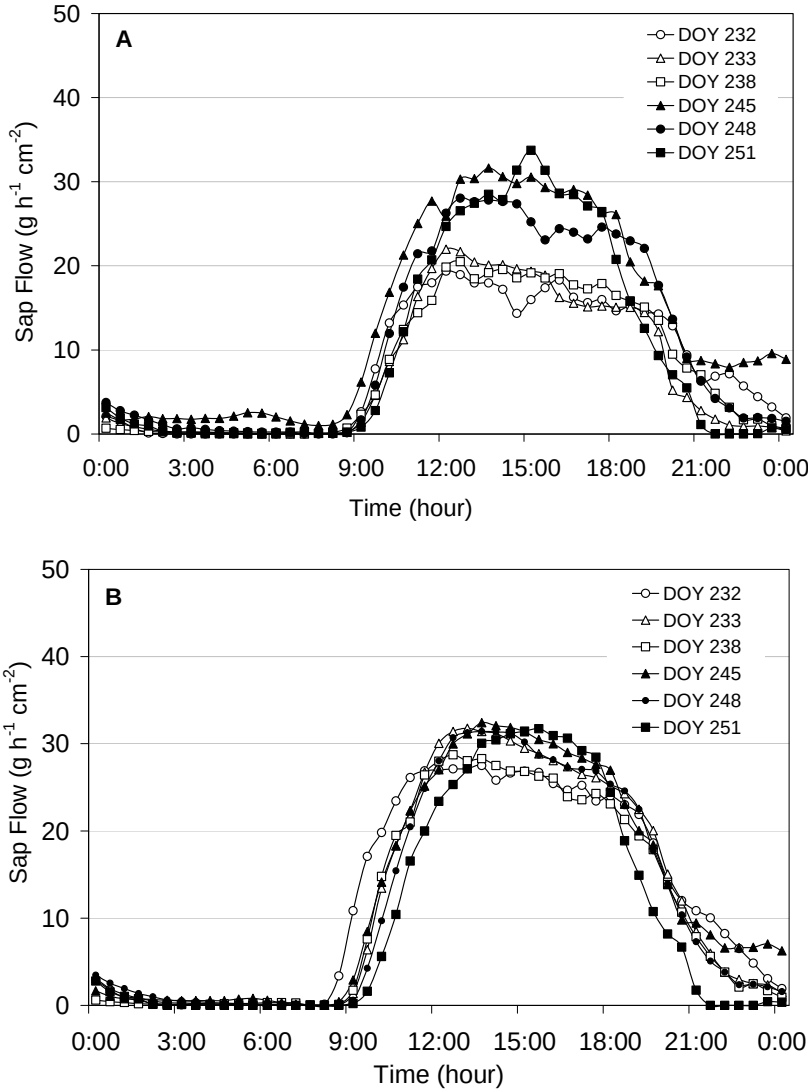

Figure 4.2 A and B. Diurnal patterns of sap flow for irrigated trees M1 (A) and F1 (B) on three representative days before irrigation (open symbols), and after irrigation (closed symbols) on 29 August (DOY 241).

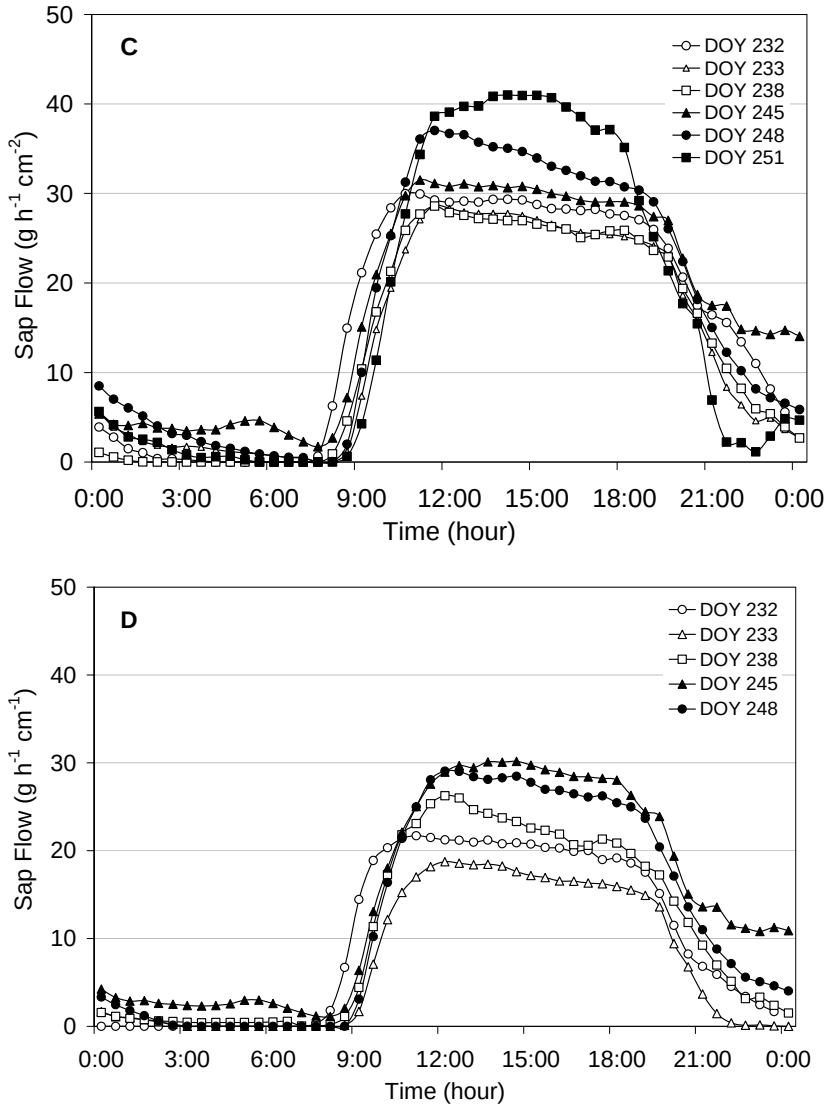

Figure 4.2 C and D. Diurnal patterns of sap flow for irrigated trees F2 (C) and M2 (D) on three representative days before irrigation (open symbols), and after irrigation (closed symbols) on 29 August (DOY 241). DOY 251 is missing from M2 due to inadequate sap flow data.

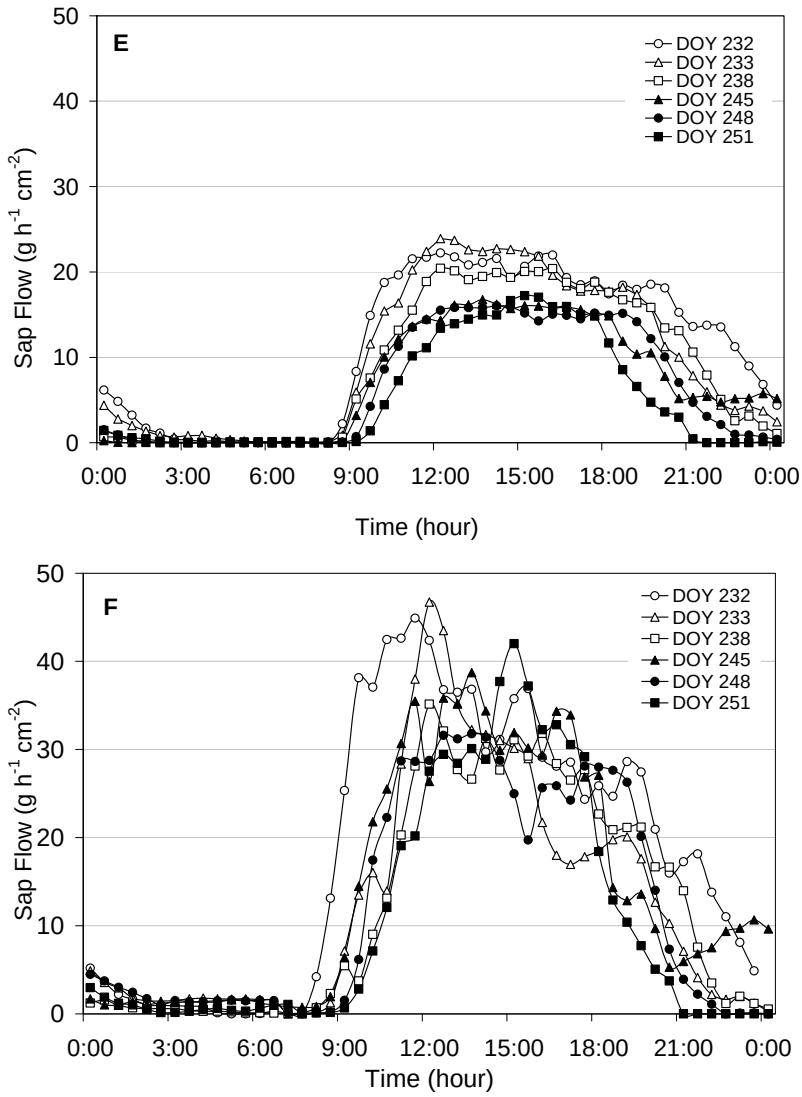

Figure 4.2 E and F. Diurnal patterns of sap flow for control (not irrigated) trees M3 (E) and M4 (F) on three representative days before irrigation of other trees (open symbols), and after irrigation (closed symbols) on 29 August (DOY 241).

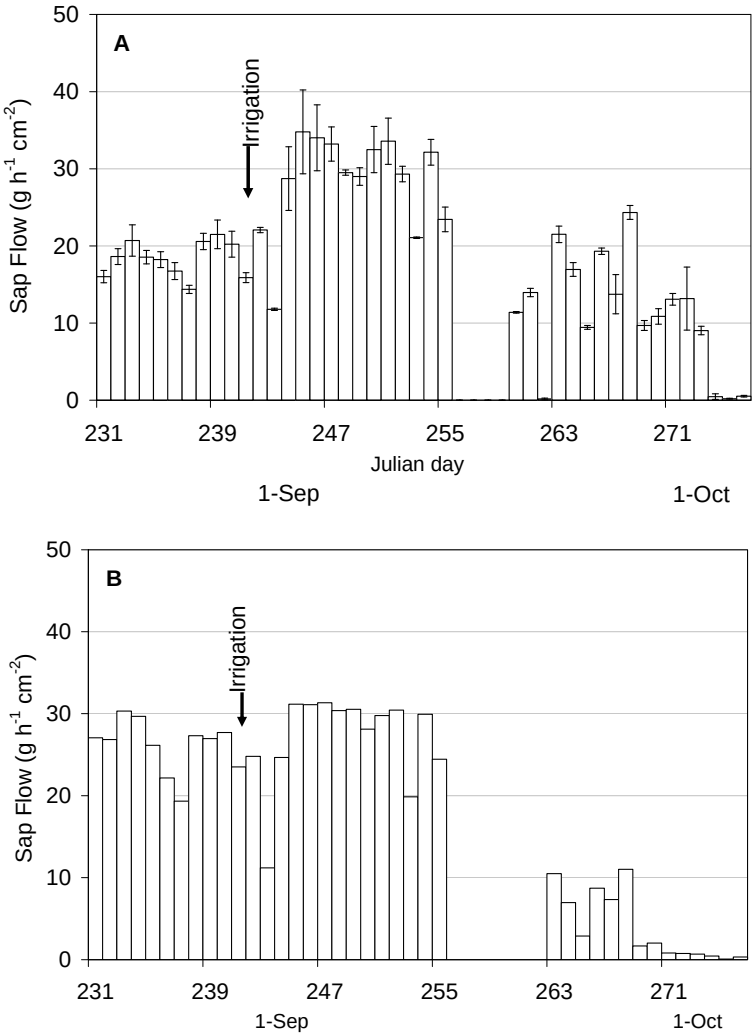

Figure 4.3 A and B. Afternoon sap flow (12:00 h to 16:00 h) for irrigated trees M1 (A) and F1 (B) from 19 August (DOY 231) to 3 October (DOY 276). Mean sap flow was calculated from two TDPs ± S.E. (A) or one TDP (B). Trees were irrigated on 29 August (DOY 241). Where no flow is shown, data was missing or inadequate**.**

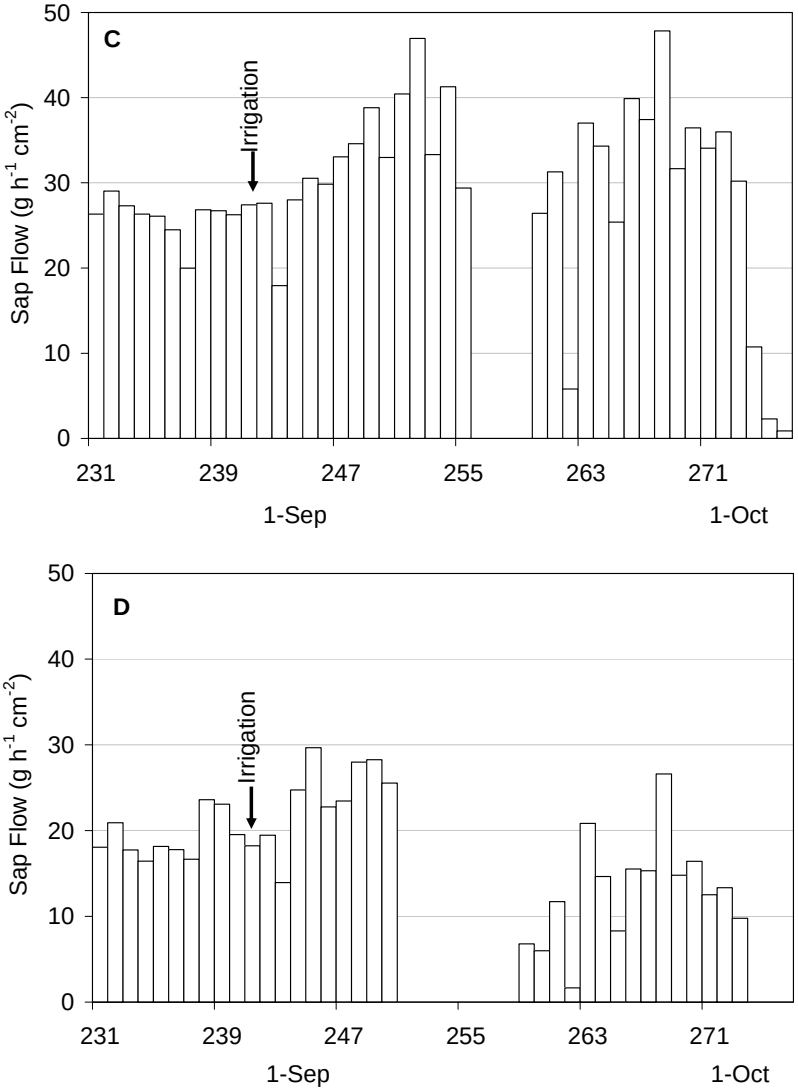

Figure 4.3 C and D. Afternoon sap flow (12:00 h to 16:00 h) for irrigated trees F2 (C) and F1 (D) from 19 August (DOY 231) to 3 October (DOY 276). Mean sap flow was calculated from one TDP. Trees were irrigated on 29 August (DOY 241). Where no flow is shown, data was missing or inadequate.

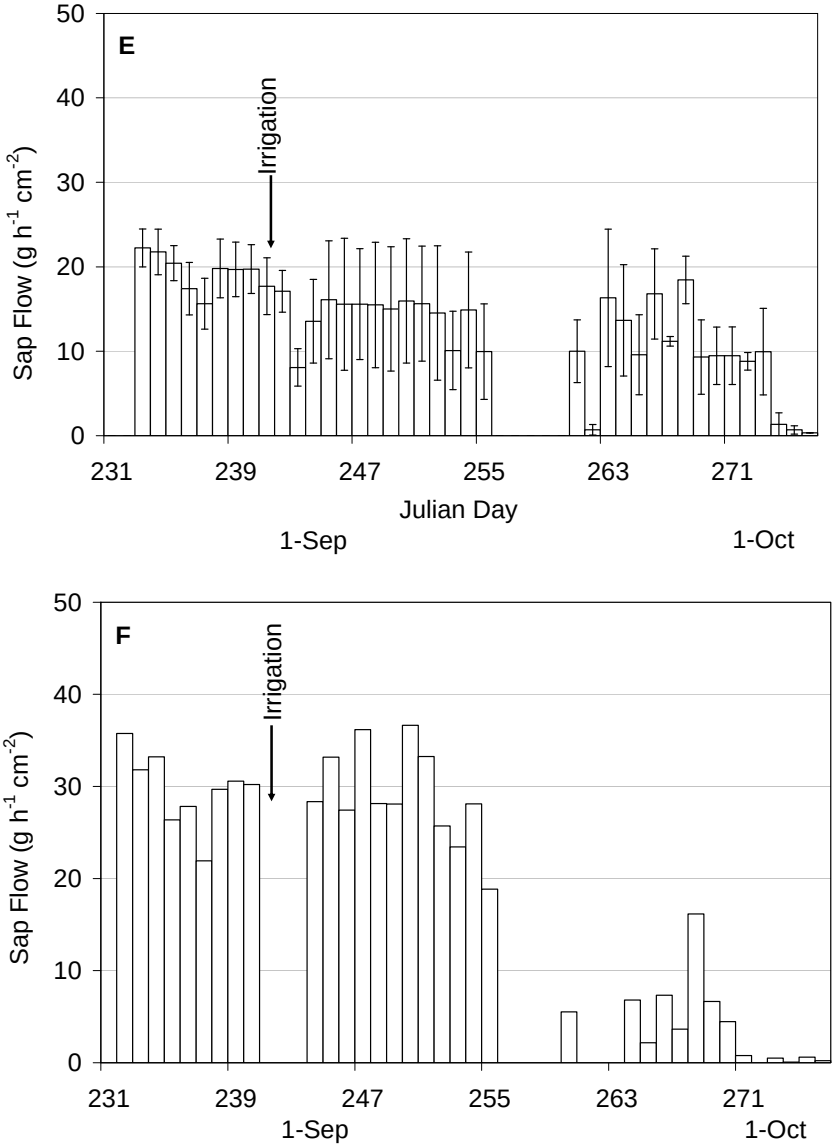

Figure 4.3 E and F. Afternoon sap flow (12:00 h to 16:00 h) for control (not irrigated) trees M3 (E) and M4 (F) from 19 August (DOY 231) to 3 October (DOY 276). Treated trees were irrigated on DOY 241, as shown by the arrow. Mean sap flow was calculated from two TDPs ± S.E. (E) or one TDP (F). Where no flow is shown, data was missing or inadequate.

4.3.3 Mean Canopy Stomatal Conductance

The response of mean canopy stomatal conductance (G_S) to irrigation differed somewhat among trees. G_S increased with irrigation in three of the trees (Figures 4.4 A, C, D) but not in the fourth (Figure 4.4 B). In two of the three trees, G_S increased evenly across the range of D. For example, the G_{Sref} (D = 1 kPa) increased and there was little difference in the G_S versus D relationship (Figure 4.4A, C). In the third tree, G_S increased at higher D, but not at lower D (Figure 4.4 D). In the two control trees, G_S was similar or decreased when comparing before- and after-irrigation periods (Figure 4.4 E and F).

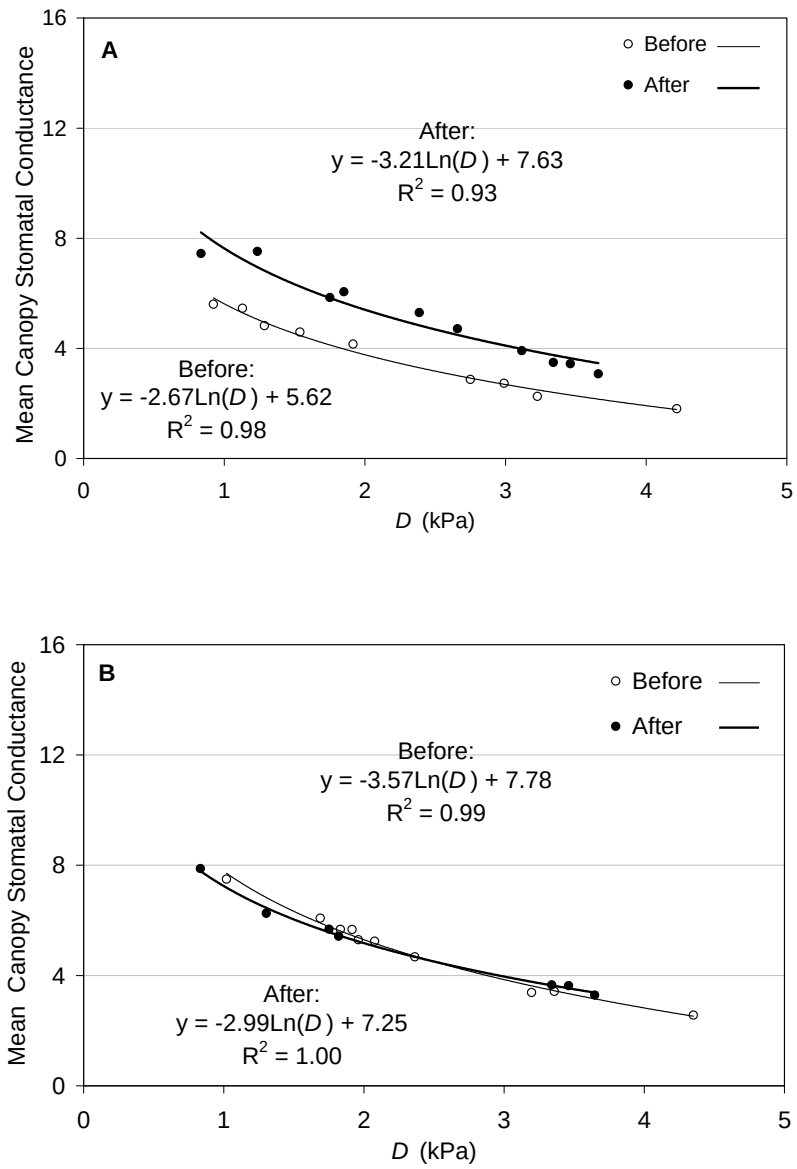

Figure 4.4 A and B. Boundary line values of G_S calculated by using the average hourly sap flow and D for each day when insolation was above 0.4 kW m^{-2}. These data are from the irrigated trees M1 (A) and F1 (B). Data were divided up to represent before- (open circles) and after- (closed circles) irrigation. Logarithmic trend lines were fitted to each group and the resulting slope and G_{Sref} (at D = 1) are shown.

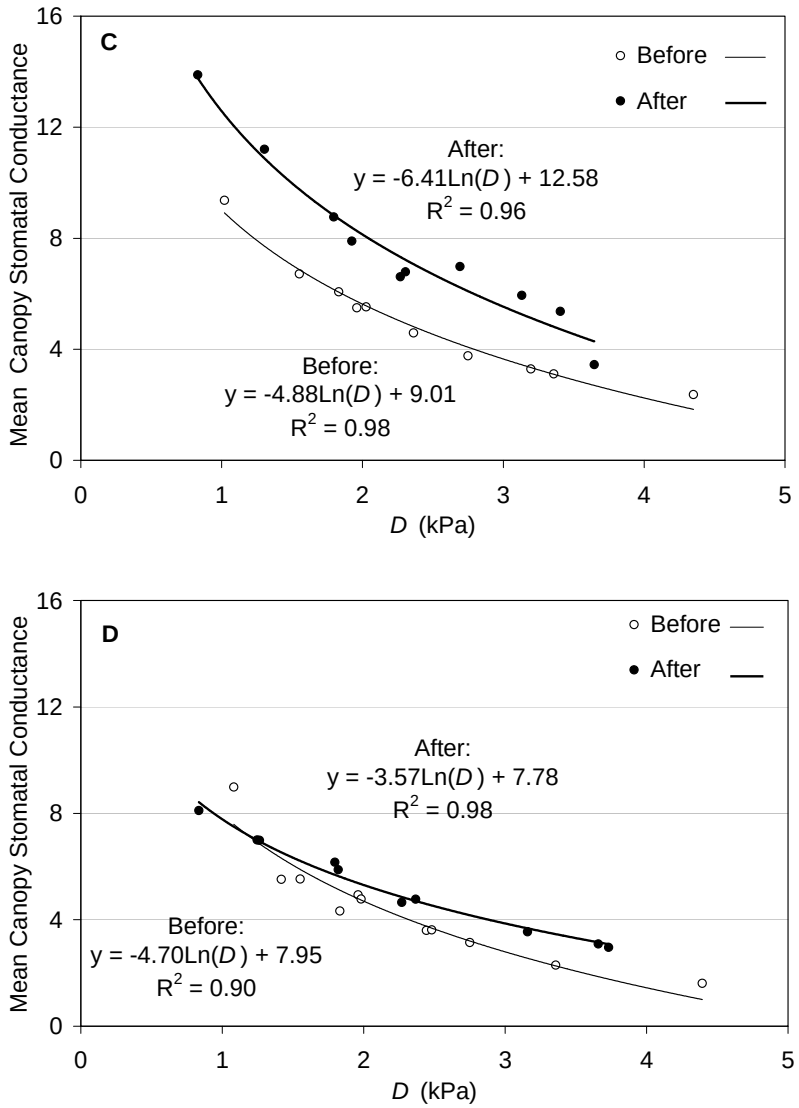

Figure 4.4 C and D. Boundary line values of G_S calculated by using the average hourly sap flow and *D* for each day when insolation was above 0.4 kW m^{-2}. These data are from the irrigated trees F2 (C) and M2 (D). Data were divided up to represent before- (open circles) and after- (closed circles) irrigation. Logarithmic trend lines were fitted to each group and the resulting slope and G_{Sref} (at $D = 1$) are shown.

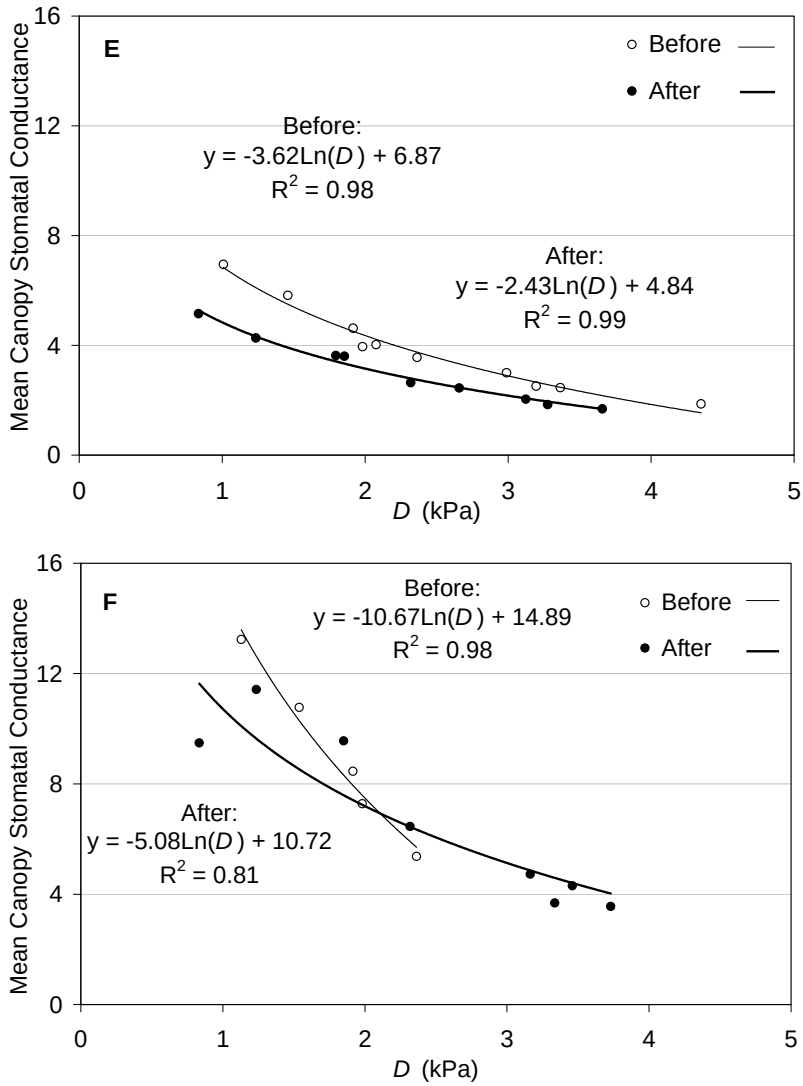

Figure 4.4 E and F. Boundary line values of G_S calculated by using the average hourly sap flow and D for each day when insolation was above 0.4 kW m^{-2}. These data are from the control trees M3 (E) and M4 (F). Data were divided up to represent before- (open circles) and after- (closed circles) the period of irrigation of the other trees. Logarithmic trend lines were fitted to each group and the resulting slope and G_{Sref} (at D = 1) are shown.

4.4 Discussion

In Chapter 3 we found stomatal conductance at the same *D* at both leaf and canopy levels decreased in association with the seasonal decline in water supply. This was a correlative analysis and in this subsequent study we manipulated water supply to test for causal association. We thus applied water to four trees in the Pearce Corner grove and predicted this would increase sap flow due to an increase in soil moisture. As expected, sap flow and canopy stomatal conductance increased in response to irrigation, consistent with an increase of the water potential difference (Figures 4.2A to E, 4.3A to E, and 4.4A to E). The increase in sap flow could have also been due to an increase in hydraulic conductance following the increased water availability in the upper soil levels (Figure 3.15, 4.1).

The addition of water increased the soil moisture surrounding each of the four irrigated trees (Figure 4.1). Given the relationship between soil moisture and soil water potential (Chapter 1), this increase in moisture would have increased the Ψ_S towards zero, and if Ψ_L was maintained around -2.0 MPa at midday (Figure 3.17) there would have been an increase in the water potential difference between Ψ_S and Ψ_L (Chapter 1).

Atmospheric demand was similar before and after irrigation (Figure 3.9), benefiting the comparison of diurnal patterns of sap flow before and after irrigation. The change in flows of irrigated trees is attributed to the change in

water potential difference and a possible larger available area of existing roots acting to increase hydraulic conductance. The slight decrease of sap flow in control trees could be due to continual seasonal drying of the riparian soil. Contributing to the response of all trees is the process of senescence which would decrease sap flow rates as trees were decreasing photosynthetic activity and CO_2 intake prior to the winter period.

Some studies involving irrigation and *Populus* have found little response in sap flow rates. Zhang et al. (1999) found soil moisture within the top 1.2 m to have a little effect on sap flow of *P. trichocarpa* x *P. tacamahaca* in a riparian area in England. Williams and Cooper (2005) found no response in ecophysiological factors such as xylem water potential and stomatal conductance within riparian Fremont cottonwoods (*P. Fremontii*) following an increase in soil water availability on a regulated river, although they concluded the dieback from previous decades inhibited the cottonwoods from responding to the short-term increase in water availability.

Sap flow is the product of the water potential difference and hydraulic conductance (the Van den Honert equation). Soil water potential became less negative after irrigation, and the water potential difference between soil and leaves would have increased. We speculate that hydraulic conductance might also have increased as a result of root distribution. Excavations under cottonwood trees have reported surface lateral roots and moderately deep roots which extend

into the saturated zone (Gazal et al. 2006). While installing soil moisture probes we also noticed a layer of lateral roots between 0.25 m to 0.5 m below the surface. The water applied during irrigation increased the availability of water at 0.5 m, where soil moisture before irrigation was low. This would increase the overall functional root zone and hydraulic path able to take up water. The variability of sap flow among trees could possibly be related to many physiology factors including root distribution, leaf area, and hydraulic conductance of the path from soil to leaves, which could differ from tree to tree.

Mean canopy stomatal conductance (G_S) was estimated and showed increases, for the same value of D, after irrigation. This is consistent with the increases observed in sap flow (Figures 4.2A to D, 4.3A to D). The controls suggest a decrease or negligible change in G_S for a given D (Figures 4.4E to F). Stomatal sensitivity to D (slope of logarithmic equation) following irrigation changed little in two trees (Figures 4.4A, B, C) and apparently decreased in one tree (Figure 4.4D). This was consistent with diurnal patterns and average sap flow (Figures 4.2 to 4.5). The increases in the magnitude and variability of G_S after irrigation are consistent with seasonal changes in sap flow and stomatal conductance (Chapter 3).

Conclusion: These results are consistent with the interpretation from sap flow and stomatal conductance measurements made in Chapter 3, further demonstrating the limitation of water supply, specifically soil water supply, that cottonwoods at

Pearce Corner experience. In Chapter 3, as water availability decreased, the majority of trees had a decrease in stomatal conductance at the same *D* for both leaf and canopy levels. Following irrigation, trees responded by increasing sap flow and canopy stomatal conductance as a likely result of an increase of the water potential difference and possibly due to an increase in the proportion of the root system in contact with sufficient moisture.

Future Work: To increase our knowledge and understanding of the physiological response of the cottonwoods to increased water availability, it would be beneficial to measure stomatal conductance, leaf and soil water potentials after irrigation. Direct measurements of soil water potential would quantify differences in water potential between the soil and leaves.

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CHAPTER 5 - Conclusions

In this study we linked the Oldman River water to the groundwater table, soil moisture, sap flow and transpiration, enabling us to take a look at the SPAC in narrowleaf cottonwoods at the Pearce Corner grove in southern Alberta. Following an initial increase in river water, the groundwater table, and soil moisture levels due to melting snow and rain these water sources declined gradually through the summer. Through measurements with thermal dissipation probes (TDPs) we were able to continuously monitor relative sap flow for six cottonwood trees and relate it to the water potential difference between soil and leaves, a condition necessary for sap flow. The decline in soil moisture corresponds to a decrease in soil water potential as evidenced by more negative predawn leaf water potentials. This, combined with the isohydric maintenance of minimum leaf water potential, decreased the water potential difference that drives sap flow. In addition, a possible alteration in hydraulic conductance will influence sap flow rates in accordance with the Van den Honert equation.

As a whole, sap flow was found to be variable across the season with increasing, decreasing, and static patterns found in the six trees analyzed. Instantaneous abaxial stomatal conductance was also measured and was found to decrease from July to August for a given vapor pressure deficit (*D*), as did the calculated canopy stomatal conductance. Thus, stomatal conductance and canopy stomatal conductance were apparently limited by declining water supply as their rates decreased over the season.

As mentioned in Chapter 1, hydraulic conductivity of the soil to leaf water pathway could be altered by many things including aquaporin activity and xylem cavitation. Cotton plants were previously found to have daily cycling in root resistance to water uptake (Javot and Maurel 2002). It was proposed that light and other environmental stimuli altered aquaporins and consequently hydraulic conductivity (Javot and Maurel 2002). Induced by low water potentials, xylem cavitations typically persist for a growing season as their refilling requires positive pressure within the xylem, which is a rare occurrence (Tyree et al. 1994). Cavitations hinder sap flow since they decrease hydraulic conductivity. Depending on the species, cavitation vulnerability within *Populus* occurs around -1.5 to -2.5 MPa, a moderately negative water potential, demonstrating riparian cottonwoods lack of drought tolerance or alternatively, a role in drought adaptation (Rood et al. 2000). While this extreme cavitation vulnerability contradicts with their native occurrence, it might reflect the abundant riparian groundwater sources (Tyree et al. 1994). The vulnerability of cottonwoods to cavitations and their natural location along rivers results in a high degree of susceptibility to alteration of river flows by upstream dams, which have resulted in their collapse on some regulated rivers (Rood and Mahoney 1990).

Given the decline in sap flow and decrease in stomatal and canopy conductance in association with the declining water supply as shown in Chapter 3, we increased soil moisture to examine the sap flow and canopy stomatal conductance response to test the causal association and increased water availability (Chapter 4). The

increase in soil moisture raised the soil water potential in the upper layer of the soil. With the consistent midday leaf water potential, the increase in soil moisture increased the water potential difference and possibly the overall hydraulic conductance by increasing the root area available to absorb water.

These findings demonstrate the water use of cottonwoods not only in terms of sap flow but also revealed how leaf and canopy level conductances and resulting transpiration rates are altered in response to changing water availability. The water supply limitation found in Chapter 3 and subsequent increase in canopy stomatal conductance following the increase in soil moistures in Chapter 4 demonstrates that the cottonwoods at Pearce Corner are opportunistic in taking up water from either the shallow soil or the deeper capillary fringe layer located above the saturated water table.

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Appendix A: Statistical Analyses

Table A1.1. There was a significant difference found by the ANCOVA for both group and D effects for M1.

Effect	F-Stat	p value
Group	9.1423	<0.0001
D	7.4565	0.0089
Group**D*	3.643	0.116

Table A1.2. Tukey's HSD found that Group 1 had significantly higher flows than Groups 2 through 5 for M1. Levels not connected by the same letter are significantly different.

DOY Range	Post Hoc		Mean
157 - 172	A		23.7000
184 - 194		B	17.0000
195 - 207		B	18.6154
211 - 225		B	19.6923
231 - 240		B	18.6000

Table A2.1. There was a significant difference found by the ANCOVA between DOY groups and the covariate D had a significant influence on sap flows for F1.

Effect	F-Stat	p value
Group	9.1567	<0.0001
D	6.1706	0.0169
Group**D*	1.3318	0.2732

Table A2.2. Tukey's HSD demonstrated that Group 5 had significantly higher flows than groups 2 through 4 for F1. Levels not connected by the same letter are significantly different.

DOY Range	Post Hoc		Mean
160 - 172	A	B	21.1294
184 - 194		B	18.4725
195 - 207		B	19.2896
212 - 225		B	20.8295
231 - 240	A		26.3542

Table A3.1. The ANCOVA for F2 revealed no statistically significant effects, thus a Tukey's HSD was not needed.

Effect	F-Stat	p value
Group	1.1743	0.334
D	2.8377	0.0986
Group**D*	2.056	0.1014

Table A4.1. The ANCOVA for M2 revealed no statistically significant effects, thus a Tukey's HSD was not needed.

Effect	F-Stat	p value
Group	0.6359	0.6395
D	0.0291	0.8654
Group**D*	1.8144	0.1423

Table A5.1. The ANCOVA analysis on M3 sap flow data revealed a significant differences between groups and a significant interaction between group and *D*.

Effect	F-Stat	p value
Group	2.6379	0.0471
D	2.5521	0.1176
Group**D*	3.7164	0.0112

Table A5.2. Tukey's HSD on M3 demonstrated that all DOY groups were the same as levels connected by the same letter are not significantly different.

DOY Range	Post Hoc	Mean
157 - 172	A	16.7000
184 - 194	A	16.4000
195 - 206	A	18.8333
214 - 225	A	19.3333
233 - 240	A	19.6250

Table A6.1. ANCOVA results for M4 demonstrate a significant difference between sap flow groups.

Effect	F-Stat	p value
Group	9.7679	0.0001
D	0.6639	0.4221
Group**D*	0.2913	0.8313

Table A6.2. Tukey's HSD revealed the difference between DOY sap flow groups with the last group having a significantly higher sap flow than from DOY 181-205 for M4. Levels connected by the same letter are not significantly different.

DOY Range	Post Hoc		Mean
160 - 171	A	B	23.9217
181 - 194		B	20.0550
195 - 205		B	18.2557
229 - 240	A		30.3618

Table A7.1. One sample t-test for mean canopy stomatal conductance reference point (G_{Sref} when the value when $D = 1$) and slope values comparing the months June, July, and August to a test value of 1.

	t	df	Sig. (2-tailed)
July to June G_{sref}	-2.6824	5	0.043694835
August to June G_{sref}	-3.8652	5	0.011818131
August to July G_{Sref}	-2.8433	5	0.036104991
July to June Slope	-8.9311	5	0.000293
August to June Slope	-7.4131	5	0.000703
August to July Slope	-3.5919	5	0.015676

Table A7.2. One sample t-test results for mean canopy stomatal conductance reference points (GSref, when D = 1) and slope values comparing before and after irrigation data for irrigated and control trees.

	t	df	Sig. (2-tailed)
Before to After Irrigated G_{Sref}	-1.208	3	0.313669
Before to After Control G_{Sref}	-38.113	1	0.0167
Before to After Irrigated Slope	0.1921	3	0.859955
Before to After Control Slope	-4.3634	1	0.143425