

**TRACING CHANGES IN UPTAKE OF PRECIPITATION AND GROUNDWATER
AND ASSOCIATED CONSEQUENCES FOR PHYSIOLOGY OF DOUGLAS-FIR
AND LODGEPOLE PINE TREES IN MONTANE FORESTS OF SW ALBERTA**

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Abstract

Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) in southwestern Alberta were studied to determine the water sources used and the effect of changing soil moisture on tree ecophysiological function. The hydrogen stable isotope ratios of water from local groundwater and precipitation were compared to tree stem water to determine the amount of stem water coming from those two sources. There were no significant differences between species in the portion of summer precipitation taken up. However, Douglas-fir shifted towards using more groundwater as shallow soil moisture declined. In addition, Douglas-fir showed large changes in shoot water potential, but maintained relatively constant rates of oxygen evolution, whereas lodgepole pine exhibited smaller changes in shoot water potential and had severely reduced rates of oxygen evolution during mid-summer drought. Lower leaf-area to sap-wood area and higher leaf $\delta^{13}\text{C}$ (carbon isotope composition) suggested a less efficient hydraulic system in Douglas-fir compared to lodgepole pine.

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List of Abbreviations and Symbols

a	leaf area (m ²)
c	fitted constant, slope at d
d	fitted constant, T _{accl} at ½O _m
DF	Douglas-fir
$f(T_{accl})$	photosynthesis function
f	fraction of precipitation
F	final chamber voltage (mV)
F _c	final chamber voltage for calibration (mV)
F _v /F _m	fluorescence (variable/maximum)
I	initial chamber voltage (mV)
I _c	initial chamber voltage for calibration (mV)
LP	lodgepole pine
MPa	megapascal
n	oxygen content (mol)
O	oxygen evolution rate (μmol O ₂ m ⁻² s ⁻¹)
O _m	modelled oxygen evolution (μmol O ₂ m ⁻² s ⁻¹)
O _{max}	maximum observed oxygen evolution rate (μmol O ₂ m ⁻² s ⁻¹)
P	pressure (bar)
PPFD	photosynthetic photon flux density (μmol m ⁻² s ⁻¹)
R	constant (8.314 × 10 ⁻² L bar mol ⁻¹ K ⁻¹)
T	temperature (K)
t	time (s)
T _{accl(i)}	acclimation temperature at time <i>i</i>
T _{accl(i+1)}	acclimation temperature at time <i>i+1</i>
T _{air}	air temperature (°C)
V	volume (L)
w _{<i>i</i>}	weight of the sample
X	calibration value (μmol O ₂ mV ⁻¹)
δD	stable hydrogen isotope composition (‰)
δ ¹³ C	stable carbon isotope composition (‰)
δD _{gw}	groundwater δD (‰)
δD _{<i>i</i>}	hydrogen isotope composition of sample <i>i</i> (‰)
δD _{precip}	seasonally-weighted precipitation δD (‰)
δD _{tree}	stem water δD (‰)
τ	time constant
Ψ _{PD}	predawn water potential
Ψ _{MD}	midday water potential
‰	part per thousand

1.0 Introduction

1.1. Climate change and the hydrologic cycle

The effects of a changing climate on the hydrologic cycle have not been clearly identified. Increasing temperatures will amplify evaporation from the oceans and intensify the hydrologic cycle, increasing precipitation globally, with substantial temporal and spatial variation (Weltzin et al. 2003, Barnett et al. 2005, IPCC 2008). Hydrological effects of climate change may also include changing precipitation patterns, intensity and extremes, reduced snow cover, widespread melting of ice, and changes in soil moisture and runoff (IPCC 2008).

The effects of climate change on local precipitation patterns are particularly unknown. Models show high variation in projected precipitation, leading to substantial uncertainty in the predictions (IPCC 2008). Increasing atmospheric concentrations of CO₂ are expected to lead to increases in annual average surface temperature, as great as 2-5°C (Barnett et al. 2005, Mote et al. 2005, Regonda & Rajagopalan 2005). Snow-dominated ecosystems such as the Rocky Mountains will be particularly affected; warming temperatures will cause a greater fraction of winter precipitation to fall as rain versus snow, decreasing the snowpack (Barnett et al. 2005, Regonda & Rajagopalan 2005, Stewart et al. 2005). Increasing winter temperatures will cause the snowpack to melt earlier (Barnett et al. 2005, Rood et al. 2008), leading to earlier spring peak flow (Gan 2000, Regonda & Rajagopalan 2005), possibly by up to one month by 2050 (Barnett et al. 2005). Earlier snowmelt will also lead to increased soil moisture earlier in the season (Barnett et al. 2005). Declines in overall streamflow have been observed in streams and rivers on the eastern slopes of the Rocky Mountains (Rood et al. 2005), reflecting declining precipitation. Historical data from western North America

suggests that a natural response to warming climates and increasing temperatures is an increase in aridity (Cook et al. 2004).

1.2. Effects of changing hydrological patterns on local ecosystems

Alterations to local hydrologic cycles and precipitation patterns will have broad effects on local ecosystems (Mote et al. 2005). It has been suggested that shifts in the amount and timing of precipitation from anthropogenic climate change will have a greater affect on ecosystems than the increasing atmospheric concentrations of carbon dioxide and rising temperatures, particularly in arid and semi-arid ecosystems (Weltzin et al. 2003). Less accumulated snow will reduce the natural store of water in the Rocky Mountains which is released throughout the summer when demand is greatest (Mote et al. 2005, Rood et al. 2008). Changes in water relations induced by modified soil moisture regimes would affect photosynthesis via stomatal conductance (Kirschbaum 2000). Plants have shown significant adaptability to changes in temperature and CO₂ concentration as long as there is sufficient soil moisture available (Kirschbaum 2004). Changes in regional precipitation will have serious effects on the distribution, structure, composition and diversity of plants and animals and their respective ecosystems (Weltzin et al. 2003). Decreasing precipitation could lead to shifts in ecoregion boundaries and ecological communities (Rood et al. 2005).

1.3. The importance of water to trees

Water is the principal limiting factor contributing to tree survival and development, and is required for physiological processes which support plant growth and health (Noy-Meir 1973). Water performs fundamental roles in tree structure and support. Through maintenance of cell turgor pressure, water is the driving force for cell enlargement and stomatal control (Jackson et al. 2000). It is the medium for transport within a cell, being the solvent which transports

carbohydrates, nutrients and hormones through a plant. Water is also a reagent in photosynthesis - one of plants most important biochemical reactions.

Despite the central function that water plays in a tree's survival and growth, trees are constantly faced with the paradox that an inevitable consequence of photosynthesis is transpiration, which by definition is the evaporation (loss) of water from plants (Mitchell et al. 2008). For photosynthesis to occur, trees must open stomata to allow diffusion of CO₂ into the leaf, simultaneously allowing a pathway for water to be released into the atmosphere (Pallardy 1997). Plants must then replace water lost from transpiration in order to maintain physiological function. Water is limiting when there are inadequate amounts and when it occurs during the season when the plant is unable to fully utilize it (Schwinning et al. 2004).

Drought, or severe water stress due to low precipitation and low soil moisture (Gan 2000), is common and causes negative hydraulic and physiological responses in trees. Water stress and drought reduce xylem conductance to water, stomatal conductance to gas exchange, the growth rate of plants and affects many other physiological processes (Tyree & Ewers 1991). Drought stress causes the productivity of a forest to decline, and may even result in large scale tree death (Breda et al. 2006).

1.4. Magnitude of precipitation events

The magnitude of a plant's physiological response to precipitation depends on the interaction between rain event size and species (Schwinning et al. 2003). The size of spring precipitation events are often irrelevant if sufficient water had been stored through snowmelt (Schwinning et al. 2003). Research has shown that the magnitude of individual summer rain events may be more important than the sum, especially in arid and semi-arid ecosystems (Sala & Lauenroth 1982, Loik et al. 2004, Fravolini et al. 2005). Small events may not even

penetrate surface organic matter, evaporating rapidly. Larger events may infiltrate shallow soil layers and only be beneficial to species with extensive shallow root systems. Large events may infiltrate deeper soil layers and be exploited by plants with deeper rooting systems, or even recharge groundwater.

1.5. Timing of precipitation events

Precipitation patterns govern ecosystem processes in semiarid ecosystems (Loik et al. 2004), with the seasonality of precipitation being as important as the quantity (Schwinning et al. 2004). Conifers in the montane and subalpine zones of the Rocky Mountains have limited windows of opportunity for growth where soil and air temperatures are adequate for high rates of water and nutrient transport, as well as biochemical reactions such as photosynthesis. Conifers are able to quickly up-regulate photosynthetic activities in response to warming air temperatures (Monson et al. 2005); however they are in need of moisture at this specific time to maintain photosynthetic activities. Precipitation which had fallen as snow in the previous winter provides springtime moisture for trees, but to maintain high rates of photosynthesis regular inputs of moisture are required during the remainder of the growing season.

1.6. Availability of precipitation and soil moisture to trees

The availability of water to plants depends on the amount and timing of precipitation, the storage ability of the soil and the plants ability to access the resident moisture. A series of abiotic and biotic factors interact with the hydrologic cycle to govern the amount of water available. Precipitation, falling as snow or rain, can travel multiple routes influenced by soil properties, vegetation characteristics and the magnitude of precipitation events (Loik et al. 2004). Precipitation may be intercepted by plant foliage, particularly in forested areas, preventing precipitation from reaching the forest floor (Loik et al. 2004). It may infiltrate the soil, recharging soil moisture and groundwater, dependent on the amount of precipitation.

Precipitation falling on saturated soils will become runoff. Stored soil moisture is eventually returned to the atmosphere via evapotranspiration from soil and vegetation.

Soils differ in their ability to store and release water and these abilities are most strongly controlled by the physical properties of soil including texture, structure and depth (Hacke et al. 2000). For any given soil texture, deeper soils are able to retain higher amounts of soil moisture in comparison to shallow soils, due simply to a greater volume of soil. Organic matter also increases the amount of water holding capacity of a soil (Brady & Weil 2002).

Soil texture is a dominant controlling factor on a soils ability to retain and release water. Finer soil textures (more clay) have the ability to absorb and retain more water than coarse textured (low clay) soils (Hacke et al. 2000, McDowell et al. 2008). Soils with finer textures release water at slower rates because of stronger capillary forces retaining water in smaller pore spaces in comparison to coarse textured soils (Hacke et al. 2000). Hydraulic differences due to differing soil textures may affect the availability of water to vegetation with different rooting systems, with fine textured soils restricting the boundary between wet and dry soils during infiltration, inhibiting the uptake of summer precipitation by deep-rooted plants (Fravolini et al. 2005).

1.7. Moisture availability and tree rooting characteristics

Roots are the first barrier that water must pass through, as it begins its journey through a tree and rooting characteristics govern the ability of a tree to access different water sources. Individual species of trees possess distinct root systems which are influenced by environmental factors including soil texture, soil moisture and soil nutrients (Bishop 1962). Most below ground production is allocated to fine and small roots (Comeau and Kimmins 1989), and fine root biomass undergoes large seasonal fluctuations, with individual root

longevity determined by soil microsite conditions (Gill & Jackson 2000), responding to soil moisture and temperature. Plants with differing rooting characteristics are able to respond to varying moisture regimes; trees with a high density of shallow fine roots are able to maximize their use of shallow soil moisture, whereas trees that possess tap roots have the ability to access deep soil moisture (Canadell et al. 1996).

1.8. Tree hydraulic architecture

Water in conifers is transported through the tree in xylem cells called tracheids, with water flowing between tracheids through pits in cell walls (Tyree et al. 1994). The driving force for water transport in trees is large tensions, or negative pressures, generated by transpirational water loss (Meinzer et al. 2001) that develops at the top of a tree, in order to pull water through the xylem in accordance with the cohesion-tension theory of sap ascent (Dixon & Joly 1894). Trees have developed diverse hydraulic systems to cope with local moisture conditions. Hydraulic architecture is the structure and design of the water conducting system in trees (Tyree & Ewers 1991) and leads to approaching the function of a tree as a hydraulic system that forms an integrated network throughout the tree (Cruiziat et al. 2002). An important parameter of hydraulic architecture is hydraulic conductance, the ratio between water flux and the pressure gradient causing the flow (Tyree & Ewers 1991).

Water under tension is in a physically metastable state (Tyree et al. 1994) and is vulnerable to cavitation, the change of phase of water in the xylem from liquid water under tension to water vapour (Piñol & Sala 2000). When cavitating the xylem is filled with water vapour and/or air instead of liquid water and this breaks the continuity of the water column, disrupting water flow and preventing the transport of water under tension. Hydraulic failure occurs when the plant can no longer transport water due to water demand exceeding water supply, resulting in cavitation and a loss of conductance (McDowell et al. 2008). When soil

moisture is low it is possible for the tension within the xylem to increase to a critical point at which cavitation can occur. Xylem cavitation results in dysfunction, therefore it is important to avoid cavitation (Tyree et al. 1994). When cavitation occurs, plants must minimize the consequences by repairing and/or isolating the cavitated section. Species that exhibit a high vulnerability to cavitation must reduce stomatal conductance before a substantial fraction of hydraulic conductivity is lost by cavitation, limiting gas exchange (Tyree & Ewers 1991, Piñol & Sala 2000).

It is possible that there is a trade off between hydraulic conductance and resistance to xylem cavitation (Piñol & Sala 2000). Wider xylem conduits may also have larger pit membrane pores, thus being more efficient conductors of water but cavitating at lower water stress. In comparison, small xylem conduits may have smaller pit membrane pores which offer resistance to cavitation but reduce hydraulic conductivity of the xylem (Tyree et al. 1994). Some studies have shown conflicting results to the hydraulic conductivity trade off with cavitation resistance (Sperry et al. 1998), but in general species adapted to drought show greater cavitation resistance, in comparison to species adapted to moister habitats which cavitate at less negative water potentials (Sperry 2000).

1.9. Isohydic and anisohydric characteristics

Both environmental and plant factors control rates of transpiration. Plants possess the ability to control their rate of transpiration by altering the size of their stomatal aperture, accomplished through sensitivity and feedback of rates of evaporative water loss and sensitivity to soil water potential (Franks et al. 2007). A continuum of stomatal regulation has been established, categorizing plants ranging from isohydric to anisohydric capabilities (Tardieu & Simonneau 1998). Plants displaying isohydric behaviour reduce stomatal conductance as soil moisture declines, maintaining a relatively constant midday water

potential regardless of drought (McDowell et al. 2008). Therefore, isohydric plants possess strong stomatal control of transpiration (Franks et al. 2007). Conversely, anisohydric plants exhibit less stomatal control, revealed through declines in midday water potential as drought progresses. Isohydric plants prevent xylem water potential from decreasing past a critical point that would induce hydraulic failure, but the consequence of such tight stomatal control is reduced leaf gas exchange in times of water stress (Franks et al. 2007). Anisohydric plants are able to maintain high rates of photosynthetic gas exchange during drought but risk the prospect of hydraulic failure if soil moisture declines too much.

1.10. Douglas-fir and lodgepole pine forests in southwestern Alberta

Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) are both members of the Pinaceae (Pine) family and native to western North America (Martinez-Vilalta et al. 2004). Douglas-fir have a very wide latitudinal range through North America, being limited by temperature at its northern limits and moisture at its southern limits. Two varieties of the Douglas-fir have been identified: *P. menziesii* (Mirb.) Franco var. *Menziesii* or coastal Douglas-fir, and *P. menziesii* var. *glauca* (Beissn.) Franco, commonly called Rocky Mountain Douglas-fir (Hermann & Lavender 1990). The species of concern in this thesis, Rocky Mountain Douglas-fir, establishes pure stands in the eastern slopes of the Rocky Mountains with areas reaching out into the foothills of southern Alberta. Lodgepole pine (*Pinus contorta*) is considered to have the widest environmental tolerance of any conifer in North America (Lotan & Critchfield 1990). *Pinus contorta* has been divided into four varieties, with the species of concern in this study being *P. contorta* var. *latifolia*, the inland form, also referred to as Rocky Mountain lodgepole pine (Lotan & Critchfield 1990). Rocky Mountain lodgepole pine dominate much of the montane ecozone from Colorado to northern Alberta (Fahey & Knight 1986). In southwestern Alberta, Douglas-fir occur on southern slopes at

lower elevations and consequently further east than lodgepole pine, a species that forms pure stands in the sub-alpine ecozone.

1.11. Determining water sources

The relative proportions of precipitation used by woody vegetation can be determined by analyzing the natural abundance of the stable hydrogen isotope composition (δD) of stem water and comparing it to the stable hydrogen isotope composition of potential water sources (Flanagan et al. 1992, Valentini 1994, Williams & Ehleringer 2000, Dawson et al. 2002, West et al. 2007a, Eggemeyer et al. 2008). The isotopic composition of xylem (stem) water remains unaltered as it is transported from soil to root to shoot, and reflects the stable isotope composition of its source water (Flanagan & Ehleringer 1991, Ehleringer & Dawson 1992). The isotopic composition of precipitation fluctuates seasonally, with summer rains showing higher δD values (Dansgaard 1964, Gat 1996, Peng et al. 2004). In comparison, the isotopic composition of groundwater is the weighted average of long-term precipitation inputs (Ehleringer & Dawson 1992, Maule et al. 1994). The differences in stable isotope composition of source water make it possible to calculate the relative proportion of stem water which is coming from each source (Dawson et al. 2002).

This method has been employed in multiple ecosystems world-wide, most repeatedly in piñon-juniper woodlands in southern Utah, determining the reliance on summer precipitation of two coexisting conifers, piñon pine and a juniper species (Flanagan et al. 1992, Williams & Ehleringer 2000, West et al. 2007a, West et al. 2007b). Stem water stable isotope composition has been used to determine the water sources of two conifer and two deciduous species in the Italian Alps (Valentini et al. 1994), to determine if surface or deep roots were most active in water uptake in four families of loblolly pine (Retzlaff et al. 2001), and also to

determine the water relations of two evergreen tree species in a karst savanna (Schwinning 2008).

1.12. Contrasting water sources of two forests

The present study is the first to examine water sources for two conifers – Douglas-fir and lodgepole pine – in southwestern Alberta. There were two primary questions addressed in this research. First, what consequences did seasonal changes in available soil moisture have on tree ecophysiological function? Secondly, what were the relative proportions of water from precipitation and groundwater that were being used by each species in their respective forests during the growing season?

It was expected that the Douglas-fir would utilize a greater fraction of groundwater/deep soil moisture because of the greater soil depth at that site. Consequently, they would be under less water stress and be able to maintain higher rates of photosynthesis throughout the growing season, regardless of soil moisture conditions. Because of the higher potential amounts of soil moisture, Douglas-fir may be more likely to exhibit anisohydric characteristics and would experience larger seasonal changes in midday water potential. In comparison, it was expected that the lodgepole pine would be more reliant on spring and summer precipitation, due to shallow soil with lower moisture storage capacity. As a result, they would be more likely to demonstrate water stress as summer progressed and soil moisture reached a minimum and a lack of precipitation input was experienced. The moisture stress could present itself in the lodgepole pine through reduced rates of photosynthesis. In addition, the lodgepole pine would also be more likely to demonstrate isohydric characteristics and maintain relatively constant midday water potentials as the growing season progressed.

Knowing a species response to changing soil moisture could provide us with insight as to how species boundaries may shift in response to changing precipitation patterns resulting from climate change. Determining the relative proportion of different water sources being used by individual species, and the effect of changing moisture conditions, may allow us to predict how each species will respond to changing temperatures and altered moisture regimes.

2.0 Methods

2.1. Study sites

The study was conducted at two sites in southwestern Alberta, Canada, in the front ranges of the Rocky Mountains (Figure 1). The Douglas-fir (DF) site (49°42' N, 114°01' W) is located 25 km north of Pincher Creek, AB, in the Montane natural subregion of Alberta (Archibald et al. 1996) at an elevation of 1402 m. The DF study site was on private ranch land owned by Bruce and Marianne Mowat. The mean annual temperature (1971-2000) at Claresholm (45 km north-east of the Douglas-fir site, elevation 945 m) is 5.2°C. The 30-year (1971-2000) average annual precipitation at Cowley (15 km south of the Douglas-fir site) is 493.8 mm, with 61% (303.3 mm) of that being rain and 39% (190.5 mm) snow. Claresholm is the Environment Canada (EC) station closest to the Douglas-fir site with long-term temperature records. Cowley is the closest EC station to the Douglas-fir site with long-term precipitation records. The Douglas-fir forest studied was on the crown of a large hill, with a west-northwest facing aspect.

The lodgepole pine (LP) site (49°49' N, 114°25' W) is located approximately 20 km north of Coleman, AB, in the Subalpine natural subregion of Alberta (Archibald et al. 1996) at an elevation of 1500 m. The LP study site was situated east of the Racehorse Creek Campground across Highway 40 (Forestry Trunk Road). The 30-year (1971-2000) mean annual temperature at Coleman (elevation 1303 m) is 3.5°C. The 30-year average annual precipitation at Coleman is 576.5 mm, with 69% (397.2 mm) of that falling as rain and 31% (179.2 mm) as snow. Coleman is the closest EC weather station to the LP study site. The lodgepole pine forest studied had a west facing aspect. The two study sites are located 30 km apart, with the Douglas-fir site being situated 30 km south-east of the lodgepole pine study site.

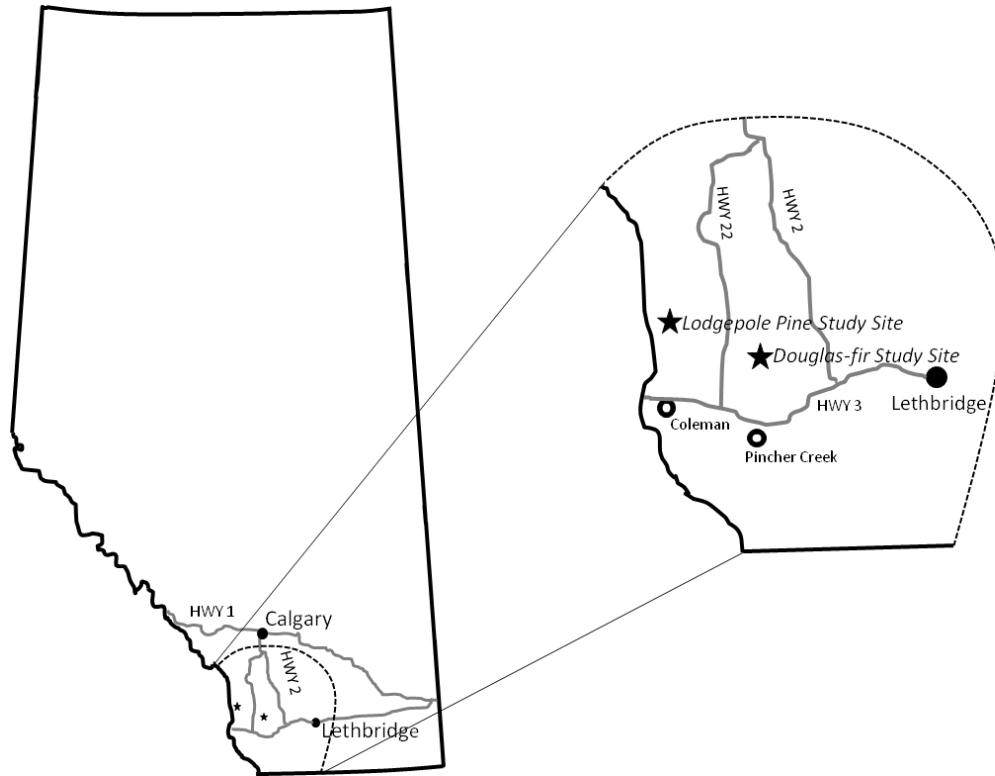


Figure 1. Map of Alberta, Canada, and the location of the Douglas-fir and lodgepole pine study sites.

2.2. *Meteorological data*

Meteorological stations were installed that consisted of 3 m tall triangular towers which served as an instrument base, with power being supplied to instruments from batteries charged by solar panels. The meteorological station at the DF site had a north facing aspect and the station at the LP site had a west facing aspect. Air temperature, relative humidity, atmospheric pressure, photosynthetic photon flux density (PPFD), precipitation, soil temperature and soil moisture were measured from May-October 2008. Air temperature and relative humidity were measured at 1.5 m above ground using a temperature and relative humidity probe (HMP45C, Campbell Scientific Ltd., Logan, Utah, USA), consisting of a platinum thermistor resistance thermometer and a Vaisala HUMICAP[®] 180 capacitive relative humidity sensor housed inside a vented radiation shield. Barometric pressure was measured using a barometric pressure sensor (CS105, Campbell Scientific Ltd.). Photosynthetic photon flux density (PPFD) was measured with a quantum sensor (LI190SB, Li-Cor, Lincoln, Nebraska, USA) installed at the top of the tower (3 m).

Soil temperature was measured at three depths (5, 15 and 30 cm) using a thermistor soil temperature probe (107B, Campbell Scientific Ltd.). Soil water content was measured (n=3) using CS616 water content reflectometers. The output period of the probes was converted to volumetric water content using manufacturer recommended calibration equations. Relative soil moisture was calculated as the ratio of the difference between a given volumetric measurement and the minimum volumetric measurement to the difference between the maximum and minimum volumetric soil water contents. The calculations were done separately for each study site. Total rainfall was measured in 30-minute intervals with a tipping-bucket rain gauge (CS700, Campbell Scientific Ltd.). Instruments were connected to a data logger (CR23X, Campbell Scientific Ltd.) and scanned at 5-second intervals, which

were recorded by the data logger as 30-minute means. Data was downloaded to a field laptop computer during field visits.

2.3. *Water samples*

Two water samples from the sites were collected during each field visit at approximately two-week intervals. At the DF site groundwater samples were taken from a spring filling a cattle watering trough and from a local house tap connected to a water well. Due to the relative proximity of the sites to each other, the spring and well are likely from the same aquifer. At the LP site samples were taken from Vicary and Racehorse Creeks to use as a proxy for local groundwater, under the assumption that water in the creek was being supplied by groundwater from the surrounding mountains, including the LP study site.

At each site, 6 precipitation collectors were attached to fence posts or trees. The precipitation collectors were constructed from 2 L Rubbermaid liquid containers with an attached funnel. A ping pong ball was placed in the funnel to prevent evaporation and wire mesh covered the funnel to contain the ping pong ball and prevent large debris from entering. During each visit to the field up to 2 L of precipitation was collected depending on the amount of precipitation since the previous sampling date.

2.4. *Stem samples*

Tree stem samples, approximately 5 cm long with a diameter of approximately 5 mm, were clipped from 5 trees chosen randomly each sampling day at each site at a height of approximately 2 m from the ground. If present, needles were plucked from the stem samples. Stem samples were cut into 1 cm segments, and placed into glass vials which were closed and sealed with Parafilm. Samples were stored in a cooler until return to the lab where they were stored in a freezer until stem water extractions were completed.

2.5. *Water potential*

Samples for predawn measurements, taken as a proxy for soil water potential, were taken immediately before dawn. Midday water potential measurements were taken between 12:00 pm and 2:00 pm mountain daylight time. Twig samples for water potential measurements were cut on an angle from 5 trees chosen randomly each sampling day using sharp hand pruners. Twig samples (approximately 5 mm diameter), including foliage, were taken from fully exposed south facing branches at a height of approximately 2 m from the base of the tree. Needles were plucked for 3 cm from the cut end, and the phloem peeled back 1 cm from the cut end to aid in determination of the end point.

Water potential measurements were immediately completed in the field using a pressure chamber (PMS Instruments Co., Corvallis, Oregon, USA) and a portable nitrogen tank. Twig samples were inserted into rubber gaskets and firmly pushed into the chamber cover of the pressure chamber. The chamber lid was attached to the chamber and pressure was slowly increased within the chamber. The cut end of the sample was closely observed using a hand lens and flashlight when needed. When the end point was reached, the pressure at which a uniform film of water appeared on the cut surface, the control valve was switched to off and the pressure immediately read and recorded.

2.6. *Needle samples*

One-year old needle samples were taken from 5 trees chosen randomly each sampling day. Samples were collected from fully exposed, south-facing branches at a height of approximately 2 m above ground level. Needles were dark-adapted for one hour by placing them in small manila envelopes. Chlorophyll fluorescence and oxygen evolution measurements were completed on the same needle samples. The needles were then sealed in

envelopes and brought back to the lab, where they were dried at 60°C for 48 hours and stored for later analysis of carbon isotope composition ($^{13}\text{C}/^{12}\text{C}$) and total nitrogen content.

2.7. *Fluorescence*

Chlorophyll fluorescence was measured in the field using a fluorescence monitoring system (FMS 2, Hansatech Instruments, Norfolk, England). After the dark-adaptation period, needles were carefully lined up on a flat black background. The fibre-optic of the fluorescence monitoring system was held in place by a clamp attached to a support stand. The fibre-optic was positioned at approximately a 45° angle, 1 cm away from the needles. Dark-adapted samples were exposed to an intense saturating pulse of light and the ratio of variable fluorescence to maximal fluorescence, F_v/F_m , was measured to provide the maximum quantum efficiency of photosystem II photochemistry (Baker 2008).

2.8. *Photosynthetic oxygen evolution*

Photosynthetic oxygen evolution was measured in the field using a leaf disc electrode chamber (LD2/3, Hansatech Instruments) (Delieu and Walker 1981). The electrode was prepared by placing 5 drops of electrolyte (50% potassium chloride) on the electrode. A 2 cm² piece of cigarette paper (as a spacer) and a 2 cm² piece of membrane were layered on top of the cathode. O-rings were applied to hold the spacer and membrane in place on the electrode and the electrode was installed in the electrode chamber.

The electrode chamber was connected to the electrode control unit (CB1-D3, Hansatech Instruments), which in turn was connected to a field laptop computer. The electrode control unit provided stable voltage to the electrode disc, and the current generated by the electrode in the presence of oxygen was converted into a voltage that was recorded on the computer. The electrode disc produces a voltage proportional to the O₂ concentration.

In the electrode chamber a series of support materials were placed in order to support the sample above the cathode while still allowing the diffusion of evolved oxygen back to the cathode. The temperature of the leaf chamber and electrode were controlled at 25°C by a water bath connected to the electrode chamber. A portable tank of air which had a CO₂ concentration of 5% was also connected to the electrode chamber.

The system was checked for leaks by filling a syringe with 1 mL of air and inserting it into an open tap. If no leaks were present, the voltage reading would increase and then remain constant. If leaks were present, an increase in voltage followed by a gradual decline would be seen and all O-rings and other connections were examined and resecured.

Calibration values were calculated prior to each sample. A known volume of air (1 mL) was injected into the gas chamber, and the change in electrode voltage reading was observed. The O₂ content of the known volume of air was calculated using the Ideal Gas Law (equation 1). The calibration value was calculated by dividing the moles of O₂ in the injected air by the change in voltage observed (equation 2).

Ideal Gas Law:

$$n = \frac{PV}{RT} \quad \text{Equation 1}$$

Where:

n = oxygen content (mol)

P = pressure (bar)

V = volume (L)

R = constant (8.314×10^{-2} L bar mol⁻¹ K⁻¹)

T = temperature (K)

Calibration value:

$$X = \frac{n}{(F_c - I_c)} \quad \text{Equation 2}$$

Where:

X = calibration value ($\mu\text{mol O}_2 \text{ mV}^{-1}$)

n = oxygen content (μmol)

F_c = final chamber voltage for calibration (mV) (after addition of 1mL air)

I_c = initial chamber voltage for calibration (mV)

Needles were then placed adjacent to each other in the leaf chamber. The chamber was closed and flushed with air containing 5% CO₂. The high intensity light source (LS2, Hansatech Instruments) was placed on top of the chamber and turned on, providing a light intensity of about 2100 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. The voltage from the O₂ electrode was observed via the computer screen and when a steady increasing trend was observed (5-10 minutes after the light source was turned on), a start time and voltage was recorded. Four minutes later the end time and voltage were recorded.

Oxygen evolution rate:

$$O = \frac{X \times \left(\frac{F - I}{t}\right)}{a} \quad \text{Equation 3}$$

Where:

O = oxygen evolution rate ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)

X = calibration value ($\mu\text{mol O}_2 \text{ mV}^{-1}$)

F = final chamber voltage (mV)

I = initial chamber voltage (mV)

t = time (s)

a = leaf area (m^2)

Sample leaf area was calculated using a standard curve that related needle area to dry weight. This curve was generated by gathering 40 needle samples from each species over two months with masses in the range of those that were used for the oxygen evolution measurements. Upon return to the lab the surface area of the needles was measured using a leaf area meter (LI3000 LiCor, Nebraska, USA). The needles were dried at 60°C for 48 h and weighed, and the resulting standard curve produced (Figure 2). The average dry weight of Douglas-fir needles used in oxygen evolution measurements was 0.15 ± 0.04 g and for the lodgepole pine was 0.15 ± 0.03 g.

2.9. *Photosynthetic oxygen evolution model*

Seasonal changes in photosynthetic oxygen evolution were modelled as a function of acclimation temperature (Makela et al. 2004). Acclimation temperature (equation 4) was determined by calculating the change in acclimation temperature (equation 5) and adding it to the acclimation temperature from the previous time step. Original acclimation temperatures for each site were determined using air temperature from a local Environment Canada meteorological station (Pincher Creek). Air temperature from Pincher Creek at the beginning of April (DOY 92) was set as the initial acclimation temperature and calculations were reiterated throughout April using the EC air temperature. When meteorological data collection began at the study sites, that temperature became the air temperature used in calculations with the previously calculated acclimation temperature. The modelled curve was fit to data measured in the field while trees were recovering from winter down-regulation, a temperature controlled response (DF DOY 123-197, LP DOY 122-186) (Figure 3). The constants “c” and “d” were determined from the modelled curve fit to the data ($d=T_{\text{accl}}$ at $\frac{1}{2}O_{\text{max}}$, $c=\text{slope at } d$).

Photosynthesis model:

Acclimation temperature: $T_{accl(i+1)} = T_{accl(i)} + \Delta T_{accl}$ *Equation 4*

Change in acclimation temperature: $\Delta T_{accl} = \frac{T_{air} - T_{accl}}{\tau} \times \text{time step}$ *Equation 5*

Modelled oxygen evolution: $O_m = f(T_{accl}) \times O_{max}$ *Equation 6*

Photosynthetic function: $f(T_{accl}) = \frac{1}{1 + e^{-c(T_{accl}-d)}}$ *Equation 7*

Where:

T_{air} = air temperature

$T_{accl(i)}$ = acclimation temperature at time i

$T_{accl(i+1)}$ = acclimation temperature at time $i+1$

τ = time constant (200 hours)

time step = 0.5 h

$f(T_{accl})$ = photosynthesis function

O_m = modelled oxygen evolution ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)

O_{max} = maximum observed oxygen evolution rate ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)

d = fitted constant, T_{accl} at $\frac{1}{2}O_m$ (DF=3.78, LP= 4.15)

c = fitted constant, slope at d (DF=0.65, LP=0.40)

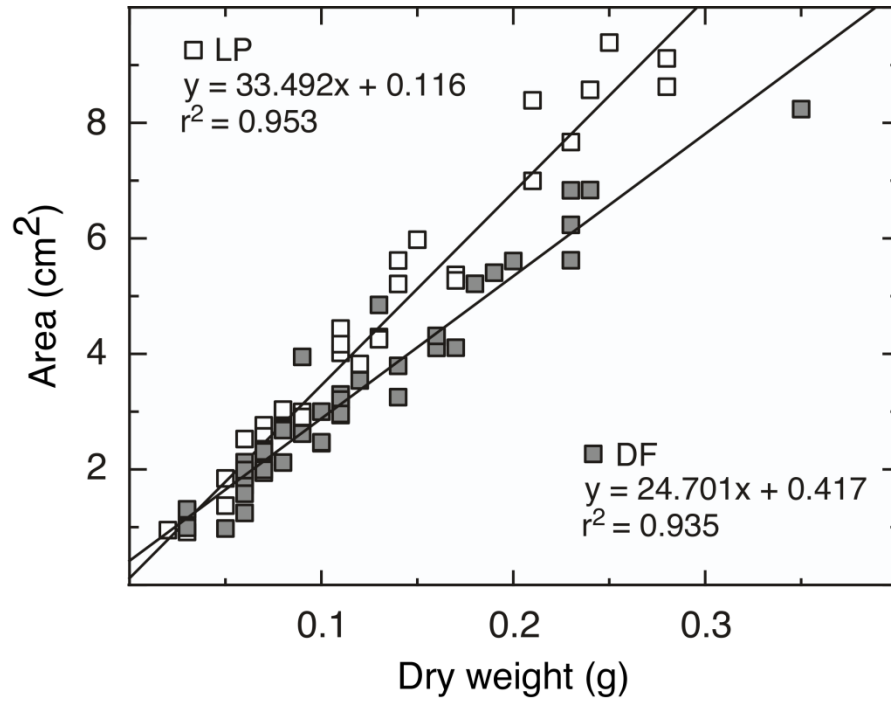


Figure 2. The relationship between needle dry weight (g) and needle surface area (cm²) for Douglas-fir and lodgepole pine in southwestern Alberta. 40 needle samples were taken from each species over July and August 2008.

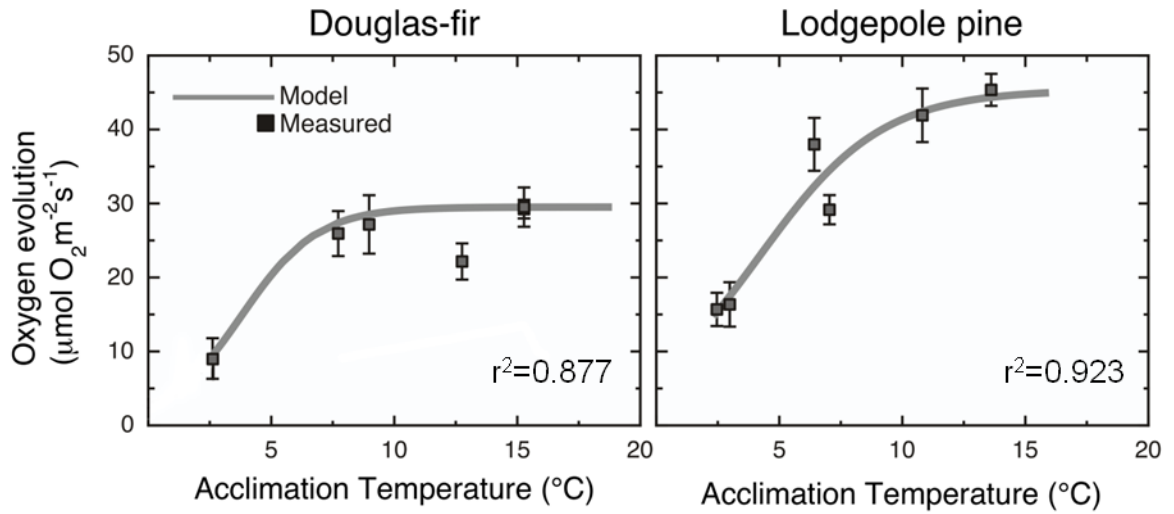


Figure 3. Modelled and measured oxygen evolution as a function of acclimation temperature (see equations 4-7), describing how photosynthesis changes with temperature. The modelled curve was fit to data measured in the field during recovery from winter down-regulation (DF DOY 123-197, LP DOY 122-186). Measured data represent the mean of 5 replicates \pm SE.

2.10. Forest description

At each study site, three 100 m transects were assessed in order to determine some basic forest attributes such as tree density, height, diameter at breast height and basal area. At the Douglas-fir site, five 25 m² quadrats were examined along each transect. At the LP site 5 or 10 quadrats of 25 m² or 100 m² were examined along each transect, depending on tree density. For each quadrat tree density was tallied, tree height was calculated using angles measured with a clinometer and tree diameter was measured at 1.35 m above the ground. Basal area was calculated using measured tree diameter and tree density. Sapwood area was measured at each study site by coring ten randomly chosen trees and immediately examining and marking the transition point from heartwood to sapwood on each core. The transition point from heartwood to sapwood was distinguished by examining the core in direct sunlight and observing the transition from translucent to non-translucent tissue, the sapwood being the translucent fraction of the core. Sapwood area was calculated using the measured basal area of the tree and the depth of the sapwood (Hall et al. 2003, West et al. 2008).

2.11. Stem water extraction

Water was extracted from stem samples using cryogenic vacuum distillation (West et al. 2006, Ehleringer et al. 2000). Vials containing pre-cut stem samples were placed in a sample tube attached to a vacuum line. An open dewar of liquid nitrogen was used to freeze the sample subsequent to the vacuum being applied. After the system was evacuated valves were closed to isolate the sample from the vacuum pump. The dewar of liquid nitrogen was then removed from the sample tube and the sample tube was heated with a beaker of boiling water, placed on a hot plate to ensure the water stayed at a constant temperature of approximately 100°C. Additional hot water was added to the beaker as it evaporated off to keep a consistent level. The tip of the collection tube was placed in a dewar of liquid

nitrogen to draw the moisture from the sample to the bottom of the collection tube. The extraction process continued for 90 minutes to ensure that all of the water had been extracted from the stem sample (West et al. 2006). After 90 minutes the collection tube was removed from the system and sealed with Parafilm.

The sample was allowed to melt and then was transferred to a glass vial containing a small amount of activated charcoal (0.01 mg), and the vials cap sealed with Parafilm. Activated charcoal was added to the sample in order to remove resins that had been extracted along with the stem water. Finally, after approximately 24 h the water sample was transferred from the charcoal vial by pipet to a 0.5 mL tube and sealed with a cap (with 'O' rings) and with Parafilm, for storage until stable isotope analyses were complete.

2.12. Hydrogen isotope composition of stem water, precipitation and groundwater

The hydrogen in water samples was reduced to H₂ through use of a zinc catalyst (Coleman et al. 1982). A Pyrex tube containing approximately 100 mg of zinc reagent was evacuated and backfilled with dry N₂ gas. A 2 µl subsample of water, loaded in a microcapillary tube, was placed in the backfilled Pyrex tube and frozen using liquid nitrogen. After the sample was frozen, the Pyrex tube and enclosed frozen sample were placed under vacuum and a propane torch was used to seal the tube. Sealed samples were placed in an oven at 500°C for 1 hour to convert the hydrogen in the water samples to hydrogen gas.

The hydrogen gas in the sealed sample tubes was analyzed for hydrogen isotope composition using a gas isotope ratio mass spectrometer (Delta Plus, ThermoFinnigan, Bremen, Germany) located in the Flanagan Lab, University of Lethbridge. The stable isotope ratio of hydrogen was expressed using delta notation (δ) in parts per thousand (‰) (equation 8), with R being

the molar ratio of heavy (²H) to light (¹H) forms, and the standard referring to Vienna standard mean ocean water (V-SMOW).

Hydrogen stable isotope ratio:

$$\delta D = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000 \quad \text{Equation 8}$$

The mass spectrometer was calibrated daily using three working standards LMX, LTP1 and RMSW (known δD values of -105.6 to -147.7‰) which had been calibrated against V-SMOW (International Atomic Energy Agency). The precision (standard deviation of 37 working standards) was 3.2‰ (LMX), 3.5‰ (LTP1), and 3.1‰ (RMSW). Accuracy was attained through daily normalization of samples relative to the working standards.

A two component mixing equation was used to determine the proportion of the tree's water supply coming from precipitation (equations 9 & 10).

Mixing equation:

$$\delta D_{tree} = f(\delta D_{precip}) + (1 - f)(\delta D_{groundwater}) \quad \text{Equation 9}$$

$$f = \frac{(\delta D_{tree} - \delta D_{groundwater})}{(\delta D_{precip} - \delta D_{groundwater})} \quad \text{Equation 10}$$

Where:

δD_{tree} = stem δD

$\delta D_{groundwater}$ = groundwater δD

δD_{precip} = seasonally-weighted precipitation δD

f = fraction of precipitation

δD_{tree} was the hydrogen isotope composition of stem water extracted from stem samples taken in the field. $\delta D_{groundwater}$ for the Douglas-fir site was the average hydrogen isotope composition of water sampled from a local well and spring over the growing season.

$\delta D_{\text{groundwater}}$ for the LP site was the average hydrogen isotope composition of water sampled from Racehorse and Vicary Creeks over the growing season. δD_{precip} refers to precipitation samples gathered at both sites and were calculated as monthly- and seasonally-weighted means (equation 11).

Monthly- and seasonally-weighted means:

$$\delta D_{\text{precipitation (weighted)}} = \frac{\sum_{i=1}^n w_i \delta D_i}{\sum_{i=1}^n w_i} \quad \text{Equation 11}$$

Where:

w_i = weight of the sample

δD_i = hydrogen isotope composition of that sample

2.13. Carbon isotope composition ($^{13}\text{C}/^{12}\text{C}$) and total leaf nitrogen content

Needle samples which weighed approximately 0.1-0.2 g were brought to the lab and dried at 60°C for 48 hours. Needle samples were ground to a fine powder with a mortar and pestle, and stored in small vials until analysis. A 1 mg subsample of ground leaf matter was sealed into tin capsules and loaded into an elemental analyzer (NC2500, CE Instruments, ThermoQuest Italia, Milan, Italy). Combustion occurred in the oxidation column of the elemental analyzer and the resulting products (CO_2 , NO_x and H_2O) were carried by the flow of a helium stream through a reduction column to remove excess oxygen and reduce nitrogen oxides to N_2 , and through magnesium perchlorate to remove water (Ehleringer et al. 2000). The remaining gases, carbon dioxide and pure nitrogen, were separated by gas chromatography and forwarded to the inlet of the gas isotope ratio mass spectrometer (Delta Plus) for analysis of $\delta^{13}\text{C}$ and the total amount of nitrogen.

The stable isotope ratio of carbon is expressed using delta notation (δ) in parts per thousand (‰), where R is the ratio of heavy isotope (^{13}C) to the light isotope (^{12}C) (equation 12), with the standard being the international standard Pee Dee Belemnite (PDB).

Carbon isotope ratio:

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad \text{Equation 12}$$

Two working standards, Rye and Mar1 ($\delta^{13}\text{C}$ values of -23.0 and -28.5‰, nitrogen contents of 2.8 and 1.5%, respectively) were interspersed throughout a run. The precision (standard deviation of 23 replicates) for $\delta^{13}\text{C}$ values of both Rye and Mar1 was 0.1‰, and for the nitrogen content of both standards was 0.1%. Accuracy was attained through daily normalization of raw sample values relative to the working standards.

2.14. Soil analysis

Soil samples were taken from 5 randomly chosen locations at each site with a soil corer pushed into the soil to a depth of 15 cm. The soil sample was stored in a tin container and cooler until return to the lab where it was weighed and then dried at 100°C for 24 h. Bulk density was determined by drying and weighing a known volume of soil (equation 13). Gravimetric water content was determined (equations 14 & 15) using soil water content and bulk density. Percent organic matter was determined through dry combustion. Soil samples were oven dried and a known mass of oven dried soil (approximately 5 g) was placed in a muffle furnace at 550°C for 2 hours. The sample was reweighed after combustion and the amount of organic matter was equal to the difference in mass between the oven dried soil and the combusted soil, and percent organic matter was then calculated (equation 16). Particle

size distribution was determined by sieving (Brady and Weil 2002) to separate coarse sizes of sand particles and the hydrometer method (Kalra and Maynard 1991) to differentiate the finest soil fractions (very fine sand, silt and clay).

Bulk density:

$$\text{bulk density} = \frac{\text{dry soil (g)}}{\text{volume (cm}^3\text{)}} \quad \text{Equation 13}$$

Gravimetric soil moisture:

$$\text{soil water content} \left(\frac{\text{g H}_2\text{O}}{\text{g soil}} \right) = \frac{(\text{wet soil (g)} - \text{dry soil (g)})}{\text{dry soil (g)}} \quad \text{Equation 14}$$

$$\text{gravimetric} \left(\frac{\text{g H}_2\text{O}}{\text{cm}^3 \text{ soil}} \right) = \text{soil water content} \times \text{bulk density} \quad \text{Equation 15}$$

Organic matter:

$$\% \text{ OM} = \frac{\text{organic matter (g)}}{\text{dry soil (g)}} \times 100 \quad \text{Equation 16}$$

2.15. Statistical analyses

Data was analyzed using Systat 10 (SPSS Inc. 2000) using one and two-way analysis of variance and correlation coefficients.

3.0 Results

3.1. Forest characteristics

Tree density at the Douglas-fir site and the lodgepole pine site were similar, with the Douglas-fir site containing 1493 ± 308 trees per hectare compared to the lodgepole pine site with 1340 ± 227 trees per hectare (ANOVA, $F(1,4)=0.16$, $p>0.05$, Table 1, Figures 4 & 5). Average diameter at breast height (DBH) was similar between sites (Kruskal-Wallis, $X^2(1)=1.19$, $p>0.05$). Average heights were also not significantly different between sites (ANOVA, $F(1,4)=1.69$, $p>0.05$), with trees at both sites having mean heights of approximately 15 m. It was determined that the DF site had $29.0 \text{ m}^2 \text{ ha}^{-1}$ more basal area than the LP site (ANOVA, $F(1,4)=10.24$, $p<0.05$). Sapwood area was not significantly different between the sites (ANOVA, $F(1,18)=4.11$, $p>0.05$), although lodgepole pine did have 13% more sapwood area than Douglas-fir (Table 1).

3.2. Soil characteristics

The DF site had a deeper soil with finer particle size compared to the soil at the LP site, which was shallow and sandy (coarse). The depth of the A horizon at the DF site was 13 cm compared to the A horizon at the LP site which had a depth of only 8 cm (Table 2). No differences were found in the amount of organic matter in the A horizon between the sites, with the DF site having $17.4 \pm 0.1\%$ organic matter and the LP site $16.0 \pm 2.0\%$ organic matter. Organic matter was 4.9% higher in the B horizon at the DF site (Kruskal-Wallis, $X^2(1)=6.82$, $p<0.01$) compared to the same horizon at the LP site.

The A horizon at the LP site had a coarse texture, containing 45.5% coarse and very coarse sand compared to 11.1% at the DF site (Table 3). Conversely, the DF site A horizon contained 53.2% fine and very fine sand compared to 19.7% at the LP site. The LP site

contained more clay than the DF site in both the A and B horizons, but still less than 5% at both sites in both horizons (ANOVA, A horizon $F(1,8)=25.04$, B horizon $F(1,6)=12.73$, $p<0.05$). The B horizon showed similar trends in particle size to the A horizon with the LP site consisting of more coarse and very coarse sand compared to the DF site which had a greater proportion of medium, fine and very fine sand. The DF site did include more silt than the LP site in the B horizon ($F(1,6)=11.11$, $p<0.05$). A C horizon was sampled at the DF site which was sandy.

The soil traits assessed suggest that the DF site would have a greater water holding capacity because of its greater depth and finer particle size. In comparison, the lodgepole pine site would be unable to store large amounts of water because of its relatively shallow depth and coarse texture.

Table 1. A description of forest characteristics at the Douglas-fir and lodgepole pine study sites. Tree density, basal area, diameter at breast height (DBH) and height were determined from three 100 m transects which were assessed at each site in July and August 2008. Each transect was sub-sampled through 5-10 quadrats which varied from 25-100 m². Sapwood area was measured from 10 randomly chosen trees at each site. Significance was determined through analysis of variance, NS = not significant.

	Douglas-fir	Lodgepole pine	Significance
Tree density (ha ⁻¹)	1493 ± 308	1340 ± 227	NS
Basal area (m ² ha ⁻¹)	58.7 ± 8.8	29.7 ± 2.3	<0.05
Average DBH (cm)	23.9 ± 6.4	17.56 ± 1.1	NS
Average height (m)	14.1 ± 1.5	15.2 ± 0.8	NS
Sapwood area (cm ²)	175.7 ± 29.8	224.9 ± 38.5	NS
Sapwood area (% of basal area)	37.7 ± 2.0	50.1 ± 5.7	NS



Figure 4. The lodgepole pine study site located across from the Racehorse Creek campground north of Coleman, AB. Photograph facing south-east towards study site with a west facing slope.



Figure 5. Douglas-fir study site located north of Pincher Creek, AB, on Bruce and Marianne Mowat's land. Photograph of the Douglas-fir forest looking west with a north facing slope.

Table 2. Soil characteristics at the Douglas-fir and lodgepole pine study sites. Samples were taken from randomly chosen points at each site in September 2008. Significance was determined through analysis of variance, NS = not significant.

	Douglas-fir	Lodgepole pine	Significance
Horizon A			
Depth (cm)	13	8	
Organic matter (%)	17.4 ± 0.1	16.0 ± 2.0	NS
Bulk density (g cm ⁻³)	0.56 ± 0.03	0.80 ± 0.13	NS
Horizon B			
Depth (cm)	18	8	
Organic matter (%)	9.6 ± 0.6	4.7 ± 0.1	<0.01
Bulk density (g cm ⁻³)	0.85 ± 0.06		
Horizon C			
Organic matter (%)	5.0 ± 0.3		

The values in the table represent the mean ± SE, n=5.

Table 3. Particle size analyses (% of total sample) of soils at the Douglas-fir and lodgepole pine study sites. Particle size was assessed using a sieve stack to separate the coarser fractions of soil and the hydrometer method to determine the finer fractions of soil. Particle size distribution was classified according the United States Department of Agriculture (USDA) classification system* (Soil Survey Division Staff 1993). Significance was determined through analysis of variance, NS = not significant.

	Douglas-fir	Lodgepole pine	Significance
Horizon A			
very coarse sand	3.4 ± 0.2	22.4 ± 0.6	<0.01
coarse sand	7.7 ± 0.4	23.1 ± 0.7	<0.001
medium sand	17.9 ± 0.5	18.0 ± 0.6	NS
fine sand	32.5 ± 0.5	17.9 ± 0.6	<0.001
very fine sand	20.7 ± 2.2	1.8 ± 0.2	<0.01
silt	16.0 ± 1.4	12.6 ± 1.4	NS
clay	1.8 ± 0.3	4.3 ± 0.4	<0.01
Horizon B			
very coarse sand	5.8 ± 0.6	27.5 ± 0.9	<0.001
coarse sand	13.5 ± 0.8	25.4 ± 0.7	<0.001
medium sand	26.0 ± 0.8	18.6 ± 0.4	<0.001
fine sand	29.6 ± 0.9	19.9 ± 0.6	<0.001
very fine sand	13.2 ± 1.0	0.9 ± 0.3	<0.05
silt	10.8 ± 1.3	4.8 ± 0.6	<0.05
clay	1.2 ± 0.2	2.9 ± 0.5	<0.05

*Particle sizes: very coarse sand (2000-1000 µm), coarse sand (1000-500 µm), medium sand (500-250 µm), fine sand (250-100 µm), very fine sand (100-50 µm), silt (50-2 µm), clay (<2 µm).

The values in the table represent the mean ± SE, n=5 except for lodgepole pine B, where n=3.

3.3. Seasonal variation in meteorological data

Variation in daily maximum and minimum temperature, daily maximum PPFD and daily maximum VPD displayed similar trends at both the Douglas-fir and lodgepole pine study sites (Figure 6). Both sites showed similar daily maximum temperatures through the growing season, although the LP site consistently showed lower minimums, and therefore slightly greater daily temperature fluctuations. The elevation of the LP site was 98 m greater than the DF site, which was the source of the slight temperature differences. The magnitude of photosynthetic photon flux density was equivalent at each site during the growing season. Precipitation followed similar trends at each study site (Figure 7), not unexpected as they are located only 30 km apart. May was a wet month at both sites with the DF site receiving a total of 108.8 mm and the LP site a total of 134.2 mm precipitation. August was a very dry month at both sites, with the DF site only receiving a 14.6 mm and the LP site 21.0 mm of rain.

Relative soil moisture measurements were measured by soil probes inserted at an angle down to a depth of 15 cm, therefore relative soil moisture measurements only assessed the top 15 cm of soil. It is important to note that relative moisture cannot be compared quantitatively between sites, as it is a measurement relative to its site specific maximum and minimum moisture levels of the season. However, relative moisture showed similar trends at both sites. Both sites began May with maximum or near maximum relative soil moisture (Figure 7). Together the sites experienced a drop in soil moisture until the middle of May (DOY 144), when a large precipitation event enhanced the soil moisture, increasing it to its maximum (DF) and near maximum (LP) levels for the season. The time period from June until the beginning of September (DOY 153-DOY 246) saw a gradual but constant decline in soil moisture at both sites. Occasional precipitation events caused increases in relative soil

moisture to occur, but it would continue to decline soon after the precipitation input. June, July and August received modest amounts of rain, resulting in relative soil moisture reaching its lowest point for the growing season at both sites in the beginning of September (DOY 246). Precipitation in the beginning of September caused soil moisture to rebound, but it resumed declining again immediately.

Gravimetric soil moisture measurements from samples taken in the field also represented the top 15 cm of soil. There were significant seasonal differences at both sites (ANOVA, DF $F(14,60)=13.81$, LP $F(14,60)=4.29$, $p<0.001$, Figure 7), but no differences between sites (ANOVA, $F(1,148)=3.90$, $p>0.05$). The DF site had a seasonal average of 0.19 ± 0.01 g H₂O cm⁻³ soil compared to the LP site which averaged 0.22 ± 0.01 g H₂O cm⁻³ soil. The trends in gravimetric soil moisture measurements were similar to the trends in relative moisture, with a gradual decrease from June until September, aside from short-term increases which were seen after precipitation inputs. Relative soil moisture and gravimetric soil moisture were highly correlated at both sites (DF site $r=0.94$, $p<0.01$, LP site $r=0.83$, $p<0.01$).

Soil temperature at a depth of 15 cm displayed parallel trends between sites during the growing season (Figure 8). Soil temperature at 15 cm at the DF site was 1.6°C at the beginning of May, with the LP site only being slightly lower at 1.4°C. Soil temperature increased as air temperatures increased, reaching its highest point at the DF site near the middle of August (DOY 231) at 16.7°C compared to 14.1°C, the maximum at the LP site that occurred one day later (DOY 232). Declines in soil temperature began in August and had declined to approximately 1°C by the end of October.

3.4. Meteorological data compared to 30-year normals

Based on 30-year normals (1971-2000) from the nearest Environment Canada meteorological station, both sites were slightly cooler in May in comparison to the average temperature ± 1 standard deviation (Figure 9). July and October at the DF site were only slightly below mean temperature ± 1 SD. All other months at both sites showed slightly cooler trends than the 30-year normal but were still within 1 SD. The Douglas-fir and lodgepole pine study sites experienced wetter conditions than normal in May of 2008 (as compared to EC 30-year normal 1971-2000, Figure 9). June, July and September 2008 had average amounts of precipitation, compared to August which received very little rain.

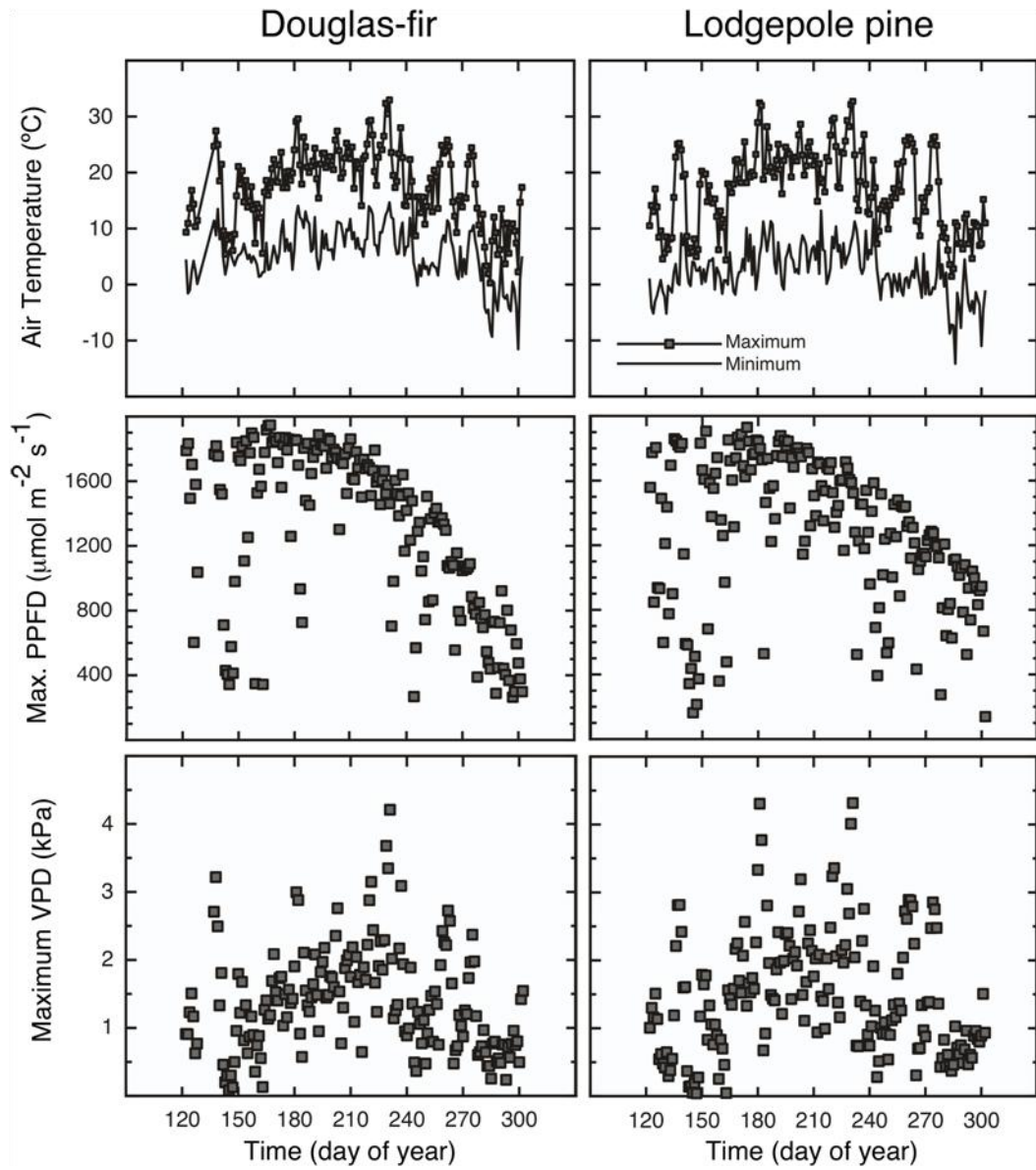


Figure 6. A comparison of the daily maximum and minimum air temperature, daily maximum photosynthetic photon flux density (PPFD) and daily maximum vapour pressure deficit (VPD) between the Douglas-fir and lodgepole pine study sites from May-October 2008.

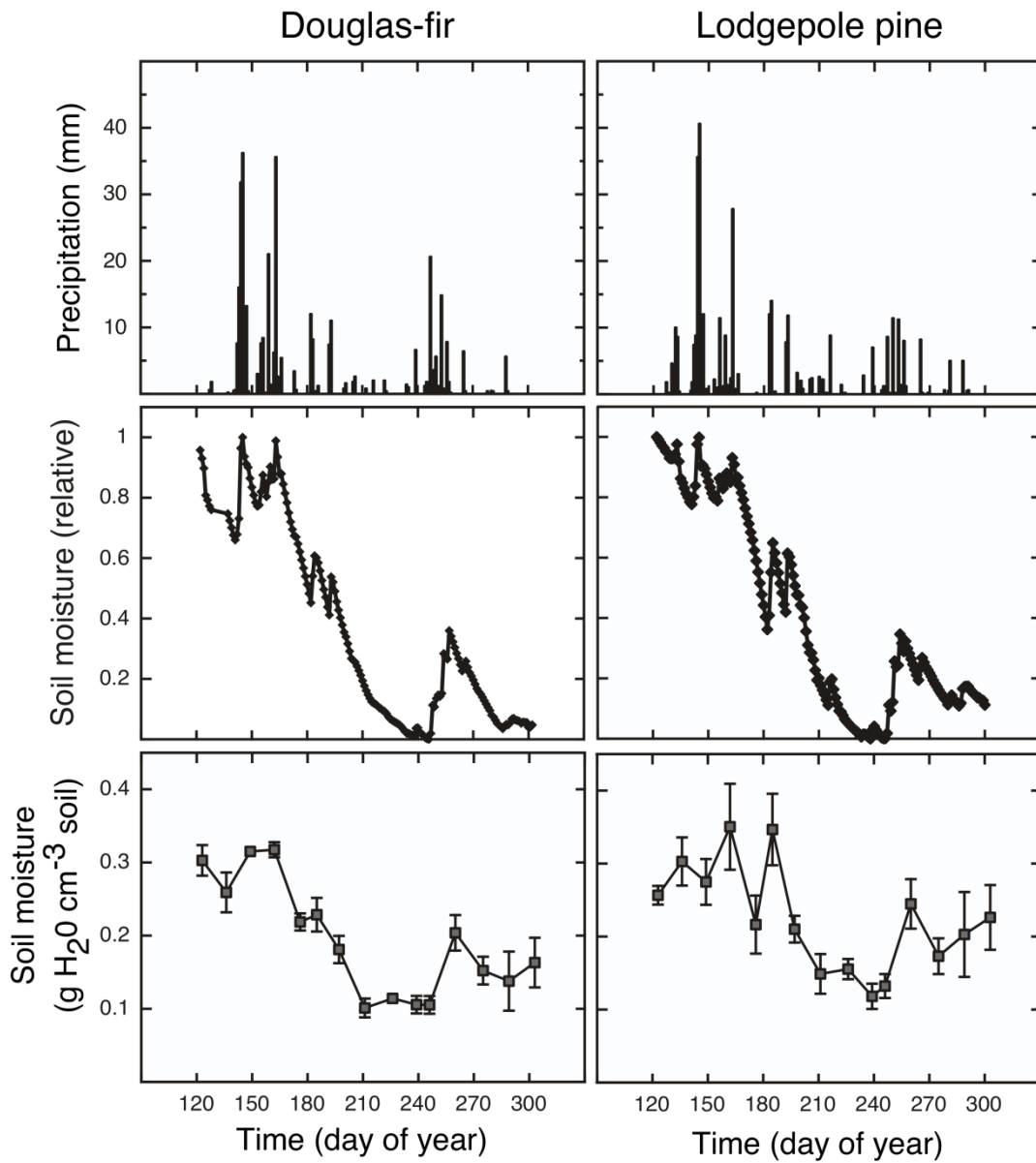


Figure 7. Seasonal variation in total daily precipitation, mean daily relative soil moisture and gravimetric soil moisture at the Douglas-fir and lodgepole pine study sites from May-October 2008. Relative soil moisture was calculated from continuous measurements recorded by the soil moisture probes ($n=3$) averaged over the 0-15 cm depth interval and are a daily average. Gravimetric soil moisture was calculated from samples taken in the field to a depth of 15 cm and are the mean \pm SE, $n=5$.

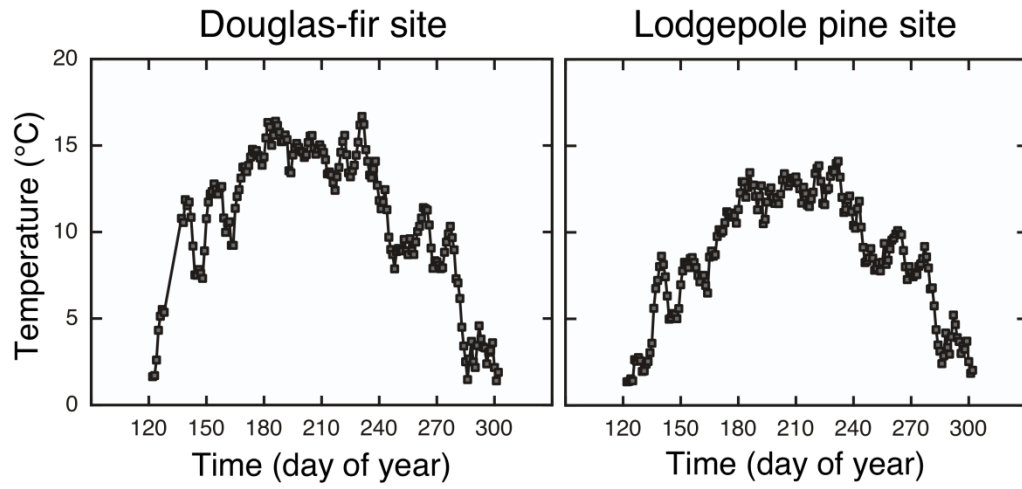


Figure 8. Mean daily soil temperature at a depth of 15 cm at the Douglas-fir and lodgepole pine study sites from May-October 2008.

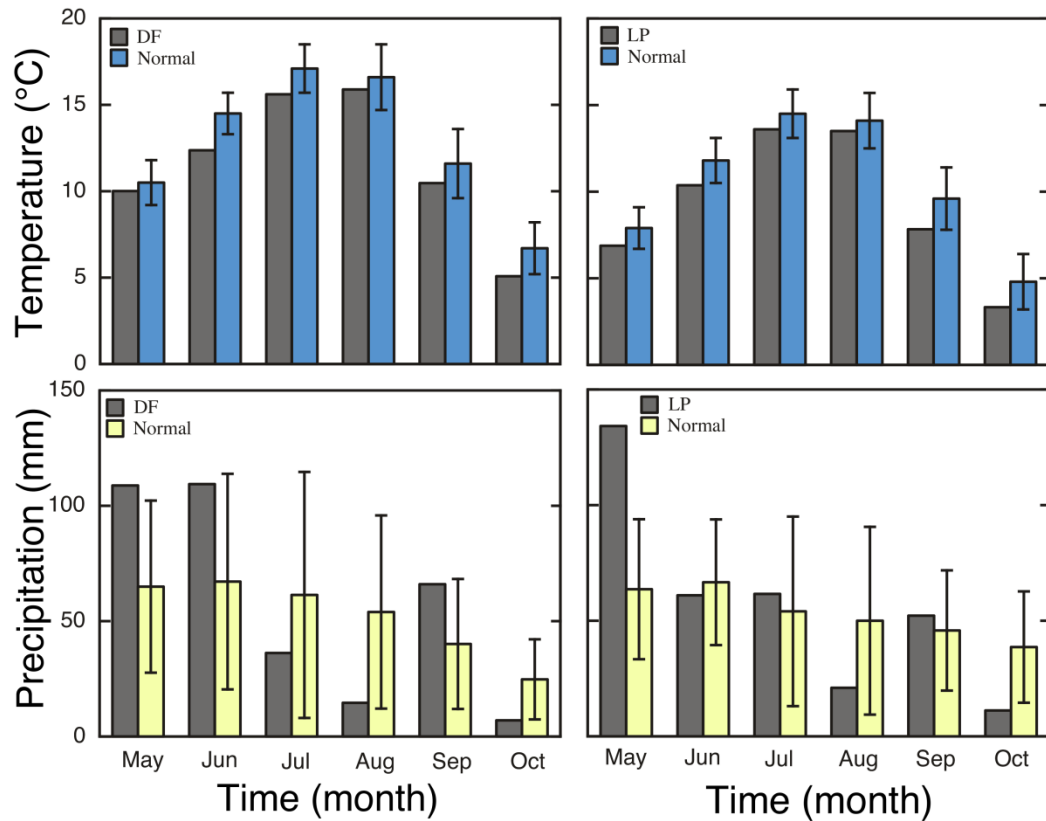


Figure 9. Comparison of Environment Canada’s average monthly temperature and total monthly precipitation 30-year normals (1971-2000) to meteorological data from the study sites. ‘Normals’ are long-term data from Environment Canada (EC) meteorological stations closest to the study sites. Claresholm was the closest EC station to the DF site with long-term temperature records, and Cowley was the closest with long-term precipitation records. Coleman was the closest EC station to the LP site with long-term records. Environment Canada data is the 30-year mean \pm 1 standard deviation.

3.5. *Predawn water potential*

Douglas-fir and lodgepole pine exhibited different predawn water potentials when examined as a seasonal average, with Douglas-fir consistently showing a lower average of -1.37 ± 0.06 MPa compared to lodgepole pine which had a seasonal average of -0.92 ± 0.04 MPa (ANOVA, $F(1,58)=43.71$, $p<0.001$, Figure 10). Both species exhibited seasonal variation in predawn water potential (ANOVA, DF $F(5,24)=22.93$, $p<0.001$, LP $F(5,24)=5.34$, $p<0.01$, Figure 11). Douglas-fir experienced a decrease in predawn water potential from mid-July (DOY 198) to the beginning of September (DOY 247), corresponding to declining soil moisture occurring at the same time. The lowest predawn water potential measurement in Douglas-fir occurred at the same time (DOY 247) that the lowest soil moisture content was recorded. Correlation between predawn water potential and soil moisture was expected because predawn water potential has often been used as a proxy for soil water potential (Schwinning 2008). Lodgepole pine showed little seasonal variation in predawn water potential from the middle of June, when predawn sampling began, until the middle of October. A significant decrease in LP predawn water potential was seen from the beginning of July (DOY 186) to the end July (DOY 212), corresponding to the onset of the decline in soil moisture (Figure 7), after which it remained constant for the remainder of the growing season. The fact that lodgepole pine predawn water potential remained static as soil moisture continued to decline implied that lodgepole pine trees were exhibiting a different physiological reaction to drought in comparison to Douglas-fir.

3.6. *Midday water potential*

Douglas-fir showed significantly lower (more negative) midday water potentials compared to lodgepole pine when data was averaged over the whole growing season. The average difference between species was -0.7 MPa (ANOVA, $F(1,146)=221.18$, $p<0.001$, Figure 10).

A species x day of year interaction was observed (ANOVA, $F(14,118)=7.93$, $P<0.001$), indicating that seasonal patterns of midday water potential differed between species.

Douglas-fir exhibited a considerable amount of seasonal variation in midday water potential (ANOVA, $F(14,58)=10.20$, $p<0.001$, Figure 11). A significant decrease in midday water potential was seen in May as the trees emerged from winter dormancy. Douglas-fir showed an increase in midday water potential from the beginning of July to the end of August that was negatively correlated to changes in relative soil moisture ($r=-0.97$, $p<0.01$) and gravimetric soil moisture ($r=-0.91$, $p<0.05$) (Figure 7). A decline in midday water potential was seen in the beginning of September (DOY 247) which coincided with the lowest values of soil moisture. Midday water potential rose in October, possibly in response to cooling temperatures and reduced rates of photosynthetic gas exchange (see below).

Lodgepole pine exhibited some seasonal variation in midday water potential, but not to the same degree as Douglas-fir (ANOVA, $F(14,60)=14.58$, $p<0.001$, Figure 11). Lodgepole pine experienced an increase in midday water potential from mid-May to mid-June (DOY 134-163). Water potential on DOY 163 was high because of rainfall in the preceding night and during the sampling day. During the time period in the growing season when soil moisture was diminishing (DOY 185-246), lodgepole pine midday water potential remained relatively constant, again suggesting that the lodgepole pine trees were responding differently to drought compared to Douglas-fir trees.

3.7. Difference between midday and predawn water potential

When examining the difference between predawn and midday water potential at each site over the whole season, Douglas-fir showed an average difference of -0.84 ± 0.15 MPa while lodgepole pine showed a smaller difference of -0.46 ± 0.14 MPa (Figure 12). The two

species showed similar trends throughout the season, however the lodgepole pine consistently had a smaller difference between predawn and midday water potential. Note that the first lodgepole pine predawn measurement only showed a 0.1 MPa difference from its midday measurement. This was expected, because it had rained the entire night before the predawn measurement, with rain continuing up to the point of the midday measurement, resulting in very low moisture stress even at midday when moisture stress is normally at its maximum for the day (Mitchell et al. 2008). The differences in predawn and midday water potential were greatest at both sites in July when soil moisture was still relatively high, resulting in high predawn water potentials, and low midday water potentials that likely resulted from high transpiration rates associated with warm air temperatures.

3.8. *Leaf carbon isotope composition*

Douglas-fir and lodgepole pine showed statistically significant differences in leaf carbon isotope composition when compared as seasonal averages (ANOVA, $F(1,146)=62.17$, $p<0.001$, Figure 13). However, the difference in seasonal average $\delta^{13}\text{C}$ was only 0.9‰ (DF mean of $-26.1 \pm 0.1\text{‰}$ and LP mean of $-27 \pm 0.1\text{‰}$). No significant seasonal variation occurred for either species (ANOVA, DF $F(14,59)=1.21$, $p>0.05$, LP $F(14, 59)=1.208$, $p>0.05$).

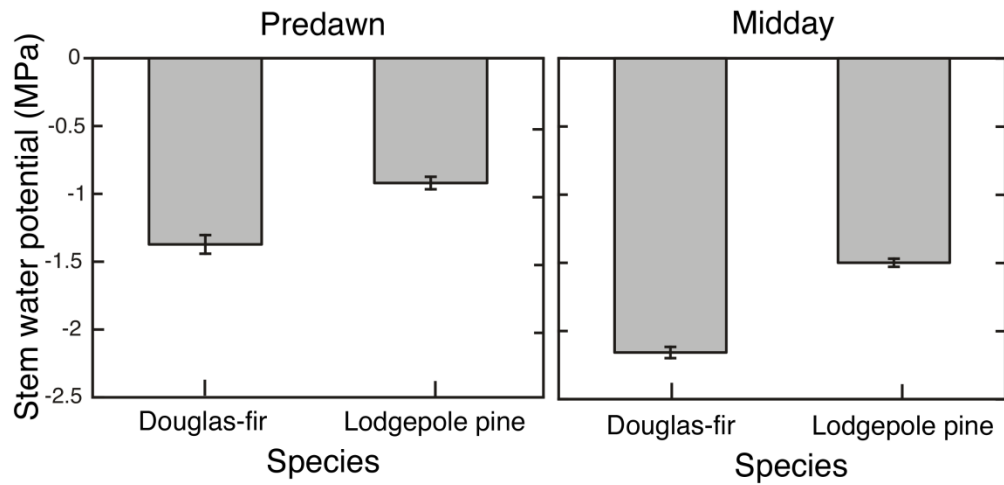


Figure 10. Predawn and midday stem water potential (MPa) as a seasonal average at the Douglas-fir and lodgepole pine study sites from May-October 2008. Predawn water potential measurements represent the mean of 6 sampling days x 5 samples per day, \pm SE. Midday water potential represents the mean of 15 sampling days x 5 samples per day, \pm SE.

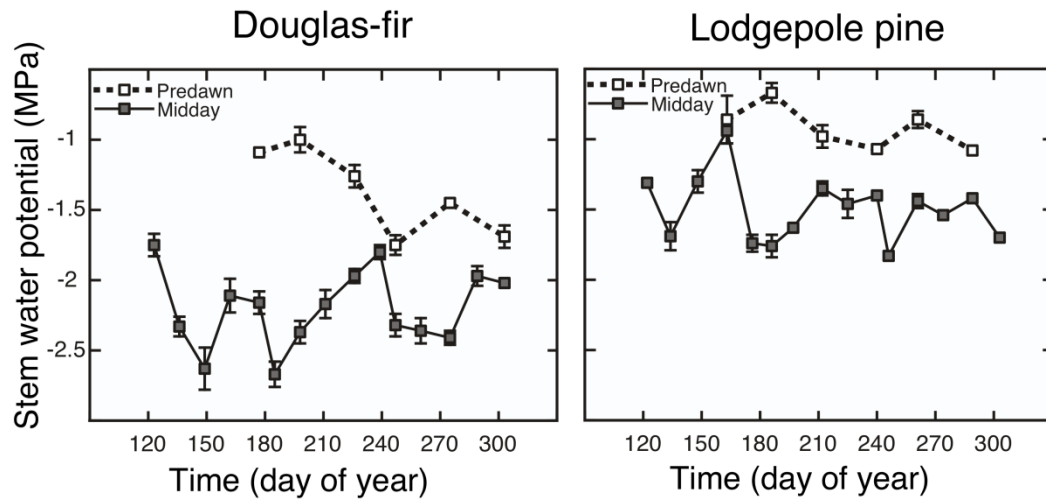


Figure 11. Predawn and midday stem water potential (MPa) at the Douglas-fir and lodgepole pine study sites from May-October 2008. Predawn samples were measured immediately before dawn. Midday samples were measured between 12:00 pm and 2:00 pm MDT. Each point represents the mean \pm SE, n=5.

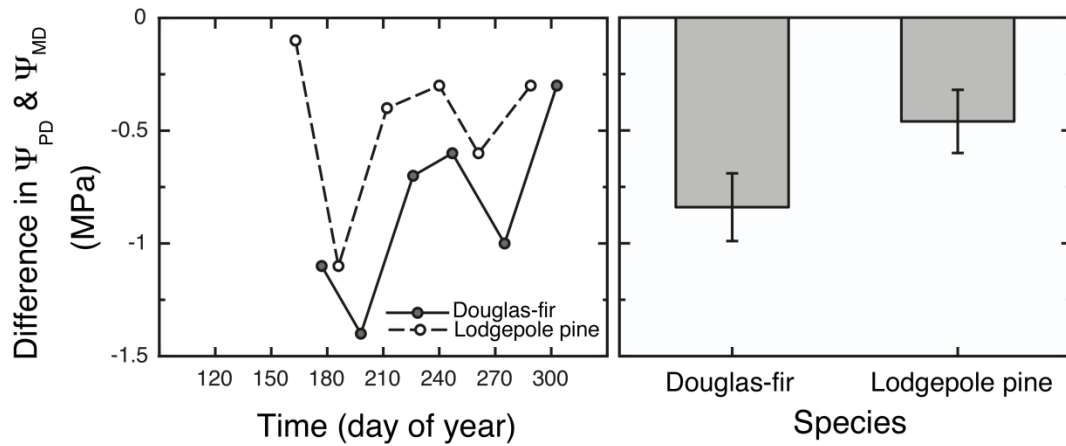


Figure 12. Difference between predawn and midday stem water potential at the Douglas-fir and Lodgepole pine study sites from May-October 2008. The left box represents the seasonal trends, with points representing the difference between the mean of 5 predawn and 5 midday samples. In the right box the bars represent the seasonal average of the difference between stem water potential at each site, bars being the mean \pm SE, n=6.

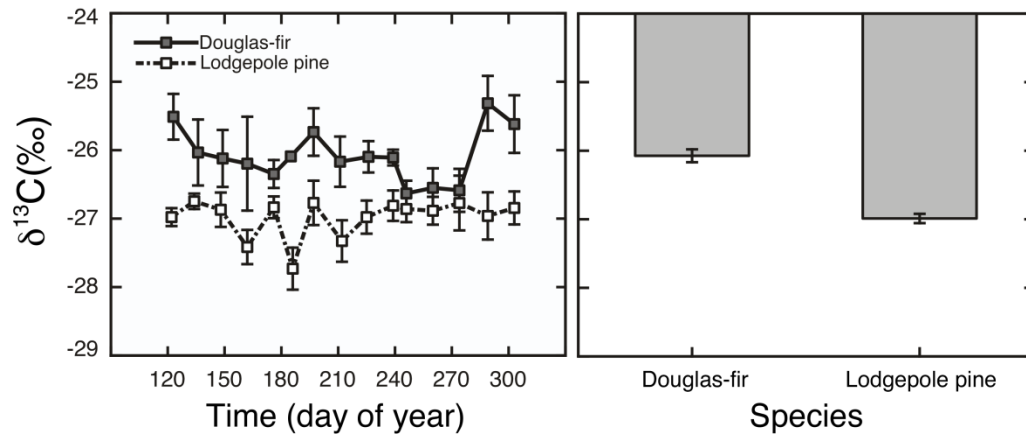


Figure 13. Comparison of carbon isotope composition of leaves at the Douglas-fir and lodgepole pine study sites from May-October 2008. The left box represents seasonal trends, with points signifying the mean \pm SE, $n=5$. The right box represents the average of the entire season with each bar being the mean of 15 sampling days \times 5 samples per day, \pm SE.

3.9. *Chlorophyll fluorescence*

Chlorophyll fluorescence rates revealed when trees had recovered photosynthetic capacity after winter down-regulation, with high values implying high photosynthetic capacity. Fluorescence values differed between the species when examined as a seasonal average, Douglas-fir demonstrating a seasonal average (May-October) F_v/F_m of 0.69 ± 0.02 and lodgepole pine having a higher seasonal average F_v/F_m at 0.73 ± 0.01 (ANOVA, $F(1,138)=4.35$, $p<0.05$, Figure 17). There was no species and day of year interaction exhibited (ANOVA, $F(13,112)=1.59$, $P>0.05$). Both species also showed seasonal variation in fluorescence (ANOVA, DF $F(13,56)=24.85$, LP $F(13,56)=18.48$, $p<0.001$, Figure 14). Similar trends were seen for each species, with increasing F_v/F_m in May as they recovered from winter dormancy, followed by a maximum which was generally maintained until photosynthetic down-regulation began in October in preparation for winter. Fluorescence was found to be correlated with soil temperature at all depths at both sites, but was most highly correlated to temperature at the 30 cm depth (DF $r=0.82$, $p<0.01$, LP $r=0.91$, $p<0.01$).

3.10. *Leaf nitrogen content*

Total leaf nitrogen content was different between species when examined as a seasonal average (DF $1.02 \pm 0.02\%$, LP $1.12 \pm 0.02\%$, ANOVA, $F(1,146)=9.78$, $p<0.01$, Figure 15). An interaction existed between species and day of year (ANOVA, $F(14,118)=2.36$, $p<0.01$), indicating that seasonal patterns of total leaf nitrogen content differed between species. Significant seasonal variation occurred for each species as well (ANOVA, DF $F(14,59)=9.99$, LP $F(14,59)=6.53$, $p<0.001$). Both species showed a general trend of increasing leaf nitrogen as the growing season progressed. Douglas-fir showed two main distinctions through the season. Mid-June (DOY 162) DF total leaf nitrogen content was significantly lower than all other sampling days of the season. Mid-September (DOY 260) DF total leaf nitrogen content

was significantly higher than all previous sampling days. High precipitation inputs occurred during the two weeks before sampling on DOY 260, possibly leading to a nutrient flush which caused the rise in DF leaf nitrogen content. Total leaf nitrogen content in lodgepole pine did not show the dramatic changes which Douglas-fir exhibited. The lack of an increase in nitrogen in lodgepole pine following high precipitation inputs late in the season may be a function of small soil volume. Both species had a reduction of leaf nitrogen in October as trees began to prepare for winter, as the photosynthetic apparatus containing nitrogen may have been disassembled.

3.11. Photosynthetic oxygen evolution

Photosynthetic capacity, as observed through light- and CO₂-saturated oxygen evolution, showed significantly higher rates in lodgepole pine ($28.3 \pm 1.8 \mu\text{mol O}_2 \text{ m}^{-2}\text{s}^{-1}$) compared to Douglas-fir ($22.7 \pm 1.2 \mu\text{mol O}_2 \text{ m}^{-2}\text{s}^{-1}$) over the whole growing season ($F(1,147)=6.8$, $p<0.05$) (Figure 17), consistent with total leaf nitrogen content being higher in the lodgepole pine (ANOVA $F(1,147)=6.78$, $p<0.05$, Figure 15). A large proportion of leaf N is normally associated with the photosynthetic apparatus (particularly Rubisco content), resulting in a positive correlation between photosynthetic capacity and leaf N concentration (Field & Mooney 1986, Warren et al. 2004). A species x day of year interaction also existed (ANOVA, $F(14,119)=5.59$, $p<0.001$) suggesting that seasonal patterns of photosynthetic oxygen evolution differed between species. Seasonal differences within each species were observed, as described below (ANOVA, DF $F(14,59)=4.93$, LP $F(14,60)=8.88$, $p<0.001$, Figure 16). The model data presented for each site, calculated using equation 6, demonstrate potential rates of oxygen evolution as controlled by acclimation temperature (Figure 16). Divergence from the model prediction suggests that other factors are contributing to any reduction in photosynthetic oxygen evolution.

During May oxygen evolution at the DF site increased as trees recovered photosynthetic capacity from their winter down-regulation (Figure 16). The end of June (DOY 176) revealed a drop in oxygen evolution, although not significant compared to the sampling days before and after, that corresponded to low levels of total leaf nitrogen content found two weeks earlier. An increase in oxygen evolution rate was seen in the beginning of July (DOY 185) which stabilized for the following four weeks. A dramatic drop was observed in Douglas-fir oxygen evolution at the beginning of September (DOY 246) which corresponded with the lowest soil moisture of the growing season. From the beginning of September to the end of October, rates of Douglas-fir oxygen evolution were correlated with gravimetric soil moisture ($r=0.91$, $p<0.05$). Low October rates of oxygen evolution matched low October fluorescence, suggesting trees had begun down-regulation processes in preparation for winter. When comparing measured oxygen evolution rates in Douglas-fir to the model calculations, measured values correlated closely to the model from the beginning of May until the beginning of September ($r=0.77$, $p<0.05$). After this point measured oxygen evolution rates diverged from the model and appeared to follow changes in soil moisture.

Oxygen evolution rates in lodgepole pine showed a very sharp increase from the middle to end of May, followed by a decline until the middle of June (DOY 162) which also corresponded to a time when leaf nitrogen content was low (Figure 15). An increase in oxygen evolution rates was seen until the beginning of July (DOY 186). The remainder of the growing season until the middle of September saw a consistent decline in the rate of oxygen evolution in lodgepole pine, which was correlated with soil moisture from DOY 186 to DOY 246 (relative soil moisture $r=0.93$, $p<0.01$, gravimetric soil moisture $r=0.83$, $p<0.05$), declines in oxygen evolution mirroring reductions in soil moisture. Dark-adapted chlorophyll fluorescence values remained elevated, confirming that functional photosynthetic machinery

was present but under some type of controlled down-regulation. These results suggest that lodgepole pine were completely dependent on shallow soil moisture and when that reservoir went dry, they were unable to maintain high rates of oxygen evolution. Rain and an increase in soil moisture were seen between DOY 246 and 260, but rates of oxygen evolution did not respond immediately to the moisture inputs and were still at low levels on DOY 260. Oxygen evolution rates rose dramatically by the next sampling date (DOY 274), but then resumed declining in October, corresponding to a reduction in fluorescence, presumably as trees began preparing for winter down-regulation. When comparing measured oxygen evolution rates in the lodgepole pine to the model, measured oxygen evolution rates were closely correlated to the model from DOY 122-134 and DOY 274-303 ($r=0.96$, $p<0.01$). Measured values diverged from the model prediction during DOY 186-260, the same time period when soil moisture was declining. The relationship between the measured rates of oxygen evolution in lodgepole pine and the model clearly shows a temperature dependence until moisture became limiting at mid-season.

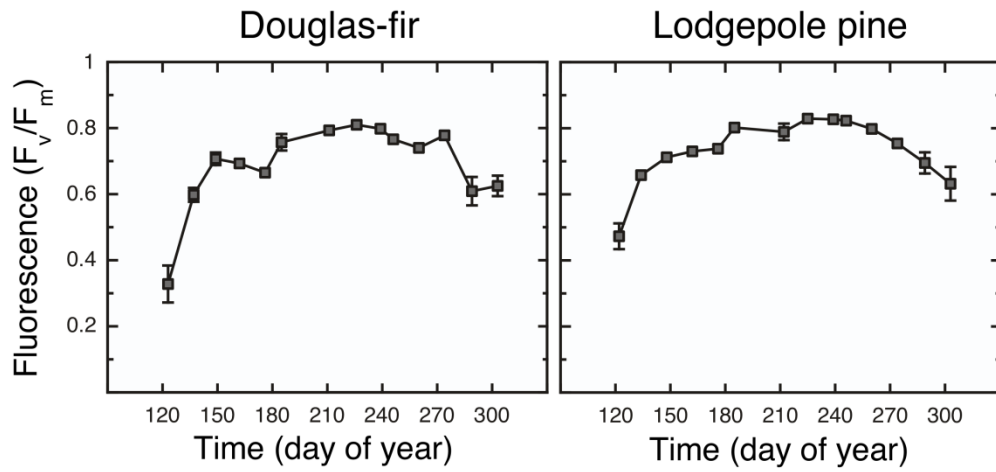


Figure 14. Seasonal trend of dark-adapted leaf chlorophyll fluorescence (F_v/F_m , variable/maximum) at the Douglas-fir and lodgepole pine study sites from May-October 2008. Points represent the mean \pm SE, $n=5$.

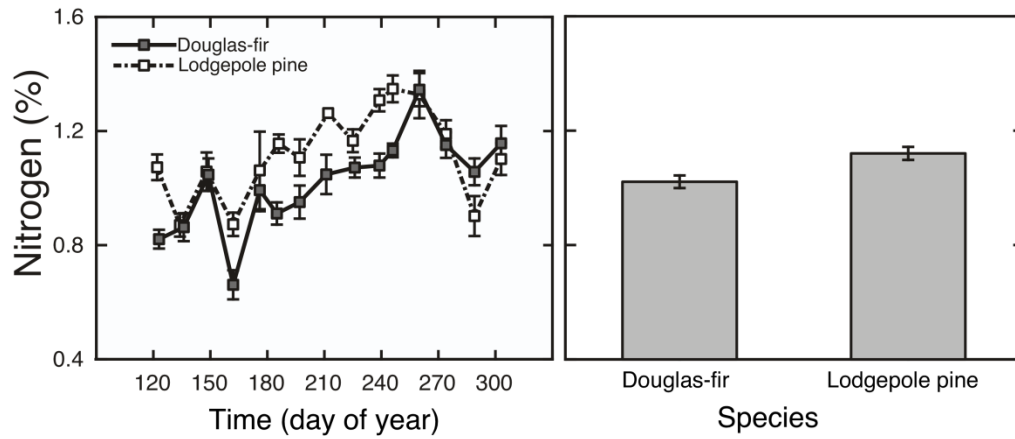


Figure 15. Total leaf nitrogen content (%) at the Douglas-fir and lodgepole pine study sites from May-October 2008. The left box represents seasonal trends, with points representing the mean \pm SE, $n=5$. The right box represents the mean of 15 sampling days \times 5 samples per day, \pm SE.

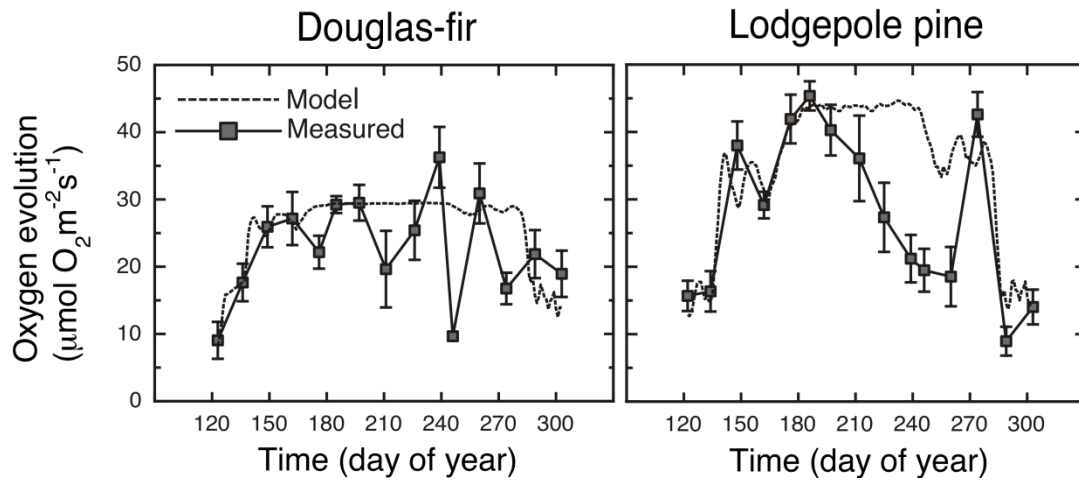


Figure 16. Seasonal changes in measured oxygen evolution ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$) from May-October 2008 in comparison to seasonal changes in modelled oxygen evolution (equations 4-7) as a function of acclimation temperature. Oxygen evolution measurements were made under stable conditions at 25°C with saturating light, 5% CO_2 . Measured oxygen evolution values are mean \pm SE, $n=5$.

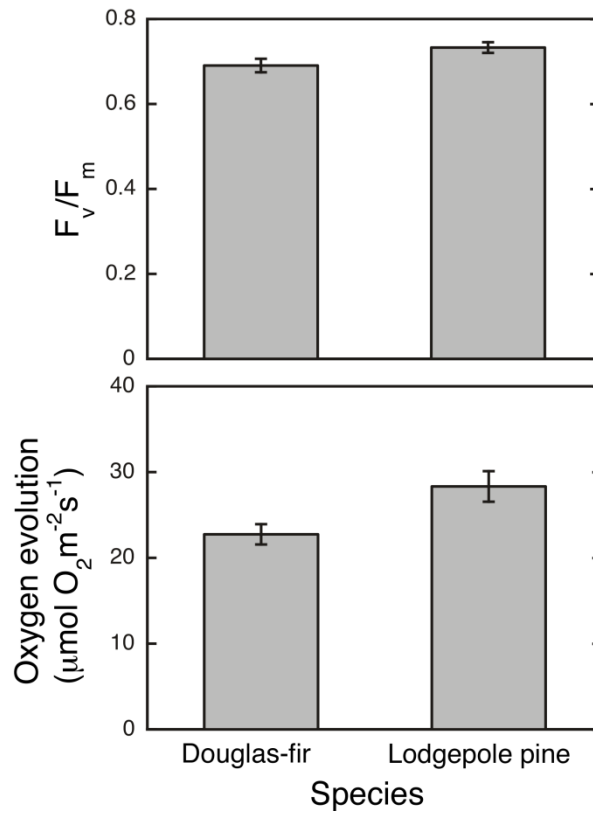


Figure 17. Fluorescence and oxygen evolution as seasonal averages at the Douglas-fir and lodgepole pine study sites from May-October 2008. Bars represent the mean of 15 sampling days x 5 samples per day, ± SE.

3.12. Precipitation stable isotope composition

In comparison to the hydrogen isotope composition of precipitation from previous studies in southern Alberta (Peng et al. 2004, L.B. Flanagan, unpublished data) the δD of precipitation during 2008 showed comparable values with perturbations above and below average as expected with only one year of data (Figure 18). The seasonally-weighted average (May-October) at the DF site was -118‰ and at the LP site it was slightly more enriched at -112‰. For comparison, the 10-year seasonally-weighted average (May-October) at Calgary, Alberta (approximately 150 km north of the study sites) was -136‰, while the 3-year data from Lethbridge, Alberta (approximately 100 km east of the study sites) showed precipitation with an average δD value of -135‰ (seasonally weighted average, May-October). Therefore, the precipitation samples at the DF and LP sites during 2008 were about 25‰ more enriched in deuterium compared to the Calgary and Lethbridge data.

When comparing both individual values and monthly-weighted averages between the DF and LP sites, very similar trends were seen (Figures 18 & 20). Precipitation samples taken during May at both sites were relatively enriched in deuterium, in comparison to June when a 50‰ decrease in δD was observed. The stable isotope composition of rain became more enriched in deuterium during July and August, as expected because precipitation falling during summer months is expected to be more enriched in deuterium (Dansgaard 1964). One difference apparent between sites in October was that precipitation at the LP site was considerably more enriched in deuterium than precipitation at the DF site.

3.13. Groundwater stable isotope composition

There were no seasonal differences in groundwater δD values at either of the study sites (ANOVA, DF $F(13,12)=0.26$, LP $F(12,12)=0.73$, $p<0.05$). This was expected as groundwater δD values are an average of local precipitation over time, however there were

significant differences between the two sites as a seasonal average (ANOVA, $F(1,49)=262.56$, $p<0.001$, Figure 19). The groundwater from the DF site had a δD value of $-150 \pm 0.6\text{‰}$ and samples from the LP site were more enriched in deuterium with an average δD of $-134 \pm 0.7\text{‰}$. Published data from the Oldman River (Rock and Mayer 2007, Figure 19), the watershed where the study sites were located, showed a site upstream of the Oldman River dam (closer to the LP site) having a δD of $-144 \pm 0.7\text{‰}$. A site downstream of the Oldman River dam (closer to the DF site) had a δD of $-138 \pm 0.6\text{‰}$. Both sites from the previous study showed stable isotope compositions that fell between the isotope signatures of groundwater sources at the DF and LP study sites.

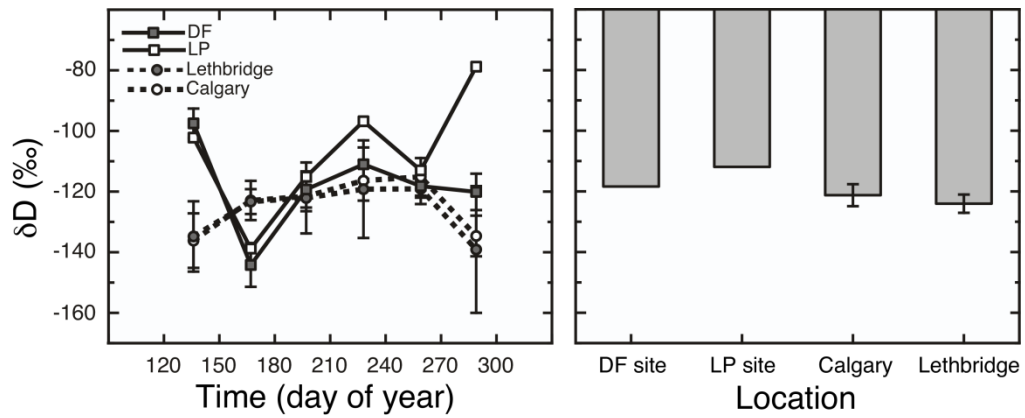


Figure 18. Hydrogen isotope composition of precipitation in southern Alberta. The left box shows δD levels of precipitation with monthly weighted averages comparing the study sites to data from Lethbridge (3-year mean) (L.B. Flanagan, unpublished data) and previously published data from Calgary (10-year mean) (Peng et al. 2004). The right box shows the seasonally (May-October) weighted precipitation δD values, with standard error for Calgary and Lethbridge.

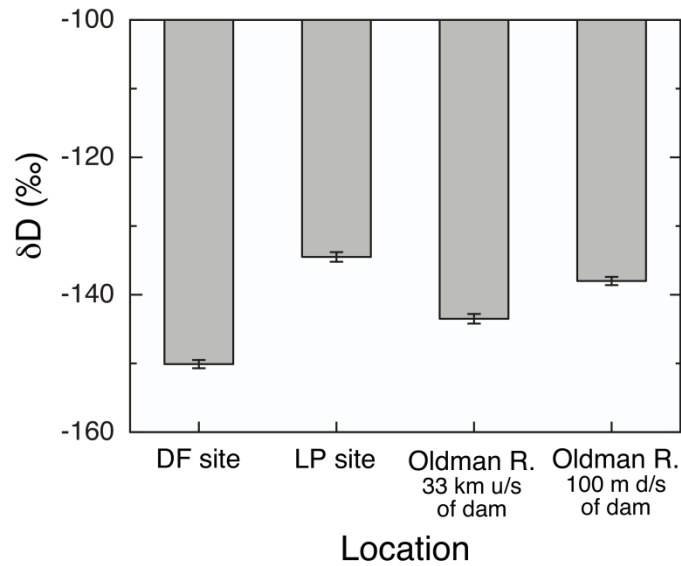


Figure 19. Comparison of hydrogen stable isotope composition of groundwater/creek water at the study sites compared to the stable isotope composition of the Oldman River (Rock & Mayer 2007). Hydrogen stable isotope composition of groundwater/creek water from the study sites from May-October 2008 and from the Oldman River from April-March 2001-2003. Values from the DF and LP sites are mean of 14 (DF) and 13 (LP) samples taken from May-October 2008, \pm standard error. Values from the Oldman River are yearly means \pm SE, n=12.

3.14. Stem water stable isotope composition

The isotopic composition of potential water sources for the trees, precipitation and groundwater, were different, therefore it was possible to determine the relative uptake of summer precipitation via analysis of plant stem water δD values. The seasonal groundwater stable isotope composition and the seasonally-weighted isotope composition of precipitation become the end members for the two component mixing equation, as the stable isotope composition of stem water should fall between the two end members (Figure 20, Table 4).

Douglas-fir stem water δD values ranged from -104‰ to -151‰ and lodgepole pine stem water varied from -90‰ to -142‰ during the growing season (May-October 2008), each having a range of about 50‰ (Figure 20). The δD of stem water was significantly different between species during the growing season (ANOVA, $F(1,145)=64.67$, $p<0.001$). Douglas-fir δD possessed an average δD of -131 ± 1.0 ‰ and the lodgepole pine was more enriched at -119 ± 1.1 ‰. Significant seasonal variation was seen in Douglas-fir stem water δD (ANOVA, $F(14,58)=3.41$, $p<0.001$), but not in lodgepole pine (ANOVA, $F(14,59)=1.81$, $p>0.05$). The largest trend observed was that Douglas-fir stem water became more negative, approaching groundwater δD values, as soil moisture decreased from the beginning of July to the beginning of September (DOY 185-DOY 246). A species x day of year interaction was also observed (ANOVA, $F(14,117)=1.82$, $p<0.05$), suggesting that seasonal patterns of stem water δD differed between species.

3.15. Plant water sources

The fraction of precipitation used (f) was determined from the two component mixing equation which used local seasonally-weighted precipitation and local groundwater (Douglas-fir) and creek water (lodgepole pine) as end members. The calculated f value showed no significant differences between species when examined as an average from May-

October 2008 (DF $61 \pm 5\%$, LP $65 \pm 5\%$, ANOVA, $F(1,27)=0.36$, $p=0.56$, Figure 21). Although the seasonal averages were not significantly different between sites, there appeared to be distinct seasonal patterns of variation in f within each species.

The Douglas-fir began May with the percentage of stem water derived from precipitation at 55% (Figure 21), suggesting the trees were utilizing soil moisture present from snowmelt. At this point in the year soil moisture was high, but soil temperatures were still low at 0.0°C at a depth of 30 cm. Trees appeared to still be in winter dormancy exhibiting low fluorescence (F_v/F_m) and minimal rates of oxygen evolution (Figures 14 & 16). During mid-May (DOY 136) the f value had increased to 86%, in response to high precipitation inputs in the days prior to stem sampling.

The mid-May increase in f occurred as soil and air temperatures increased and trees emerged from dormancy, based on high levels of fluorescence and increased rates of oxygen evolution. Decreasing midday water potential at the same time (Figure 11) suggested the trees had increased rates of transpiration. From the end of May to the end of June (DOY 149-DOY185) there were fluctuations in f which seem to be linked to changing precipitation inputs, with f showing rapid increases after precipitation events as soil moisture increased. For Douglas-fir, changes in f were correlated with both relative soil moisture ($r=0.60$, $p<0.05$) and gravimetric soil moisture ($r=0.67$, $p<0.01$), with f increasing as soil moisture increased.

The correlation between f and soil moisture was expected. Soil moisture measurements represented soil to a depth of 15 cm, the zone of precipitation infiltration, which would provide a moisture source for shallow roots and the resultant higher fraction of f . From the end of June until the beginning of September, f showed a consistent decline which mirrored a

corresponding summer drop in soil moisture (Figure 7) and an increase in midday water potential, suggesting the trees were shifting to a deeper water source and stomatal conductance and transpiration rates were declining. At the beginning of September (DOY 246) Douglas-fir displayed the lowest seasonal value of f at 21%, which matched the lowest level of soil moisture over the growing season and the lowest predawn water potential, suggesting that shallow moisture reserves had been completely depleted. A dramatic increase was seen two weeks later as f returned to 66%, in response to late summer precipitation inputs. There was no significant relationship observed between Douglas-fir f and rates of oxygen evolution.

Lodgepole pine began May with a high proportion of stem water (95%) reflecting the isotopic signature of precipitation (Figure 21). A substantial drop in the value of f was seen from the beginning of May until the end of May (DOY 148, $f=47\%$), even though there was substantial precipitation in the preceding two weeks. It is likely that the soil was saturated at this point and any precipitation inputs were not infiltrating the soil but running off. The rest of the season consisted of a series of increases and decreases in the proportion of precipitation in stem water which seem to be related to rain events. For example, between DOY 185 and DOY 197 the f value increased from 53 to 73%, in response to 19.6 mm of precipitation in the 5 days before sampling stem water.

Lodgepole pine showed no significant correlation between f and either measurement of soil moisture content. This was possibly due to small precipitation events which did not register as increases in soil moisture but did get utilized by the lodgepole pine while the trees were under water stress. The lowest f value in lodgepole pine (34%) was observed at the same time that soil moisture reached its lowest seasonal value, which also coincided with the lowest midday water potential experienced by the lodgepole pine. Although the small

precipitation events were utilized by trees as seen through increases in f during the dry summer period, they were not large enough to release the lodgepole pine from their controlled down-regulation of photosynthetic capacity, observed through decreased rates of oxygen evolution (Figure 16). The beginning of September saw the input of over 30 mm of rain to the ecosystem which caused a sharp increase in f and the rain input was substantial enough to break the state of controlled photosynthetic down-regulation that the lodgepole pine were under.

Different patterns in the percentage of stem water derived from precipitation were observed between sites. Lodgepole pine began and ended the growing season with much higher values of f compared to Douglas-fir. Lodgepole pine also exhibited more seasonal fluctuations and appeared to be more sensitive to precipitation inputs compared to Douglas-fir. The fraction of precipitation in the stem water of lodgepole pine responded to smaller amounts of precipitation than Douglas-fir. Similar patterns were seen when there were large precipitation inputs, which caused f to increase in both Douglas-fir and lodgepole pine.

Table 4. Comparison of hydrogen isotope composition of groundwater to seasonally-weighted precipitation at the Douglas-fir and lodgepole pine study sites. These values are the end members used in the two component mixing equation.

	Douglas-fir site	Lodgepole pine site
Precipitation (‰)	-118	-112
Groundwater (‰)	-150 ± 0.6	-134 ± 0.7

Precipitation values are seasonally-weighted averages from May to October. Groundwater values represent the mean ± SE, DF n=14, LP n=13.

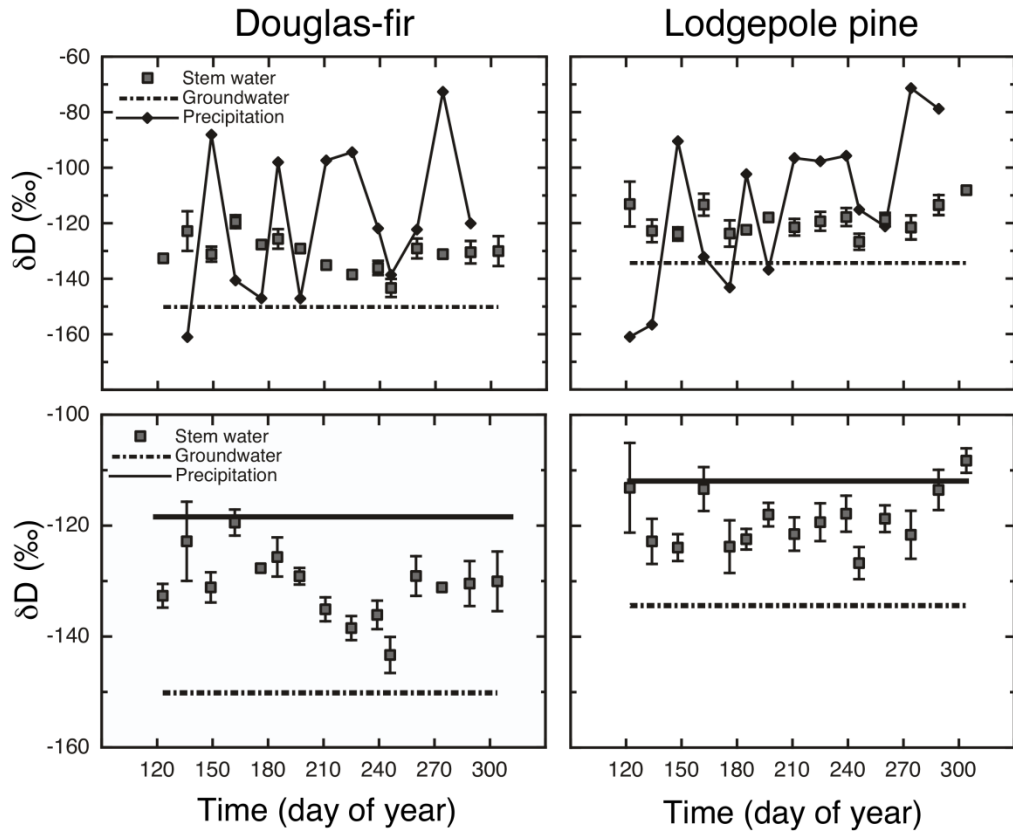


Figure 20. Stable isotope composition of stem water compared to stable isotope composition of precipitation and groundwater. Top boxes represent the hydrogen stable isotope composition from the Douglas-fir and lodgepole pine study sites of individual precipitation samples, stem water samples (mean \pm SE, $n=5$), and the seasonal groundwater average in 2008. Bottom boxes display the same groundwater and stem water data, but with the addition of the seasonally weighted precipitation average for both sites.

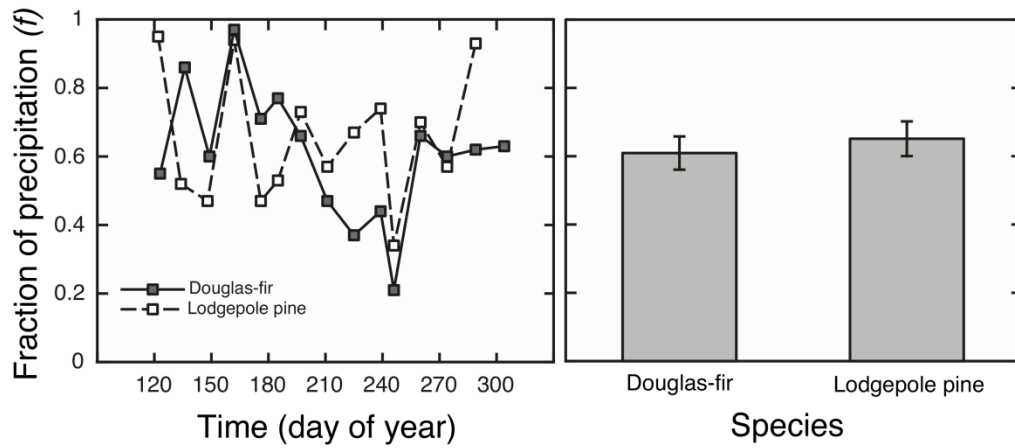


Figure 21. The fraction of precipitation in the stem water of Douglas-fir and lodgepole pine calculated with a two component mixing equation (Equation 6). The left graph demonstrates the seasonal variation in the fraction of precipitation (f) found in stem water. The box on the right shows the seasonal comparison between species (mean \pm SE, DF n=15, LP n=14).

4.0 Discussion

4.1. *Water availability and use*

White et al. (1985) suggested that three scenarios existed when considering water sources for trees. First, the groundwater extreme exists where the water table is near the surface and trees have an abundant supply of groundwater, even during periods of high precipitation. In this case stem water will have a δD value equal to that of groundwater. Second, the summer rain extreme occurs in locations where soil development is poor and soil water storage negligible, the only source of water for trees is rain and stem water δD completely reflects precipitation. Finally, the intermediate case exists where groundwater is available to deep roots and precipitation is available to shallow roots; the δD of stem water is an intermediate of those two sources. In this study it has been demonstrated that Douglas-fir and lodgepole pine are intermediate cases, with stem water in Douglas-fir showing a trend toward groundwater δD values and stem water in lodgepole pine showing a trend toward growing season precipitation δD (Figure 20).

There was no significant difference in the fraction of growing season precipitation in the stem water of Douglas-fir and lodgepole pine when observed over the whole growing season (May-October) (Figure 21). Despite the fact that the seasonal averages of f in both species were the same, Douglas-fir and lodgepole pine showed two distinctions in seasonal water use.

The first distinction observed was that Douglas-fir appeared to be shifting to use deeper water sources as soil moisture declined in the top 15 cm of soil over the growing season. In mid-summer, the declining δD of Douglas-fir stem water (approaching groundwater δD values) (Figure 20) as shallow soil moisture declined (Figure 7) indicated that Douglas-fir was

accessing deeper water sources, implying deeper rooting systems. Previous studies have shown Douglas-fir to have deeper rooting depth than lodgepole pine (Nicoll et al. 2006). The fraction of precipitation in Douglas-fir stem water was highly correlated to soil moisture content during summer (DOY 185-225, Figures 7 & 21). This was expected because soil moisture measurements were representative of water content in the top 15 cm of soil, the zone where fine root biomass would be contributing to precipitation uptake.

The second distinction observed was that lodgepole pine appeared to have been displaying greater sensitivity to inputs of summer precipitation. Large oscillations in the fraction of precipitation in stem water (Figure 21) and frequent seasonal changes of stem water δD (Figure 20) indicated a greater sensitivity to input of summer precipitation. Lodgepole pine stem water δD did not show a trend towards groundwater signatures (Figure 20) as shallow soil moisture levels declined (Figure 7), suggesting that lodgepole pine were dependent on shallow moisture, a consequence of shallow rooting systems and low soil volume. Lodgepole pine roots have been shown to be adaptable, but vertical development is especially sensitive to soil texture and structure (Bishop 1962), and at the LP study site vertical development was likely impeded by shallow and rocky soil.

The distinctions observed in the different patterns of precipitation use by Douglas-fir and lodgepole pine were consistent with differences in soil characteristics at each site. Soil at the DF site had greater depth, finer soil texture and greater amounts of organic matter, indicating a greater ability to retain high amounts of moisture. In comparison, soil at the LP site had shallow depth and coarse texture, indicating a low ability to maintain long-term water storage (Hacke et al. 2000, Sperry et al. 2002). Soil is a reservoir of moisture for trees. The total volume of water available to a tree depends on the total volume of soil explored by the plant, which is in turn governed by the total depth of soil above a root-restricting layer.

Consequently, Douglas-fir had access to larger amounts of soil moisture because of greater soil volume in comparison to lodgepole pine. Deeper soils act to buffer vegetation against high variation in precipitation inputs.

Two points should be made regarding assumptions about groundwater at the study sites. First, creek water at the LP site was used as a proxy for groundwater under the assumption that water in the creek was being supplied by groundwater from the surrounding mountains (including the LP study site). It is not known for certain that groundwater was available at the lodgepole pine study site. It is possible that a bedrock layer could cause snow melt and precipitation inputs to flow through the surface layer and runoff, resulting in a lack of groundwater. If there was no groundwater present at the LP site, but groundwater δD values were being used as an endpoint in the two component mixing equation, the calculations would underestimate the contribution of precipitation to stem water. Secondly, when this study considers Douglas-fir to be shifting to dependence on groundwater, another caveat should be taken into account. At the DF site, it is possible that trees were not actually rooted into groundwater, but in deep soil layers close to groundwater. Groundwater and soil moisture are conceptually different, but deep soil moisture is also a mixture of seasonal precipitation events and would have an isotopic ratio approaching that of groundwater (White et al. 1985).

Previous data has shown that there are specific precipitation size thresholds for species, below which they do not respond and above which they respond actively (Schwinning et al. 2003). Douglas-fir and lodgepole pine stem water showed similar responses to large inputs of precipitation (40-50 mm) with large increases in the fraction of precipitation in stem water (DOY 149-162, DOY 246-260, Figure 21). Lodgepole pine were more responsive to smaller inputs of precipitation in comparison to Douglas-fir. During the beginning of July (DOY

185-197) lodgepole responded to 20 mm of precipitation in the 5 days previous to the sampling day, shown by an increase in stem water reflecting the isotope signature of precipitation (Figure 21). During the same time period with the same precipitation input, Douglas-fir showed a decrease in f . It is possible that small amounts of precipitation were not even infiltrating the soil at the DF site and evaporating rapidly, because of finer textured soil and greater surface organic matter. The ability to respond to small rain events depends on the density of roots in shallow soil (Canadell et al. 1996), a characteristic more important to lodgepole pine in reference to the sites in this study. Douglas-fir and lodgepole pine have both been shown to increase allocation of resources to fine and small roots on dry, xeric sites (Keyes & Grier 1981, Comeau & Kimmins 1989), making it possible to take advantage of pulsed moisture events.

Other conifer species have been observed to exhibit varying degrees of dependence on growing season precipitation vs. groundwater or deep soil moisture, depending on site-specific moisture holding capacity and species-specific rooting habits. In the Italian Alpine region, Scots pine (*Pinus sylvestris*) have exhibited greater use of rainwater, a function of a shallow rooting system in poor and rocky soils, where another co-occurring conifer, European larch (*Larix deciduas*), showed almost exclusive use of groundwater using a deep rooting system (Valentini et al. 1994).

4.2. *Physiological response of water relations to changing soil moisture*

Douglas-fir predawn and midday water potential measurements displayed very different trends in comparison to the lodgepole pine predawn and midday water potential throughout the growing season, suggesting different physiological responses to changes in soil moisture. Douglas-fir reached midday water potentials that may have been bringing them very close to hydraulic failure, where as lodgepole pine maintained a greater buffer between their midday

water potential and the xylem tension needed to induce hydraulic failure (unpublished data, L.B. Flanagan).

Soil moisture content was almost identical at both sites to a depth of 15 cm during the growing season (Figure 7). Given identical moisture conditions, soil characteristics at the LP site (coarser soil texture and low soil volume) would have exposed the lodgepole pine to much more negative soil water potentials, theoretically leading them to experience lower plant water potential in comparison to Douglas-fir. This was not observed at the study sites and suggested that the lodgepole pine were strongly restricting transpirational water loss via reduced stomatal conductance.

Douglas-fir exhibited distinct seasonal differences in predawn and midday water potential, with midday water potential declining as predawn water potential declined in response to seasonal changes in soil moisture (Figure 11), a behaviour characteristic of anisohydric species (Franks et al. 2007, McDowell et al. 2008). Anisohydric behaviour facilitates higher levels of photosynthetic gas exchange even as water stress increases (Franks et al. 2007). Douglas-fir also consistently exhibited greater differences between predawn and midday water potential, displaying larger fluctuations in water potential, a trait exhibited by anisohydric plants (Franks et al. 2007, Figure 12).

Lodgepole pine water potential displayed less variation throughout the season, maintaining relatively constant predawn and midday water potential as soil moisture decreased (Figure 11), features characteristic of isohydric species which demonstrate strong stomatal control of transpiration (Franks et al. 2007). Stomatal conductance in lodgepole pine has been found to be strongly correlated with soil moisture (Pataki et al. 2000). The advantages of isohydric behaviour include strong stomatal control which prevents xylem cavitation in water-limited

situations (Franks et al. 2007, McDowell et al. 2008), features which are beneficial in an environment with high fluctuations in soil moisture, as experienced by the lodgepole pine. However, isohydric species run the risk of carbon starvation as they maintain limited stomatal conductance during water stress, thereby restricting CO₂ entry for photosynthetic gas exchange (McDowell et al. 2008).

Although not statistically significant, lodgepole pine had a larger proportion of sapwood in comparison to Douglas-fir. Sapwood conducts water, consequently more sapwood results in more efficient water flow through the tree. An allometric relationship exists between whole-tree leaf area and sapwood area (Waring et al. 1982), which suggests that a given unit of leaf area is supplied with water from a fixed amount of conducting “pipes”. Research has shown Douglas-fir to have a higher leaf area to sapwood area ratio than lodgepole pine (Waring et al. 1982). This indicates that for a given leaf area Douglas-fir would have lower sapwood area, less conducting tissue and more hydraulic restrictions in comparison to lodgepole pine.

Unpublished data (L.B. Flanagan) from the Douglas-fir and lodgepole pine study sites show the vulnerability curves of both species (percent loss conductivity graphed vs. tension needed to induce cavitation (MPA)) to be nearly identical. Lodgepole pine have a slight tendency to withstand even slightly larger tensions than Douglas-fir before hydraulic losses occurred. This is in contrast to data from Piñol & Sala (2000) which suggested that lodgepole pine were more vulnerable to cavitation than Douglas-fir. Taking into account leaf area to sapwood area, Douglas-fir appear to have a less efficient hydraulic system, resulting in greater tension being required to transport water in comparison to lodgepole pine. Douglas-fir had to reach lower leaf water potentials in order to continue to transport water and allow photosynthetic gas exchange. It appeared that soil at the LP site dried so rapidly that lodgepole pine had to

strongly reduce stomatal conductance and drastically reduce rates of photosynthesis in order to prevent catastrophic hydraulic failure.

Other species have also demonstrated strong stomatal control during drought. Piñon pine have displayed tight stomatal control to prevent catastrophic cavitation, with the consequence of reduced photosynthesis during drought (Cochard 1992, West et al. 2007a). In Scots pine strong stomatal closure has been observed in response to soil drying (Irvine et al. 1998).

Douglas-fir needles were significantly more enriched in ^{13}C compared to lodgepole pine $\delta^{13}\text{C}$ values (Figure 13), likely a result of differing responses to declining soil moisture in mid-summer, as well as different hydraulic efficiency. It was initially anticipated that $\delta^{13}\text{C}$ values in lodgepole pine would be higher (less negative) in comparison to Douglas-fir, based on the water potential data which suggested that lodgepole pine were maintaining tighter stomatal control, theoretically resulting in lower intercellular concentration of CO_2 and less discrimination against $^{13}\text{CO}_2$ (Marshall & Zhang 1994).

Lodgepole pine appeared to undergo controlled down-regulation of photosynthesis in July and August as levels of soil moisture declined, observed through decreasing rates of oxygen evolution, suggesting that photosynthetic gas exchange and associated carbon metabolism were being strictly limited. With little CO_2 exchange occurring carbon isotope discrimination would also not occur (Panek 1996, Panek & Waring 1997). In comparison, Douglas-fir appeared to maintain relatively stable rates of oxygen evolution over the entire growing season, but were experiencing some water stress seen through declining water potential measurements (Figure 11). Therefore Douglas-fir were likely experiencing stomatal constraints resulting from lower hydraulic conductivity as water demand increased relative to supply, reducing intercellular levels of CO_2 and causing a decrease in ^{13}C

discrimination. Panek and Waring (1997) previously found interior Douglas-fir to have higher $\delta^{13}\text{C}$ values (lower ^{13}C discrimination) than they had predicted based on climate, because lower leaf-specific conductivity constrained stomatal conductance, decreasing internal concentrations of CO_2 , thereby producing a decline in discrimination and the resulting increase in $\delta^{13}\text{C}$. Stem hydraulic properties have been found to strongly influence carbon isotope discrimination, through influences on stomatal conductance as stomata respond to transpiration rates and associated tension in the xylem (Panek 1996).

4.3. Physiological response of photosynthesis to changing soil moisture conditions

The dark-adapted chlorophyll fluorescence measured at both study sites (Figure 14) confirmed that the function of photosystem II was not compromised during the regular growing season, regardless of soil moisture status. High dark-adapted F_v/F_m values indicated the presence of a healthy photosynthetic apparatus (Nippert et al. 2005). Fluorescence at both sites was correlated to soil temperature over the growing season; low soil temperatures are known to inhibit photosynthesis (DeLucia & Smith 1987). Fluorescence measurements reported here were similar to results from studies of Colorado Douglas-fir and lodgepole pine, where F_v/F_m reached a summer maximum of 0.8 (Zarter et al. 2006). The lowest spring time averages of F_v/F_m observed in this study were 0.3 for Douglas-fir and 0.5 for lodgepole pine, while Zarter et al. (2006) found minimum winter-time F_v/F_m values of 0.2 for both species. The slightly higher minimum F_v/F_m values reported here suggest that lodgepole pine had already begun photosynthetic recovery from winter dormancy before sampling in May. Had F_v/F_m been measured directly on the tree with no dark-adaption, it is likely that decreases in F_v/F_m would have been recorded as plant water stress increased (Baker 2008). PSII operating efficiency can be adversely affected by biochemical changes (carboxylation efficiency, rate of regeneration of 1-5-bisphosphate), intercellular CO_2 concentration,

photorespiration and the rate of carbohydrate transport, which all influence the rate of NADPH and ATP consumption and reduce PSII efficiency (Baker 2008). The dark-adaption process releases PSII from feedback inhibition and allows all of the PSII reaction centers to become capable of performing photosynthetic reduction (Maxwell & Johnson 2000).

Oxygen evolution measurements showed very different trends between species over the growing season (Figure 16). It is important to note that the rates of oxygen evolution determined for Douglas-fir and lodgepole pine were not associated with stomatal limitations because they were measured under saturating CO₂ (5%). Initial maximum rates of oxygen evolution were higher in lodgepole pine than Douglas-fir, likely a function of higher leaf N content (Zarter et al. 2006, Figure 15). The low chlorophyll fluorescence and oxygen evolution rates seen in spring and fall in Douglas-fir and lodgepole pine were correlated with soil temperature and air temperature, a common relationship observed in conifers (DeLucia & Smith 1987, Strand et al. 2002). A down-regulation process is employed by conifer trees in order to protect themselves from excess light energy during winter, accomplished through the degradation of proteins and the rearrangement of photosynthetic reaction centers, thus removing the source of excitation energy to protect the remaining photosynthetic apparatus (Adams et al. 2002, Oquist & Huner 2003).

Seasonal rates of oxygen evolution in Douglas-fir responded as expected for a species with anisohydric characteristics. After spring up-regulation, oxygen evolution rates remained fairly constant over the growing season despite declines in soil moisture, because they were accessing groundwater or deep soil water to meet their moisture requirements, as seen through declining *f* values (Figure 21). The close correspondence of the observed photosynthetic rates in Douglas-fir to modelled predictions based on changes in temperature (equation 7) also suggests moisture was not a major factor limiting gas exchange. An

exception was DOY 246 which showed a drastic drop in oxygen evolution rates corresponding to the lowest level of shallow soil moisture of the growing season at the DF site.

Observed oxygen evolution rates in lodgepole pine were highly correlated with modelled predictions based on changes in temperature (equation 7) when soil moisture levels were high, but as soon as soil moisture levels declined significantly measured rates of oxygen evolution departed from the model predictions. Rates of photosynthesis in lodgepole pine remained high through spring while soil moisture was high, but trees responded to decreasing soil moisture by reducing stomatal conductance to limit water stress and prevent hydraulic failure, as suggested by constant water potential measurements (Figure 11). The seasonal pattern of oxygen evolution rates shown by lodgepole pine were consistent with what would be expected of a species with isohydric characteristics facing water stress. Previous studies with spruce (*Picea glauca* x *Picea engelmannii* hybrid) have shown reduced rates of oxygen evolution in response to moisture stress due to reduced diffusion through the mesophyll and reduced carboxylation capacity, which decreases biochemical demand for reducing power and the need for electron transport through the photosystems (Eastman & Camm 1995, Eastman et al. 1997). This was also likely the cause for the reduction in lodgepole pine oxygen evolution observed in this study.

A sharp rise was seen in lodgepole pine oxygen evolution rates approximately two weeks after a large input of precipitation in early September. Trees can respond to pulses of summer rain, especially after prolonged periods of drought (Fravolini et al. 2005), but the effects of a rain event on photosynthesis may be delayed (Schwinning et al. 2002), by up to two weeks in this study.

4.4. Implications of a changing hydrologic cycle on Douglas-fir and lodgepole pine health and distribution

The 2008 growing season at both of the study sites, for the most part, had typical temperatures and precipitation (in comparison to 30-year normals, Figure 9). Temperatures were within normal ranges, with June possibly being slightly cooler. More precipitation than normal was received in May at both sites. August and October received slightly less precipitation than normal. If climate was to change significantly from the “normals”, what would the effect be on the individual species health and distribution?

It is clear that warmer temperatures will occur in the near future, especially in high latitude regions such as Canada, but scenarios for hydrologic changes in specific areas are ambiguous (Weltzin et al. 2003). Warming temperatures in the Rocky Mountains could decrease the amount of snowpack, with warmer winter and spring temperatures leading to earlier melting of the snowpack and earlier peak spring flow (Gan 2000, Cook et al. 2004, Mote et al. 2005). Changes in precipitation are unknown, but even if precipitation actually increases, it is likely that Rocky Mountain areas would still be drier during the growing season because of increasing evaporation associated with warmer temperatures (Schneider et al. 2009). Changes in the magnitude and timing of precipitation will also affect soil moisture regimes (Weltzin et al. 2003).

Smaller snowpacks would result in less water being available to recharge deep soil moisture and groundwater. This could seriously impact Douglas-fir, a species that was observed in this study to rely on deep soil moisture later in the growing season. Lesser amounts of deep soil moisture would be depleted more rapidly, potentially making Douglas-fir more susceptible to catastrophic xylem failure. Lodgepole pine require early spring moisture as photosynthesis begins to rapidly up-regulate from winter dormancy. Soil at the LP site was

unable to store high amounts of water, so the amount of snowpack is not as critical at this site as consistent inputs of rain during the growing season.

Earlier snowmelt may not have any effects on either species in this study if the trees are also responding to warmer temperatures by earlier up-regulation of photosynthesis. Other species in North America (lilac and honeysuckle) have demonstrated earlier blooming correlated to earlier snowmelt (Cayan et al. 2001). Trees could be detrimentally affected if they are unable to begin photosynthesizing earlier and miss the spring ‘pulse’ of moisture.

Less precipitation during the growing season would have detrimental effects on both tree species, which are already somewhat limited by water availability in the summer growing season. Water limitation is often the cause of vegetation mortality world-wide (McDowell et al. 2008). Douglas-fir may not be as severely impacted as lodgepole pine by reduced growing season precipitation if deep soil moisture continued to be recharged by snowmelt at the DF site. However, my results suggest that lodgepole pine restrict photosynthesis when growing season soil moisture declines. If early spring precipitation was reduced, water stress could induce stomatal closure in lodgepole pine earlier in the season, leading to the risk of carbon starvation. McDowell et al. (2008) hypothesized that future droughts will initially kill isohydric species (lodgepole pine). The effects of carbon starvation would slowly reduce the health and fitness of isohydric trees, making them more susceptible to insect and pathogen attacks. Anisohydric species (Douglas-fir) would perish if droughts became so severe that midday water potentials were pushed to the point where catastrophic hydraulic failure occurs.

More intense growing season precipitation events may be beneficial to both species. If the frequency of extreme events were to increase (Easterling et al. 2000), the DF site may be at

an advantage by having the ability to store excess moisture, whereas the LP site could lose excessive moisture through runoff. Precipitation events that were more severe but less frequent would be unfavourable for lodgepole pine.

The effects of climate change on forest carbon sequestration are also unclear. A large fraction of annual carbon sequestration in sub-alpine forests occurs in the first 30 days of the growing season – when respiration is low and moisture is still adequate enough for high photosynthetic rates (Monson et al. 2002). The reduction in carbon sequestration after the first 30 days of the growing season is caused by either high ecosystem respiration when soil moisture is high, or reduced photosynthetic carbon gain when soil moisture is low (Monson et al. 2002). It has been suggested that earlier springs would have the potential to extend the growing season and increase carbon storage. However, an extended growing season may not result in increased carbon sequestration in conifers because of increased respiration and decreased maximum photosynthetic capacity in the mid to late portions of the growing season (Busch et al. 2007). The timing of spring snow melt may be a primary control over annual rates of carbon sequestration in higher elevation subalpine forests, leading to lower annual carbon sequestration with earlier spring melt (Monson et al. 2002). The effects of climate change on carbon sequestration in the Douglas-fir and lodgepole pine forests in this study are unknown. Earlier snowmelt coupled with less precipitation during the growing season could result in reduced rates of carbon sequestration. Lodgepole pine showed serious reductions in gas exchange mid-summer in 2008, which was an average year. Further reductions in precipitation could result in earlier reductions in gas exchange and even less carbon sequestration.

Models have demonstrated that changes in the distribution of tree and shrub taxa in response to climate change will be large, with shifts being difficult to predict (Shafer et al. 2001).

Douglas-fir may be limited by warming temperatures because of a required chilling period, whose absence would be detrimental to seedling recruitment (Shafer et al. 2001). Lodgepole pine have been shown to respond poorly to heat and drought stress from late summer of the prior growing season, likely because late summer conditions affect bud formation and carbohydrate storage for the following year (Chhin et al. 2008). Results from this study suggest Douglas-fir would be confined to locations that have large soil moisture reserves.

Forests in Alberta are important ecologically and economically. Transpiration and evaporation are the major routes of water loss as it returns to the atmosphere, resulting in forests having massive influences on the hydrology of terrestrial ecosystems (Diaz et al. 2007). Responses of individual species to shifts in hydrology may depend on their ability to adjust root physiological or morphological characteristics at individual and population levels (Williams & Ehleringer 2000). Acclimation is possible (Kirschbaum 2000), but if rates of climate change occur too rapidly, forests will face declines in productivity which may lead to wide-spread mortality of important tree species.

4.5. Conclusions

- Deep soil moisture was available at the Douglas-fir site because of greater soil volume and finer soil texture. This provided the opportunity for Douglas-fir to shift towards using deep soil moisture as shallow soil moisture declined during mid-summer.
- The lodgepole pine site lacked significant water storage capacity because of shallow soil with coarse texture, resulting in lodgepole pine down-regulating photosynthesis during mid-summer when soil moisture declined from lack of precipitation inputs.

- Douglas-fir operated close to xylem tensions which could cause catastrophic hydraulic failure but maintained high rates of photosynthetic oxygen evolution throughout the summer growing season.
- Lodgepole pine kept a large margin of safety between the midday water potential experienced and that which would cause hydraulic failure, but were forced to restrict leaf gas exchange and down-regulate photosynthetic metabolism during mid-summer because of water stress.

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