Analyzing the influence of environmental conditions and anthropogenic disturbance on *Picea mariana* xylem traits in boreal peatlands of northern Alberta

By

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

In the Athabasca Oil Sands Region (AOSR), wetlands dominate 55 500 km^2 (54%) of the landscape despite its subhumid climate and prevailing moisture deficits. The variability and complexity of the AOSR landscape has allowed for the formation and function of several wetland types (i.e. fen, bog, swamp), with treed fens being the most prevalent. Wetlands of the AOSR function as vital water and carbon storage systems as well as niche habitats for vegetation communities and wildlife. Wetlands of the AOSR are largely dominated by conifer species (*Picea mariana, Larix laricina*), of which are vulnerable to extreme weather and both natural and human disturbances. Thus, shifts in species development of wetland systems, due to climate warming and human disturbance, could have substantial implications for regional water and carbon storage. To define future resilience of northern wetlands to climate change and increasing ecosystem disturbance, it is critical to investigate retrospective species-specific responses to environmental conditions. To this end, we correlate long-term, intra-annual level wood anatomical parameters of 10 *Picea mariana* (black spruce) trees across two sites at differing elevations (320 and 740 m a.s.l.) and with varying growing season water table depths, as well as 20 trees across a treed swamp disturbed by an unpaved road. Regional daily maximum and minimum temperature and daily precipitation totals were compiled for the study period (1961-2019) for the three study sites. Ring width chronologies of all three sites indicated a potential influence of large-scale atmospheric patterns, such as the Pacific Decadal Oscillation and should be examined further. Enhanced previous summer temperature at both elevations could reduce lumen size, impede water transport to the tree apex and thus, diminish forest productivity. However, higher winter temperatures at higher altitudes and greater winter precipitation at lower altitudes could increase wood density and thus, mitigate potential for cavitation and/or tree mortality in reoccurring drought conditions. Black spruce sensitivity to drier conditions at topographic lows may limit cell lumen enlargement and hydraulic efficiency impacting stem overall water transport efficiency. The observed divergent and complex climatic responses of the study areas are likely the result of localized conditions (i.e. elevation and water table depth). Within the treed swamp study area, fugitive dust load was measured at varying distances away from the unpaved road to infer its influence on black spruce development. There was no evident shift in climatic influence on tree anatomy following road disturbance. Water table depth on opposing sides of the road showed similar temporal trends, suggesting minimal impediment of groundwater flow despite disturbance. Fugitive dust load was highest 2 m west of the road (4.01 gm^{-2}day^{-1}) and exhibited an exponential decline away from the road. Interestingly, cell size and cell wall thickness of the trees west of the road increased ($p < 0.05$) following road construction indicating a potential shift in water availability rather than fertilization via dust deposition. Nevertheless, intense human activity surrounding the treed swamp at the time of road construction prevents a definitive conclusion. These findings highlight the need for additional black spruce xylem anatomy research in disturbed wetland systems of northern landscapes.

Acknowledgements

I would first like to recognize that this field research was conducted within Treaty 8, the traditional territories of the Cree, Métis, and Denesuline Peoples. Both my lab and computer work were conducted on the traditional lands of the Haudenosaunee, Anishnaabeg, and Neutral Peoples. Reconciliation is a critical aspect of both my personal and academic life as an environmental scientist.

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Chapter 1: Introduction

1.1 Western Boreal Plains: Hydroclimatology and Climate Change

The Western Boreal Plains (WBP) make up approximately 58% of the landscape of Alberta, Canada, and is characterized by a sub-humid climate, with cold winters and mild to warm summers (Brown et al., 2014; Kompanizare et al., 2018). 30-year climate normals demonstrate mean annual air temperature ranges between -2° to 4°C and mean annual precipitation (P) between 430-640 mm (Ireson et al., 2015). The majority of P and evapotranspiration (ET) occurs in the growing season (May to September). In a sub-humid climate, potential ET (PET) demands often exceed P, meaning the WBP is often vulnerable to moisture deficits (Spennato et al., 2018), which are typically replenished via wet cycles every 10 to 15 years (Marshall, 1999). ET is a principal component of an ecosystem's water balance and is influenced by a collection of environmental variables including vegetation composition and maturity, leaf area index (LAI), soil moisture regimes and microclimatic behaviour (Brown et al., 2010; Brümmer et al., 2012). However, the landscape mosaic as well as rapid urban and industrial development within the WBP complicates the quantification of both current and future ET trends of the region.

Analogous to other northern biomes, shifts in hydrological regimes and climatic trends in the WBP are expected to continue in this century (Suncor Energy Inc, 2007). Northern ecosystems, such as those within the WBP, are considered more at risk than their southern counterparts due to the lengthening of the snow-free period and reduced albedo effect, which may enhance water losses (Ireson et al., 2015). Further into the 21st century, the WBP may experience changes in average annual temperature, growing season length, and frequency of severe weather events (Wang et al., 2014). Specifically, the WBP has thus far (1950-2010) experienced an overall increase in average air temperature, with the greatest impact observed in both winter (~2 to 3°C) and spring (~1 to 2°C) seasons (Ireson et al.,2015). An increase in average air temperature, as well as growing season length, may promote growth of plant and tree species. However, this may be outweighed by an increase in frequency and severity of drought-like conditions (Barber et al., 2000; Girardin et al., 2014; Ireson et al., 2015; Walker & Johnstone, 2014). If the WBP experiences greater moisture deficits in the future, peatland landscapes may be most at-risk (Petrone et al., 2011). However, peatland resilience to predicted future moisture availability is poorly understood. At the very least, it is estimated that the physical environment (i.e. nutrients, soil, water availability) will be impacted and consequently, alter current ecosystem ecology (Suncor Energy Inc, 2007). Despite research findings thus far, it is still unclear exactly to what extent and magnitude climate change will impact the WBP due to the complexity of its landscapes, rate of land-use change, and adaptive capacity.

1.2 Boreal Wetlands

Approximately 45% of the WBP is classified as wetlands, the majority of which are classified as fen and bog peatlands (Graf, 2009; Schneider et al., 2016; Vitt et al., 1996), with more than half being treed fens (AESRD, 2015). However, swamps cover ~11570 km^2 (12% of the WBP landscape; AEP, 2018) of the WBP, with greater than 50% being conifer-dominated (AESRD, 2015). Swamps often act as transition zones between other wetland types and uplands and as such may play important roles in the conveyance of water among landscape units (Alberta Government, 2015). Although, swamp systems are able to accumulate peat, they are typically considered mineral wetlands (AESRD, 2015).

Western boreal peatlands receive water inputs from both P (snowfall and rainfall) and runoff, and lose much of their water via ET and runoff processes. Hydrological regimes influence peatland plant function (i.e. photosynthesis, respiration, water-use efficiency), nutrient concentrations (Waddington & Roulet, 1997), and peat accumulation (Zoltai & Vitt, 1990). As such, carbon storage capacity and emissions are heavily intertwined with peatland water availability. Peatlands within the Canadian Prairies (Alberta, Saskatchewan, and Manitoba) occupy 0.25% of the global land cover but hold 2.1% (48.0 Pg) of the world's terrestrial carbon reserves (Vitt et al., 2000). Wooded peatlands of the continental west hold the majority of carbon stocks per unit area relative to shrubby and open wetland systems (Vitt et al., 2000).

Boreal wooded fens, which comprise the majority of WBP peatlands, are dominated by stunted *Picea mariana* (black spruce) and *Larix larcinia* (tamarack) tree species (Schneider et al., 2016). Black spruce and tamarack species are commonly found in nutrient-poor and nutrient-rich fens, respectively (AESRD, 2015). Fen tree species often lack the biomass observed in an upland stand due to anoxic soil conditions suppressing carbon uptake and ET rates (Dang et al., 1991). Understory vegetation in boreal wooded fens typically consists of *Betula spp., Salix spp.,* and *Rhododendron groenlandicum*, with a thick ground cover of brown and sphagnum mosses, graminoids, and forb species.

Wooded coniferous swamps, found scattered throughout the WBP, typically have >25% of tree cover (of which ~75% is conifer species) (AESRD, 2015). Black spruce and tamarack dominate the landscape with occasional white spruce (*Picea glauca*). In closed canopy settings, trees can grow beyond ten meters in height with shrub species (i.e. bog birch, Labrador tea) populating the understory. The ground surface of a wooded swamp is hummocky and often covered by assorted vascular species (i.e. *Cornus Canadensis, Rubus pubescens*) and feathermosses (AESRD, 2015).

Schneider et al. (2016) suggest that if future precipitation outputs do not rise with air temperature, the WBP may experience shifts toward aspen-dominated upland systems within this century as water tables decline. Peatlands will exhibit differences in water-table changes based on local biotic and abiotic factors (i.e. peatland type, tree cover, surficial geology, and topography) (Devito et al., 2005). It is likely that wetlands with adequate hydrologic connectivity will illustrate greater resilience compared to those without (Waddington et al., 2015; Kompanizare et al., 2018). Tree and vegetation distribution are anticipated to change but will differ based on their specific moisture requirements and topographic position (Ireson et al., 2015). For example, peatland black spruce transpiration rates may change with rising air temperatures, thus catalyzing a positive feedback of further drying of boreal peatlands (Choi, Chang, & Bhatti, 2007; Dang & Lieffers, 1989). Regardless, climate change impacts on wetland ecosystems are likely to be exacerbated by anthropogenic disturbance.

1.3 Western Boreal Plains: Anthropogenic Disturbance

Expansion of the oil and gas, and forestry, industries in the WBP intensifies the demand for road construction and thus, disrupts the regular functionality of many peatland ecosystems (Plach et al., 2017). Wetland ecosystems are an integral component of global nutrient and water budgets (Price & Waddington, 2000) and hold 30% of the world's carbon. Therefore, the destruction of peatlands often leads to loss of carbon storage. Approximately 21% of Alberta's Boreal Ecozone is considered disturbed (ABMI, 2012), with 80% of the anthropogenic disturbance due to linear disturbances (Pasher et al., 2013). Linear disturbances such as roads, seismic lines, and pipelines, can detrimentally alter the hydrological, ecological, and nutrient cycling processes of WBP peatlands. Winter access roads and seismic lines often alter vegetation dynamics, hydrological and nutrient cycles, and lead to a reduction in canopy biomass and overall tree net primary production (Strack et al., 2018). van Rensen et al. (2015) state that relatively wet peatland sites lack plant biomass regeneration even 50 years post-seismic line construction. Landscapes adjacent to roads in the Athabasca Oil Sands Regions (AOSR) of Alberta demonstrate elevated levels of N, specifically in areas of high vehicle traffic (Howell et al., 2014; Wood et al., 2016). It is estimated that the available gaseous nitrogen (N) in a watershed could be underestimated by up to 25% if road traffic is not considered (Bettez, 2013). Road construction also holds indirect implications for peatland ecological function and carbon storage (Saraswati et al., 2019; Saraswati et al., 2020) through impediment of water flow due to beaver damming in culverts (Bocking et al., 2017), and/or inadequate engineering design (Park et al., 2008). The degree of disruption to subsurface hydrological regimes varies depending on the orientation of the road relative to water flow direction (Saraswati et al., 2019). A significant obstruction of subsurface flow can result in drier conditions downstream and thus, shifts in vegetation communities (Bocking et al., 2017).

Fugitive dust, the suspension of particulates in the atmosphere, is a common form of pollution from traffic on unpaved roads. Dust from unpaved roads is known to cause both chemical and physiological changes in plant foliage including reduced photosynthetic processes (Sarma et al., 2017) and altered water-use efficiency (Sharifi et al., 1997). However, few studies in the AOSR have explored the ecological impacts of fugitive dust from unpaved roads. Ecological impacts of unpaved roads have primarily been studied in controlled (McGranahan & Poling, 2021) or semi-arid environments (i.e. Matsuki et al., 2016; Sarma et al., 2017; Sharifi et al., 1997) where rainfall is scarce. Rainfall acts to wash-off dust deposited on plant foliage (Omstedt, Bringfelt, & Johansson, 2005) therefore, the ecological effect of dust may differ in the sub-humid climate of the AOSR. Very few studies have demonstrated the impacts of permanent, unpaved roads on long-term tree development in northern Alberta, specifically at an intra-annual scale.

1.4 Quantitative Wood Anatomy in Conifers

Quantitative wood anatomy (QWA) is the analysis of xylem anatomical characteristics of plant species to better understand both historical and current plant-ecosystem dynamics. Plant xylem are responsible for the transport and storage of nutrients, sugars, hormones, and water, all necessary components for photosynthesis (von Arx et al., 2016). The process of xylem formation is heavily linked to the water and carbon cycles as it requires continual water intake and carbon assimilation in the growing seasons (Fonti et al., 2013). The rate and volume of carbon assimilation over time is moderated by several external variables such as solar radiation, air temperature, soil moisture, and nutrient availability. Inter- and intra-annual fluctuations in these variables thus, heavily influence when and how the xylem develop. This cause-and-effect relationship is investigated via QWA to understand how external variables have both influenced xylem growth in the past and in the current threat of climate change (i.e. Castagneri et al., 2015; Girardin et al., 2015; Ueyama et al., 2015). Xylem features that are commonly studied include cell wall thickness, lumen dimensions, and number of cells (Figure 1-1).

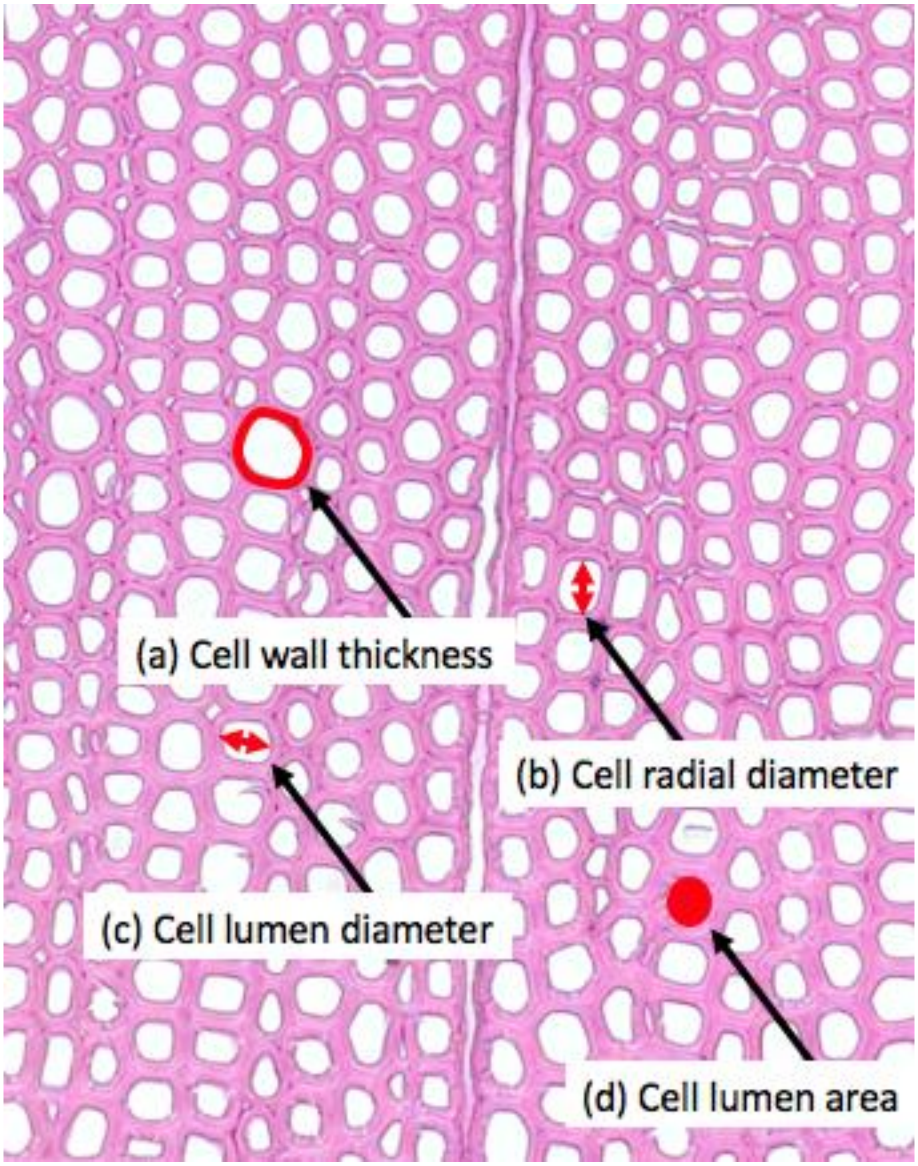


Figure 1-1. Xylem anatomical traits that are measured and analyzed for quantitative wood anatomy. (a) Cell wall thickness; (b) cell radial diameter; (c) cell lumen diameter and; (d) cell lumen area.

Plant xylem can often be further subcategorized by earlywood and latewood (Figure 1-2). Earlywood cells differentiate in early spring and summer time and as a result, have larger cell lumina and thinner cell walls. Latewood cells differentiate in the later months of the growing season and thus, have smaller cell lumina and thicker cell walls. Cartenì Fabrizio et al. (2018) suggested these differences in xylem traits could be a result of low and high sugar availability in the early and late growing season, respectively. Unlike traditional dendrochronology, xylem traits can be measured at intra-annual scales to help identify ecological sensitivities to seasonal climatic trends and ecosystem disturbances.

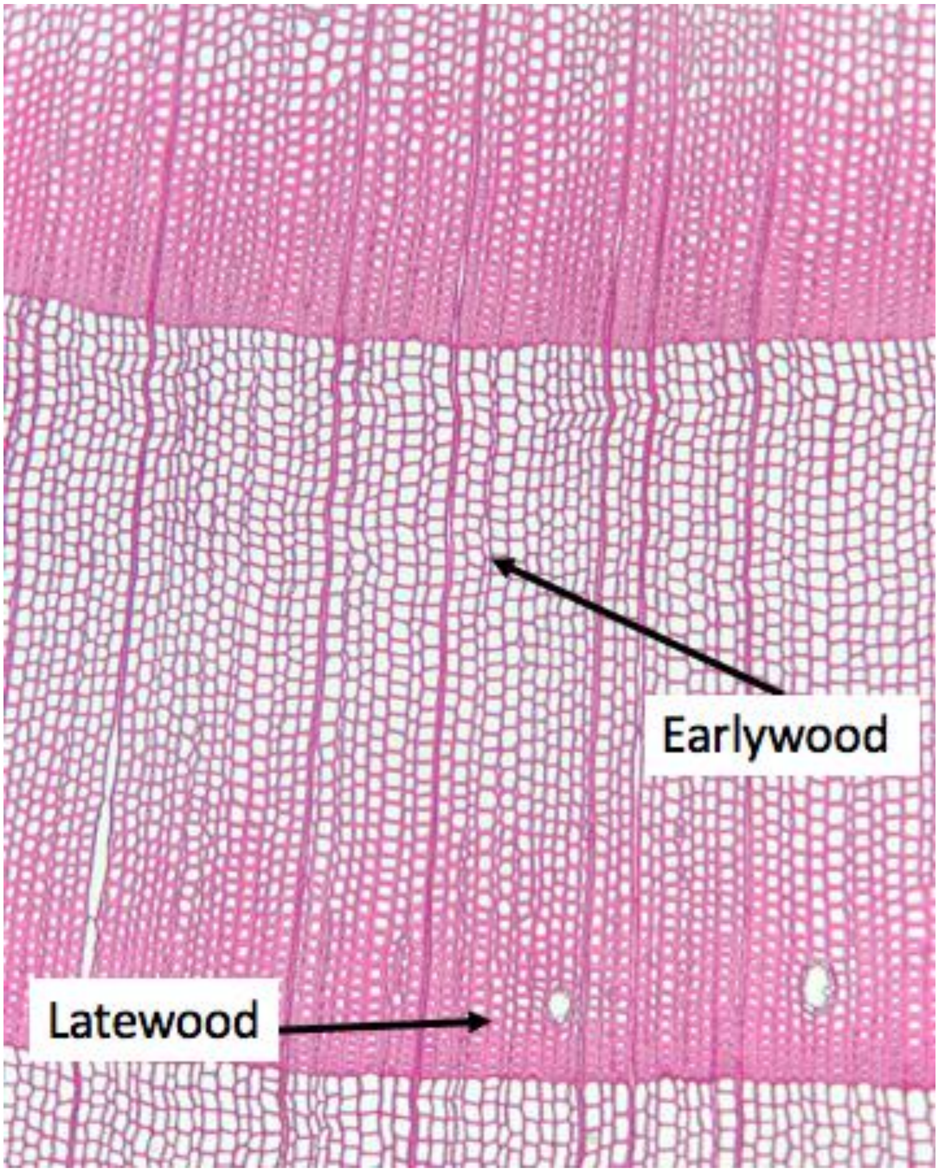


Figure 1-2. Image depicting the earlywood and latewood cells within a conifer (black spruce) tree-ring boundary.

Research surrounding black spruce growth in northern Canadian boreal forests is somewhat limited. Thus far, progress has been made to better characterize the environmental demands and thresholds of black spruce development and how climate change may pose new challenges for the species. Much of what is currently known about boreal conifer xylem formation originates from xylogenesis studies (i.e. Buttò et al., 2019; Rossi et al., 2014; Vaganov et al., 2009). Xylogenesis examines the timing and dynamics of xylem production rather than anatomical features. Non-xylogenesis QWA studies in Canada focused primarily on black spruce sapling development. More importantly, the characterization of mature black spruce anatomical features has yet to be adequately explored in the boreal peatlands of northern Canada. Black spruce sapling xylem cell production and differentiation was found to be positively related to water, carbohydrate, and carbon availability (Deslauriers et al., 2016). Greenhouse experiments also suggest that in both drought and post-drought conditions, black spruce saplings exhibit lower rates of photosynthesis and stomatal conductance (Balducci et al., 2015). This was attributed to the reduction of hydraulic conductivity of the leaf stem due to cavitation. Cavitation is the blockage, typically by air pockets, of water transport through plant xylem and can often lead to tree mortality.

At higher latitudes, phenological processes (i.e. wood formation) tend to disproportionately depend on air temperature (Kramer, Leinonen, & Loustau, 2000; Vaganov et al., 2006). Contrastingly, a QWA study conducted in the closed boreal forest of Quebec, Canada (Puchi et al., 2020) demonstrates water availability as a prominent factor for northern black spruce development, specifically in the coming decades, and will ultimately outweigh the benefits of a longer growing season (Babst et al., 2019; Buermann et al., 2018; D’Orangeville et al., 2018).

Advancements in sampling and preparation methods, as well as data analysis tools, in the last 20 years has increased the quality and efficiency of QWA studies. It was only in 2014 that a synthesis of standardized sampling and preparation methods for QWA was made available (von Arx & Carrer, 2014). The field of QWA is rapidly expanding however, uncertainties still remain around plant species development in northern Canadian forests specifically those vulnerable to climate change and anthropogenic disturbance.

1.5 Knowledge Gaps

Several uncertainties regarding the limiting factors of tree species growth in northern ecosystems still remain. This is especially true for peatlands in the AOSR of northern Alberta, where changing climatic trends and rapid industrial expansion are observed. Peatlands are considered global carbon sinks, nutrient reservoirs, and discharge basins with distinctive ecological communities.

Although progress has been made, inconsistencies among results is one of the biggest challenges in conifer wood-anatomy research. It is suggested that a large reason for this is due to localized environmental factors such as altitude and water availability (Castagneri et al., 2015). Environmental constraints on tree xylem anatomical features (and thus, tree growth) differs according to altitude and climatic conditions (Castagneri et al., 2015). This has a direct effect on carbon assimilation, transpiration rates, and tree survival (Wilkinson et al., 2015). Despite this, few studies have analyzed northern conifer tree species long-term development at various altitudes in tandem. Much of what we know in regard to boreal conifer xylem production is limited to xylogenesis studies (i.e. Buttò et al., 2019; Rossi et al., 2014; Rossi et al., 2016; Vaganov, E.A et al., 2020). The need for conifer wood-anatomy research in northern peatlands of Canada is required, considering conifer xylem anatomy research has been conducted mainly in eastern continents and/or upland landscapes (i.e. Castagneri et al., 2015; Dufour & Morin, 2013; Martin-Benito et al., 2013; Puchi et al., 2020).

Due to the sheer complexity of individual ecosystem function and resilience, it is difficult to determine a universal anticipated response of conifer species to anthropogenic disturbance. Studies have addressed the impact of seismic line disturbance on carbon, water, and nutrient cycling, as well as vegetation regeneration (van Rensen et al., 2015; Strack et al., 2018). The impact of road construction on nutrient cycling (Howell et al., 2014; Wood et al., 2016) and shifts in hydrological regimes (and subsequent tree mortality) have been investigated (Bocking et al., 2017; Saraswati et al., 2019; Saraswati et al., 2020). However, the effect of road construction on intra-annual conifer growth in northern latitudes has yet to be examined. It is still unclear how road development will impact ecological succession and therefore, peatland carbon storage (Plach et al., 2017), ET rates, and susceptibility to fire. The abundance of both boreal peatland conifer species and linear disturbances in the AOSR of Alberta demonstrates a great need for further research.

Retroactively determining the type and magnitude of climatic and land-use changes that alter conifer xylem formation is critical for estimating future ecological and hydrological (i.e. ET) trends of boreal peatland ecosystems.

1.6 Research Objectives

The overall research objective of this thesis is to further understand the impact both climate and anthropogenic disturbance have on northern boreal black spruce development. These findings will improve future planning, engineering, and monitoring practices related to peatland conservation. This thesis, divided into a four-chapter manuscript, focuses on three natural peatland sites within the Greater Fort McMurray region of northern Alberta. Chapter 1 will discuss current research, research gaps, and significance of the study. The second chapter will examine the role altitude and climate plays into the long-term annual growth of boreal peatland black spruce trees at two sites. Chapter 3 investigates the impact of an unpaved road on boreal black spruce development in a treed swamp. The final chapter will highlight the findings and conclusions of the study, as well as study limitations and suggestions for further research.

Chapter 2: Manuscript 1: The impact of hydrogeomorphology on *Picea mariana* tree-ring anatomy, Alberta, Canada

Abstract

The Athabasca Oil Sands Region (AOSR) consists of approximately 54% wetlands, which act as a significant water source for the region. Fen systems are the most abundant wetland type in the region, with more than half of fen systems being treed fens, typically dominated by conifer species (*Picea mariana, Larix laricina*). *Picea mariana* (black spruce) are predominantly found in poor fens of headwater regions, and as such have the potential to influence downstream water supply. Thus, shifts in species development, due to climate warming, could have substantial implications for local and regional water balances. To define future ecohydrological resistance of northern wetlands to climate change, it is critical to investigate retrospective species-specific responses to environmental conditions. To this end, we correlate long-term, intra-annual level wood anatomical parameters of 10 trees across two sites at differing elevations (320 and 740 m a.s.l.) and with varying growing season water table depths. Daily maximum (T_{max}) and minimum (T_{min}) temperature and daily precipitation (P) totals were compiled for the period of 1961 - 2019 at Pauciflora Fen and 1961-2016 at Poplar Fen to investigate a potential drift in species growth responses. Ring width chronologies of both study sites indicated a potential influence of large-scale atmospheric patterns, such as the Pacific Decadal Oscillation and should be explored further. Enhanced previous summer temperature at both study sites could reduce lumen size, impede water transport to the tree apex and thus, diminish forest productivity. However, higher winter temperatures at higher altitudes and greater winter precipitation at lower altitudes could increase wood density and thus,

mitigate potential for cavitation and/or tree mortality in reoccurring drought conditions. Black spruce sensitivity to drier conditions at topographic lows may limit cell lumen enlargement and hydraulic efficiency impacting stem overall water transport efficiency. The observed divergent and complex climatic responses of the study areas are likely the result of localized conditions, such as hydroclimate. These findings highlight the need for additional black spruce xylem anatomy research in wetland systems of northern landscapes.

2.1 Introduction

The Athabasca Oil Sands Region (AOSR) of northeastern Alberta covers roughly 93000 km^2 of the Western Boreal Plains (WBP) (ABMI, 2017) and is characterized by a sub-humid climate (Alberta Environment and Parks, 2018). The region is typically in a moisture deficit with potential evapotranspiration (PET) often exceeding precipitation (P; mm) (Devito et al., 2012). Despite this, wetlands (25% being fen systems) occupy ~54% of the AOSR (AEP, 2018) and are significant sources of water for the region (Devito et al., 2017). In particular, wetland-dominated high elevation areas (i.e. The Stony Mountain Uplands; ~740 m a.s.l) often receive above average P and act as headwater basins for downstream ecosystems and regional groundwater flow (Barson et al., 2001). Fen systems are the most abundant wetland type in the region (Vitt & Chee, 1990; AESRD, 2015), with more than half of fen systems being treed fens (AESRD, 2015; AEP, 2018), typically dominated by conifer species (*Picea mariana* and *Larix laricina*). *Picea mariana* (black spruce) are more commonly found in poor fens (pH < 5.5) of headwater regions, but do exist in moderate-rich fens (pH between 5.5-7.0) in topographic lows (AESRD, 2015). Peatland black spruce trees are often stunted as a result of low oxygen levels in the rooting zone from inundation, which limits photosynthesis and transpiration rates (Dang et al., 1991; Thompson et al., 2014). However, how peatland black spruce productivity will change under predicted warming is currently unknown (Schneider et al., 2016). The prevalence of black spruce in the AOSR implies that shifts in species development could hold substantial implications for local and regional water balances, as well as carbon storage. For example, receding water tables, as a result of rising temperatures, catalyze black spruce photosynthesis and transpiration thus, amplifying a strong (drying) positive feedback loop (Dang & Lieffers, 1989; Choi et al., 2007). Though, trees growing in water saturated conditions often have shallow root systems (Mannerkoski, 1985) thus, moisture deficits in wetland systems could lead to water stress. Fluctuations in water table are a result of temperature and precipitation. Low-frequency atmospheric patterns, such as the Pacific Decadal Oscillation (PDO), are known to influence annual tree growth in western Canada through hydroclimatic variability (Hart, Smith, & Clague, 2010; Pisaric, St-Onge, & Kokelj, 2009). *Pinus banksiana* (jack pine) of Yellowknife, Northwest Territories showed a possible connection between early-growing season P and large-scale oscillations over the Pacific (Pisaric et al., 2009). However, little is understood about the influence of these large-scale atmospheric patterns on black spruce growth, which dominate much of this region. To define future growth and carbon storage capacity of black spruce trees, it is critical to investigate species-specific responses to multi-scale environmental conditions (i.e. air temperature, precipitation).

Quantitative Wood Anatomy (QWA) is the analysis of plant xylem anatomical features relevant to functionality, support, and growth (von Arx et al., 2016). Once formed, xylem features, such as cell size, often define the transportation of water, nutrients, sugars, and hormones throughout the tree. Xylem cell wall thickness provides structural support for plant stems and foliage (von Arx et al., 2016). The number of xylem present is also often considered in QWA due to its relationship with both plant structure and growth. Current QWA research demonstrates wood formation and xylem anatomical features and thus, sap transport and carbon fixation capacity (i.e. Castagneri et al., 2015; Fonti & Babushkina, 2016; Puchi et al., 2020; Rossi et al., 2016), are heavily influenced by external factors such as climate and elevation (i.e. Castagneri et al., 2015; Fonti & Babushkina, 2016; Puchi et al., 2020; Rossi et al., 2016). Compared to traditional dendrochronology methods that evaluate ring-width variability and growth response to climate and disturbances at annual resolution, QWA provides a higher temporal resolution of plant-environment associations. Although progress has been made to understand the plasticity of boreal conifer xylem formation with respect to current and future external conditions (i.e temperature and precipitation) through xylogenesis monitoring (Dufour et al., 2013; Rossi et al., 2014; Rossi et al., 2011), there is little knowledge of the controls of boreal black spruce anatomical features at larger temporal scales. A few long-term studies on boreal conifer species showed contrasting relationships between anatomical features and environmental conditions (Belokopytova et al., 2019; Belokopytova et al., 2020; Zhirnova et al., 2021). This may be the result of localized growing conditions (Castagneri et al. 2015), which subsequently emphasizes the critical need for QWA research in Canada’s northwest boreal landscape. More specifically, there is little research conducted on the sensitivities of western Canada’s boreal peatland black spruce development despite the species’ prevalence.

Due to the localized, long-term nature of climate change, multi-decadal analyses of plant-climate relationships in northern Alberta will help to characterize future ecosystem sensitivities (Moreno-Gutiérrez et al., 2012). The objective of this study is to retrospectively determine the long-term impacts of climate on black spruce radial growth and earlywood and latewood anatomy characteristics at two fen sites of differing site conditions.

In this research, it is hypothesized that:

(i) The number of cells per ring will be positively related to spring and summer temperature, specifically at the wetter, cooler site.

(ii) Dominant environmental controls on conifer growth differs along altitudinal gradients thus, temperature will be a prominent control for black spruce at the wetter, cooler site while precipitation will be the dominant control at the drier, warmer site.

(iii) Given the sensitivity of cell enlargement to drought, anatomical features related to cell size will have a negative relationship with temperature and positive relationship with temperature during the growing season at the drier, warmer site.

2.2 Study Area

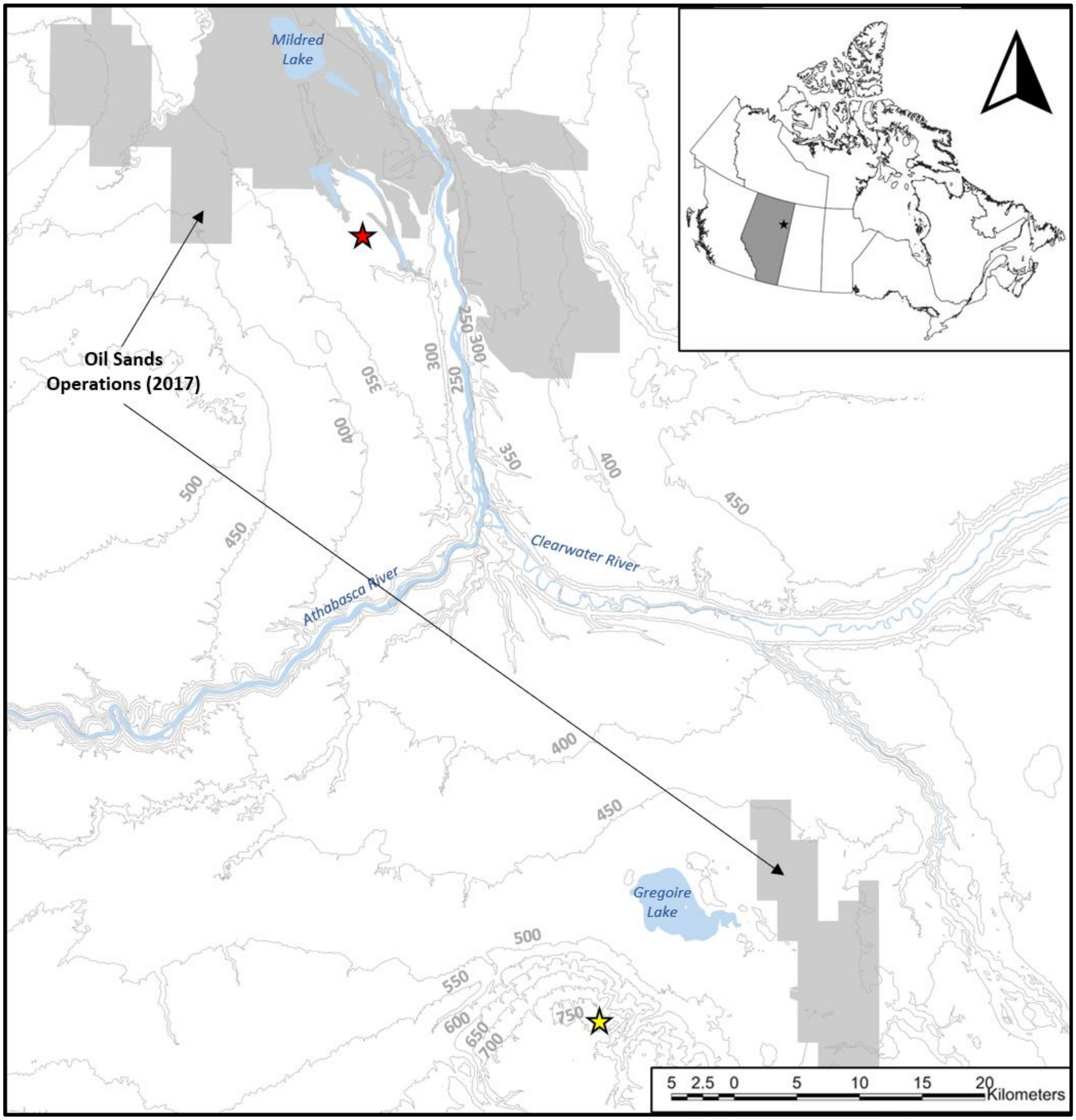


Figure 2-1. Map of the study areas, Pauciflora Fen (yellow) and Poplar Fen (red), and oil sands operations (as of 2017) of the Fort McMurray region, Alberta, Canada.

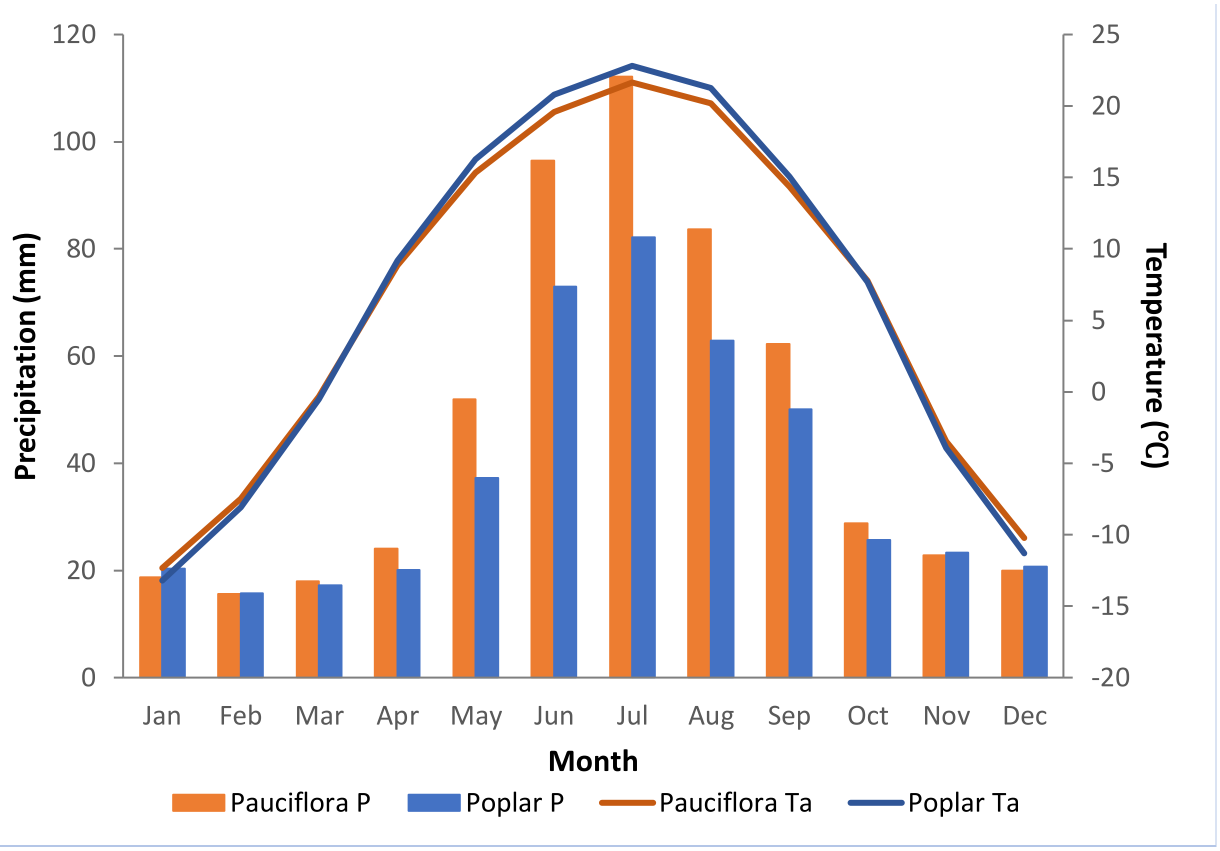


Figure 2-2. Monthly average air temperature (T_a; °C) and precipitation (P; mm) at Pauciflora Fen and Poplar Fen, Fort McMurray, Alberta, Canada, based on the Alberta Climate and Information Service record from 1961-2019 (Alberta Agriculture and Forestry 2019).

2.2.1 High Elevation Site

The first study site (56°56’ N, 111°13’ W) is an 8-hectare natural, poor fen peatland on a local topographic high (~740 m a.s.l) in the Boreal Plains Ecozone of the AOSR. The study site, herein referred to as *Pauciflora Fen*, is approximately 45 km south of Fort McMurray and lays within a basin built upon glacial deposits (silt, clay), surrounded by forested uplands (Fenton et al., 2013). Peat depth in the basin varied from 0.5 in transition zones to >12 m in the northern reaches of the fen (Wells, Ketcheson, & Price, 2017); shallow groundwater of the fen had a pH of 5.5 (Murray, Barlow, & Strack, 2017). Pauciflora Fen had an annual average air temperature (T_a) of ~0.4°C and received on average annual P of 586 mm during the study period (1961-2019; Alberta Agriculture and Forestry, 2019). Approximately 40% of all P that falls in the Fort McMurray region is in the form of snow. July was the wettest month with an average rainfall of 112 mm; daily maximum air temperature (T_{max}) peaked in July at an average of 21.6°C (Figure 2-2; Alberta Agriculture and Forestry, 2019). The fen consisted primarily of stunted and lichen-draped *Picea mariana* (non-uniformly distributed) and *Larix laricina* tree species. The understory of the open-fen system was characterized by hummock-hollow microtopography. *Sphagnum* mosses (particularly *S. angustifolium*, *S. capillifolium* and *S. magellanicum*) and flowering shrubs (*Rhododendron groenlandicum*, *Vaccinium vitis-idaea*) dominated the low-lying species of Pauciflora Fen (Bocking, Cooper, & Price, 2017).

2.2.2 Low Elevation Site

The second site, herein referred to as *Poplar Fen* (56°56' N, 111°32' W), is a moderate-rich treed (pH = 6.6) fen approximately 25 km north of Fort McMurray and 70 km from Pauciflora Fen (Figure 2-1). Poplar Fen covers an area of 250 hectares and contains both sand and gravel uplands and discontinuous fen systems (Elmes, Thompson, Sherwood, & Price, 2018). Near-surface layers of Poplar Fen were comprised of fine-grained silty sand, with a maximum peat depth of 1.2-3.0 m (Elmes et al., 2018). From 1961 to 2019, annual T_a averaged 0.7°C, with daily T_{max} peaking in July (22.8°C); average annual P (rain and snowfall) was 440 mm, peaking in July at an average of 82 mm (Figure 2-2; Alberta Agriculture and Forestry, 2019). The annual average P totals for the region were lower and daily T_a were higher for Pauciflora Fen. *Picea mariana* and *Larix laricina* species dominated the fen landscape, however ground cover mosses including

Sphagnum, Pleurozium schreberi, Aulacomnium palustre, and Tomenthypnum nitens were also present (Elmes et al., 2018). Much of the tree population at Poplar Fen was eradicated by the 2016 Horse River fire (fire ID: MWF-009, area burnt ~590,000 ha) (Elmes et al., 2018; MNP LLP, 2017). However, some clusters of live, mature trees still remained in the southern region of the watershed after the fire.

2.3 Materials and Methods

2.3.1 Climate Data

Daily meteorological data was obtained through the Alberta Climate and Information Service (ACIS) for both Pauciflora and Poplar Fen during the period of interest (1961-2019) (Alberta Agriculture and Forestry, 2019). ACIS classifies land area by township and approximates regional weather data using interpolation and inverse distance weighting (IDW) methods. Daily T_{max} and minimum air temperature (T_{min}) values for both Pauciflora (township: T085R08W4) and Poplar Fen (township: T091R10W4) were estimated using a linear IDW procedure, with the 8 closest stations or a within a 200 km radius (Alberta Agriculture and Forestry, 2019). Daily P totals were estimated using a hybrid IDW approach and the closest 8 stations or within a 60 km radius. If there was no station within the given radii, the nearest neighbor was used (Alberta Agriculture and Forestry, 2019). For every year of the study period, February 29th was removed from analysis due to leap years and December 31st was removed due to missing regional climate data for that day.

Site-level meteorological data was installed in 2011, at Pauciflora Fen and Poplar Fen, to record meteorological variables at 30-minute intervals. T_a (°C) was measured at 1 and 6 m at Pauciflora and 1,3 and 6 m at Poplar (HOBO U23 Pro v2, Onset Computer

Corporation, Bourne, MA). P (mm) was measured nearby at both site towers using a tipping bucket rain gauge (HOBO U23 Pro v2, Onset Computer Corporation, Bourne, MA). Site-level T_a and P was compared to the historical IDW data collected from the Alberta Climate Information Service (ACIS) to verify an accurate representation of site conditions from 1961-2019 (Figure A-1).

2.3.2 Hydrology

A monitoring well, north of the Pauciflora Fen and Poplar Fen tree sampling area (Figure 2-3), measured fluctuations in water table depth (WTD; cm) in the growing seasons of 2011-2019. WTD measurements were collected using logging pressure transducers (Schlumberger Mini-Diver, Houston, Texas) at half-hour increments and averaged per day.

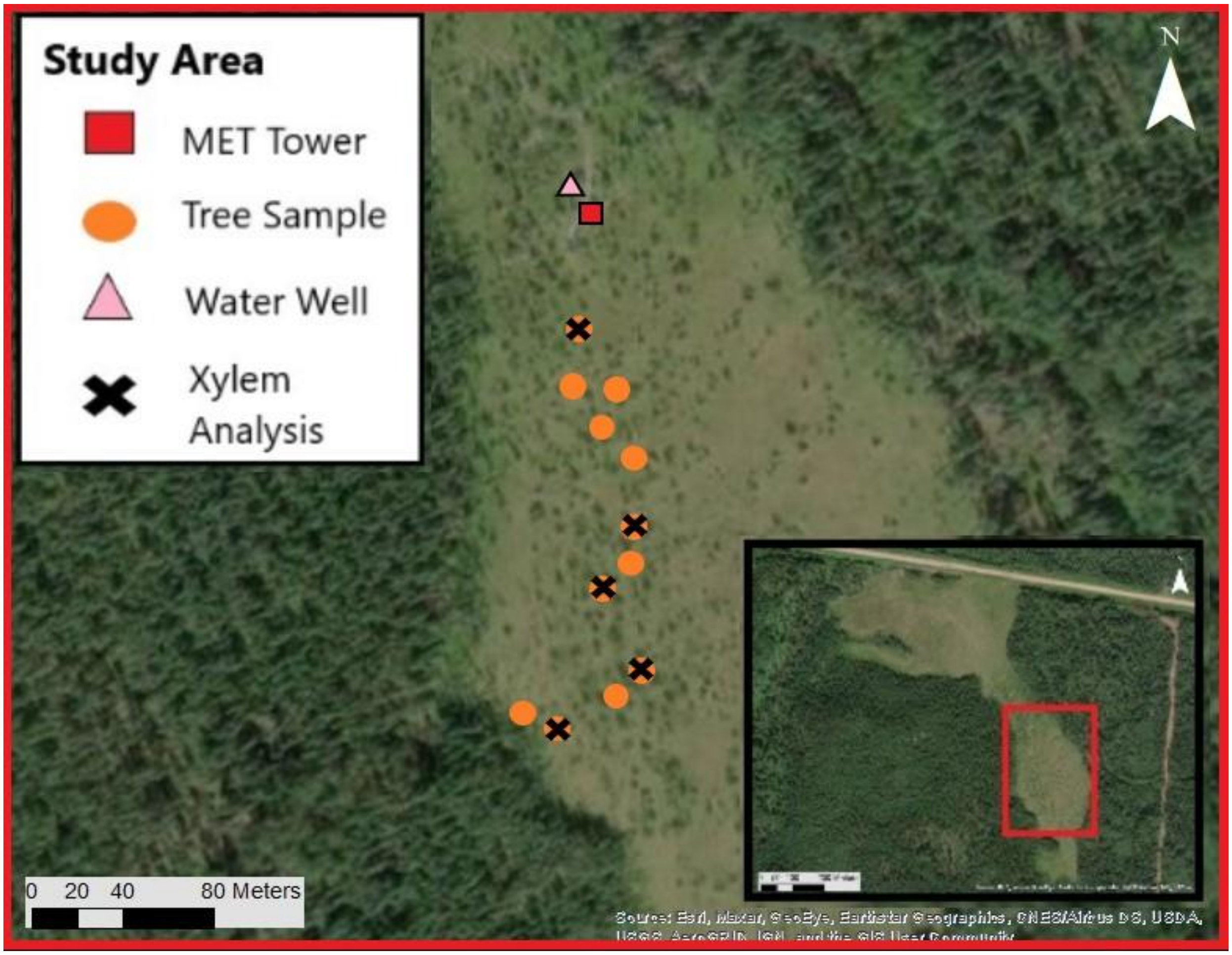
Growing season daily WTD measurements collected from Pauciflora Fen and Poplar Fen from 2011-2019 were sorted from highest to lowest value and ranked. An intensity-duration-frequency (IDF) curve value for each daily measurement was developed for both study sites using

$$IDF = \left(\frac{rank\ value}{n+1}\right) \text{ x } 100 \qquad [1]$$

where *rank value* is the rank (1 to n) the WTD daily measurement is assigned and *n + 1* is the lowest rank value plus 1. An IDF curve was produced for both study sites by plotting the sorted daily WTD measurements by rank against its corresponding IDF value.

2.3.3 Tree-ring Sample Collection

Black spruce tree cores and stem disks were collected from live, mature stands regarded as “undisturbed” in the growing season of 2019. All sampling points were at a minimum distance of 100 m from any human activity/disturbance (i.e. roads, seismic lines, mining and lumber sites) and 10 m from known fire devastation (Poplar Fen). Tree sampling areas at Pauciflora and Poplar Fen were measured at 0.42 and 7 hectares, respectively. Sampled trees were selected based on physical health, stature, and maturation. Trees in high-density areas (due to competition), as well as those with non-vertical growth and lichen-covered branches, were avoided when possible. At each sample tree, GPS coordinates, physical characteristics, height, and diameter at breast height (DBH) were recorded (Speer, 2010). At Pauciflora, stem disks were collected from 10 living trees within the open mid-fen area and 2 in the upland-fen transition zone (Figure 2-3).



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

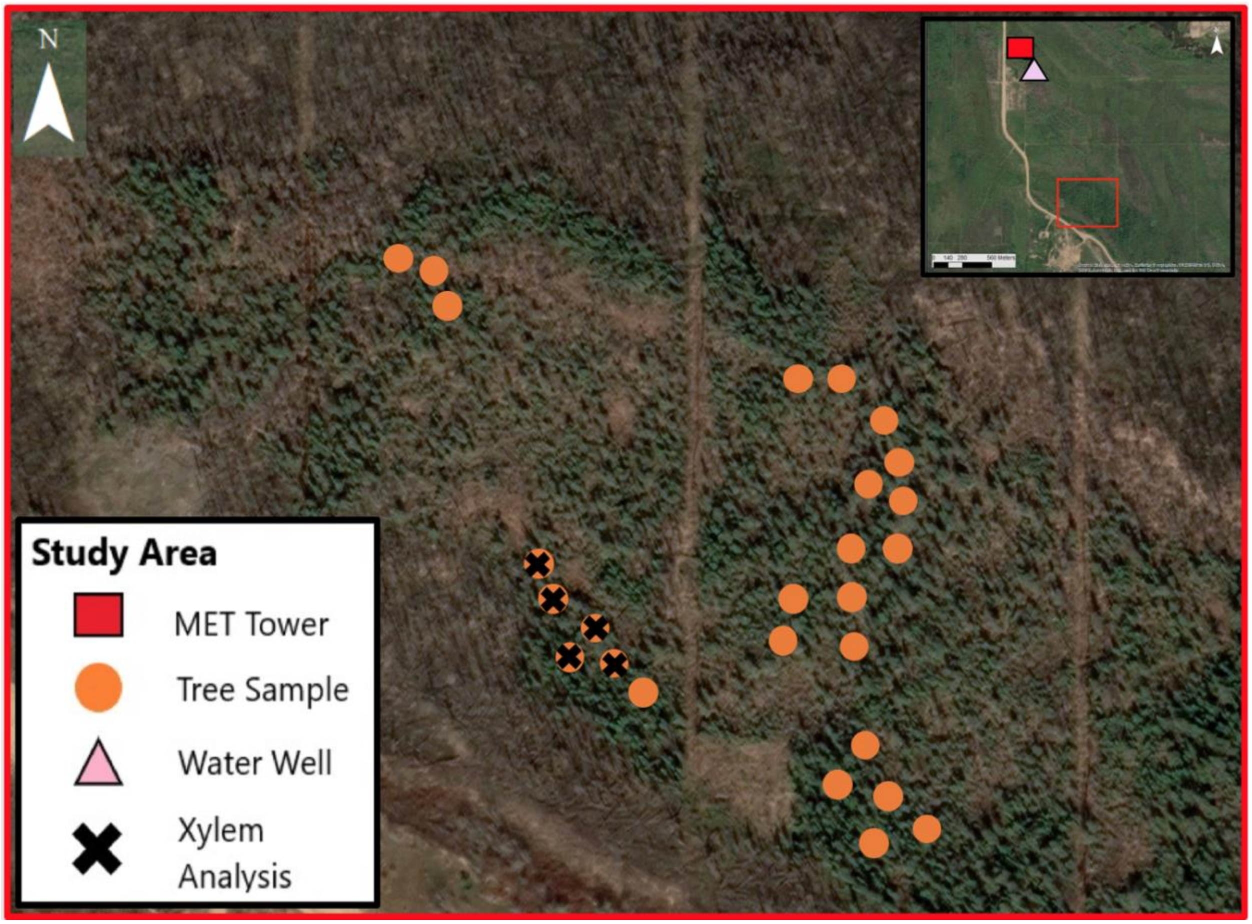


Figure 2-3. Site map of Pauciflora Fen (above; high elevation) and Poplar Fen (below; low elevation) study area and relevant sample points, Fort McMurray, Alberta, Canada.

All twelve trees at Pauciflora were cut down using a circular saw and radial cross-sections were collected at breast height (1.3 m). Stem disks, rather than tree cores, were collected at Pauciflora because all sample trees measured <10 cm DBH. Four sampled trees were immediately removed from analyses due to young age and/or rotting. 27 tree samples (16 cores, 4 stem disks) were collected at Poplar Fen using a 5.15 mm Haglöf increment borer (Haglöf, Långsele, Sweden) or circular saw. All samples were air dried in paper straws (cores) and boxes (stem disks) to prevent molding during transport back to the lab (Speer, 2010).

2.3.4 Master Chronology Development

Black spruce stem disks were sanded at progressively finer grits (P100, P220, and P320) using a belt sander and digitally scanned at 2400 dots per inch (dpi) using the Epson Perfection 4990 Photo scanner (Hillsboro, Oregon, USA). Core samples were hand-sanded using P400 grit, followed by P600 grit sand paper. All tree samples were dated manually using a stereo microscope and a dot notation system beginning at the most recent growth ring (2019) (Wilford, Cherubini, & Sakals, 2005). Ring width measurement files for all stem disks were constructed using the dendrochronology software, CooRecorder and CDendro (v9.4). CooRecorder enables automatic measurement of ring widths (to the nearest 0.001 mm) within a scanned image. The CDendro program groups CooRecorder output ring width measurement files into a collection for cross-dating purposes. Ring widths of tree core samples were measured using the Velmex (New York, USA) and Measure J2X systems to the nearest 0.001 mm. One master chronology was created for Pauciflora and one for Poplar Fen. A previously established site chronology for Pauciflora (Bocking et al., 2017) and 13 tree cores sampled at Poplar Fen in 2020 (Elmes, unpublished) were cross-dated with 2019 samples, as a robust site chronology typically consists of 40 samples (Speer, 2010). The dendrochronology statistical program, COFECHA, was used to evaluate the robustness of intra-site cross-dating for each master chronology (Holmes, 1983; Speer, 2010). COFECHA is a quality control software that computes series inter-correlation values (Equation 2) which identify the recorded stand-level signal of a site (Speer, 2010). A series inter-correlation value is the correlation of one tree record against the master chronology (Speer, 2010) and is measured using

$$r_{xy} = \frac{\sum_{t=1}^{t=n}(x_t - m_x)(y_t - m_y)}{(n-1)S_x S_y} \qquad [2]$$

where x_t is the core's index value at year *t*, y_t is the master chronology index value at year *t*, m_x is the mean index value for the core, m_y is the mean index value for the master chronology, *n* is the number of years of interest, S_x is the standard deviation for the core, and S_y is the standard deviation for the master. Series inter-correlation values fall between 0 and 1 however, a value of >0.4 is ideal. Each measured tree series was standardized using the R package dplR (Bunn, 2008), to remove age-related growth influence, and subsequently combined using a robust bi-weight mean to create a standardized ring-width index (RWI) chronology. Chronologies were standardized by dividing annual ring width values by a best-fit negative exponential or linear regression function. This technique preserves low-frequency climate signals present in a tree ring series. A residual master chronology was created for both study sites using the R package dplR (Bunn, 2008) to observe inter-annual fluctuations in ring width throughout the period of interest, as a result of high-frequency climatic influence. Pacific Decadal Oscillation (PDO) values were collected from Japanese Meteorological Agency (2020) to assess the influence of large-scale atmospheric patterns on local hydroclimates and thus, black sprue tree growth. Pearson correlation coefficients were calculated for standardized RWI and annual PDO values.

2.3.5 Quantitative Wood Anatomy Analysis

Five intact tree samples were selected from each site master chronology for anatomical analysis based on age and absence of physical defects (Castagneri et al., 2017).

Standard tree anatomical protocols were followed in preparation of cores for anatomical analysis (Castagneri et al., 2017; von Arx et al., 2016). Stem disks were cut into ~2.5 cm wide sections from bark to pith and cut again into 4-5 cm long cross-sections for transverse cutting (12 μm thick) with the rotary microtome (Leica, Heidelberg, Germany) using Feather N35 blades (Feather Safety Razor Co., Ltd, Osaka, Japan) (Castagneri et al., 2018). Transverse sections were stained with safranin (1% in distilled water) and Astrablue (0.5%), rinsed in ethanol (70, 95, and 100% concentration), and fixed on a microscope slide using Eukitt (BiOptica, Milan, Italy). Slides were dried in the oven for 48 hours at 60^{o}C and scanned at 100x magnification using the Zeiss Axio Scan.Z1 (Zeiss, Oberkochen, Germany). The scanned images were processed using the Zen software and subsequently, in ROXAS (v3.1) (von Arx & Carrer, 2014). ROXAS is an image analysis software that measures a number of anatomical parameters (i.e. cell wall thickness, cell area, lumen diameter, number of cells) of tracheids in a ring. ROXAS also detects annual ring boundaries and measures ring width. ROXAS ring width measurement output files and manual ring width measurements, produced by Velmex and CooRecorder, were cross-dated to match ROXAS images with a calendar year. ROXAS image output files are grouped per tree record and compiled using the R package plyr (Wickham, 2011) including the removal of problematic rings that exhibited non-climate related anomalies. Additionally, to understand climatic influence on xylem anatomy at an intra-annual scale, earlywood (EW) and latewood (LW) cells were separated based on the ratio between cell lumen diameter and cell wall thickness (Mork's index; Denne 1989). Thin EW cells compose the early part of the ring, and have developed within the early growing season (May to early July). Thick LW cells, in the last part of the ring, are formed towards the end of the growing season (late July to end of September). Tree anatomical traits demonstrate long-term trends (Carrer, von Arx, Castagneri, & Petit, 2015; Castagneri et al., 2017), therefore, a cubic spline with 50% frequency cut-off of 32 years was fitted to each parameter series (Cook & Kairiukstis, 1990). EW and LW standard chronologies for each xylem anatomical parameter were built using the robust mean from the detrended series, with the R package dplR (Bunn, 2008; Castagneri et al., 2017). These anatomical traits included cell wall thickness (CWTALL50), number of cells per section (NUM), cell area (CA90), cell radial diameter (DRAD50), and lumen diameter (LD90). Wood anatomical analysis was limited by available meteorological data to 1961-2019.

2.3.6 Climate-anatomy Relationships

The role climate conditions play in the radial growth and xylem anatomical characteristics was examined using Pearson correlation analysis at an intra-annual timescale. Pearson correlations were calculated for earlywood and latewood chronologies of all anatomical traits (i.e. CWTALL50, NUM, CA90, DRAD50, and LD90) and daily P, T_{max}, and T_{min} over 30-day time-windows (centered to the end of the window), moving with a 1-day step. Pearson correlations were calculated for 10, 14, 20, 30, and 40-day moving windows however, the 30-day window provided a more robust result and will be the focus for this paper. Correlations were established for the previous year's June through to the current year's December for the period of 1961-2019 (Pauciflora Fen) and 1961-2016 (Poplar Fen), because of the known impact previous year's environmental conditions have on current year's growth (Vaganov et al., 2009). Red and yellow correlations (Figure 2-8) signified strong and moderately positive correlations ($p < 0.05$), respectively, and dark blue and light blue represented strong and moderately negative correlations ($p < 0.05$), respectively. Positive correlations demonstrate an increase in a climatic variable (i.e. temperature) caused a proportional response in black spruce anatomical traits. Negative correlations imply an increase in a climatic variable caused a proportional opposite response in black spruce anatomical traits. Theoretically, the stronger and more persistent a correlation, the more likely the anatomical trait was influenced by the given climatic variable. The greater the number and intensity of correlations present for black spruce of a study area, the greater the likelihood that the climatic variable holds influence over anatomical traits of that particular hydroclimate. Short and weak correlations are considered noise and are therefore, not considered further.

2.4 Results

2.4.1 Historical Climatic Conditions

During the period of interest (1961-2019), annual average T_a at Pauciflora Fen was 0.4°C and 0.7°C at Poplar Fen. Annual average T_a peaked in July for Pauciflora Fen (21.6°C) and Poplar Fen (22.8°C). Both study sites demonstrated increasing trends in average annual T_a (Figure 2-4). Annual average P, falling as snow in winter time, was 448 mm and 586 mm for Poplar Fen and Pauciflora Fen, respectively (1961-2019). Average monthly P peaked in July for both Pauciflora Fen (112 mm) and Poplar Fen (82 mm). Pauciflora Fen showed a slight increasing trend in annual average P (slope = 0.79), unlike the decline observed at Poplar Fen (slope = -2.99) over the study period (Figure 2-4).

Daily T_a and monthly P values collected at both study sites, from 2011-2019, were consistent with historical datasets of regional climate data collected from the ACIS (Figure A-1; Alberta Agriculture and Forestry, 2019). Site- and regional-scale daily T_a at Pauciflora

Fen and Poplar Fen had R^2 values of 0.81 and 0.92, respectively, while monthly P totals exhibited R^2 values of 0.79 (Pauciflora Fen) and 0.87 (Poplar Fen).

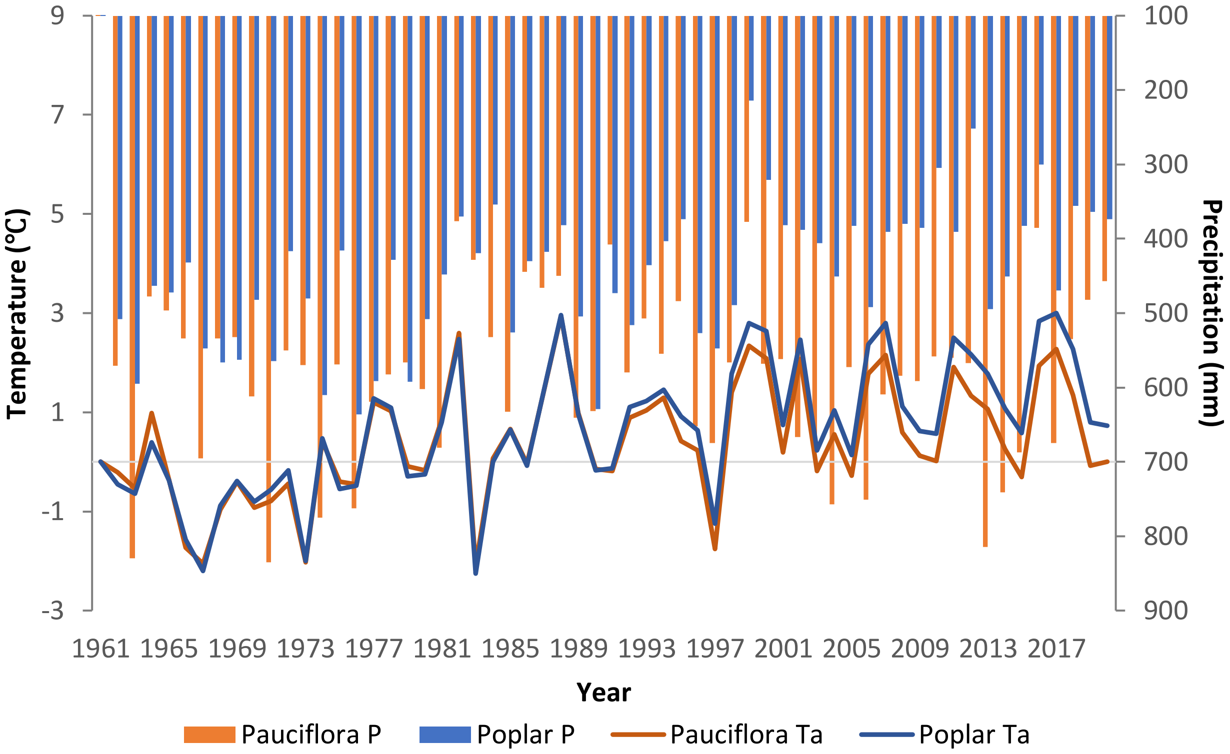


Figure 2-4. Average annual precipitation and air temperature for Pauciflora Fen and Poplar Fen, Fort McMurray, Alberta, Canada (1961–2019; Alberta Agriculture and Forestry, 2019).

2.4.2 Water table levels over the growing season

The hydrogeological setting of Poplar Fen allowed for a wider range in WTD between 2011-2019 compared to Pauciflora Fen (Figure 2-5), where WTD was more stable. However, the average WTD of each site is comparable with a difference of approximately 10 cm.

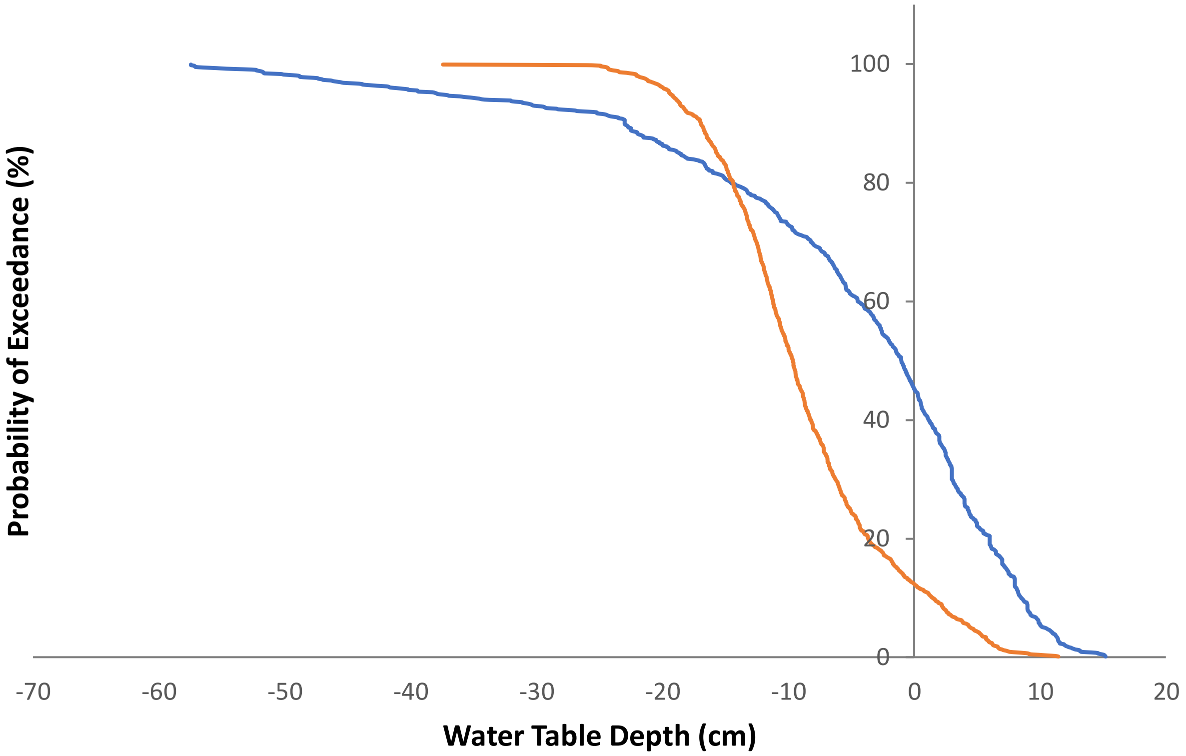


Figure 2-5. Probability of exceedance (y) for WTD (cm) (x) at Pauciflora Fen (orange) and Poplar Fen (blue) from 2011-2019, Fort McMurray, Alberta, Canada.
Note: notch in Poplar Fen curve (~23 cm) is attributed to a well-top shift in the field.

2.4.3 Inter-site comparison of black spruce characteristics

Samples collected for tree xylem anatomical analysis from Poplar Fen had above average DBH, tree height, ring width, and number of rings per series compared to samples used for the master chronology (Table 2-1). In contrast, the five samples selected for xylem analysis at Pauciflora were lower than the master chronology average for all aforementioned characteristics, with the exception of DBH (Table 2-1). Black spruce at Pauciflora were older on average, yet exhibited smaller ring widths than those at Poplar Fen.

Table 2-1. Tree samples collected for site master chronology (Master) and quantitative wood anatomy analysis (QWA), Pauciflora Fen and Poplar Fen, Fort McMurray, Alberta, Canada.

Site	No. of samples	Period (years)	DBH (cm)	Height (m)	Ring width (mm)	No. of rings
Pauciflora (Master)	40	1804-2019	7.67 ±1.77	7.01 ±3.33	0.61 ±0.40	79 ±34
Poplar (Master)	40	1926-2016	10.35 ±2.73	13.5 ±2.79	0.77 ±0.43	61 ±22
Pauciflora (QWA)	5	1946-2019	6.74 ±2.36	7.69 ±1.03	0.53 ±0.27	55 ±15
Poplar (QWA)	5	1930-2016	11.19 ±0.87	14.02 ±4.42	0.78 ±0.48	65 ±20

Values demonstrate the mean ± standard deviation of sampled trees at both Pauciflora and Poplar Fens.
DBH, Height values: n = 12 (Pauciflora), n = 27 (Poplar)
Note: 28 Pauciflora and 13 Poplar tree samples of the master chronology were sourced from Bocking (2015) and Elmes (unpublished), respectively.

2.4.4 Tree-ring width and anatomical features of varying hydroclimates

The black spruce ring width of both study sites were relatively sensitive and deviated from both standardized and residual RWI throughout the study period. Standardized RWI showed greater inter-annual variability for both sites, relative to residual RWI. Inter-site RWI Pearson correlation coefficient was moderate (r = 0.34) in the study period (1961-2019), with black spruce at Poplar Fen rarely aligning with that of Pauciflora Fen.

While in the negative phase of the PDO, from 1961-1976, Poplar Fen standardized RWI exhibited a moderately negative correlation coefficient (r = 0.22) with annual PDO values (Figure 2-6). Pauciflora Fen RWI showed a positive, but negligible, relationship with annual PDO values from 1961-1976 (r = 0.09). Interestingly, in the positive PDO phase (1977-1999) Poplar Fen (r = -0.16) and Pauciflora Fen (r = 0.25) RWI demonstrated low negative and positive relationships with annual PDO values, respectively. Poplar Fen RWI exhibited a low correlation (r = 0.24) with the annual PDO in the most recent period (2000-2019) whereas, at Pauciflora Fen, the standardized RWI-PDO relationship was moderately negative (r = -0.42). Overall, black spruce RWI at Poplar Fen had a low, negative correlation with annual PDO (r = -0.23) and black spruce RWI at Pauciflora Fen had a negligible correlation (r = -0.01). It should be noted that PDO-RWI correlations were calculated for relatively short timeframes thus, correlations may be disproportionately high.

Cell lumina is considered the opening or inside space of a tubular structure and in black spruce xylem, the size of the lumina determines the transport of water, nutrients, and hormones through the tree. The cell walls of black spruce xylem are structural layers surrounding the cell lumina that provide support and stability to the tree. Poplar Fen black spruce showed larger cell lumina but comparable cell wall thickness to black spruce at Pauciflora Fen (Figure 2-7) throughout the period of interest. The number of cells, or xylem, present in black spruce annual growth is directly relevant for water transport to the tree apex and thus, tree productivity (Couvreur et al., 2018). The annual number of cells of black spruce at Poplar Fen were generally higher since the 1980s, relative to Pauciflora Fen. However, it is important to consider that these disparities may exist between sites not because of environmental conditions but rather black spruce height.

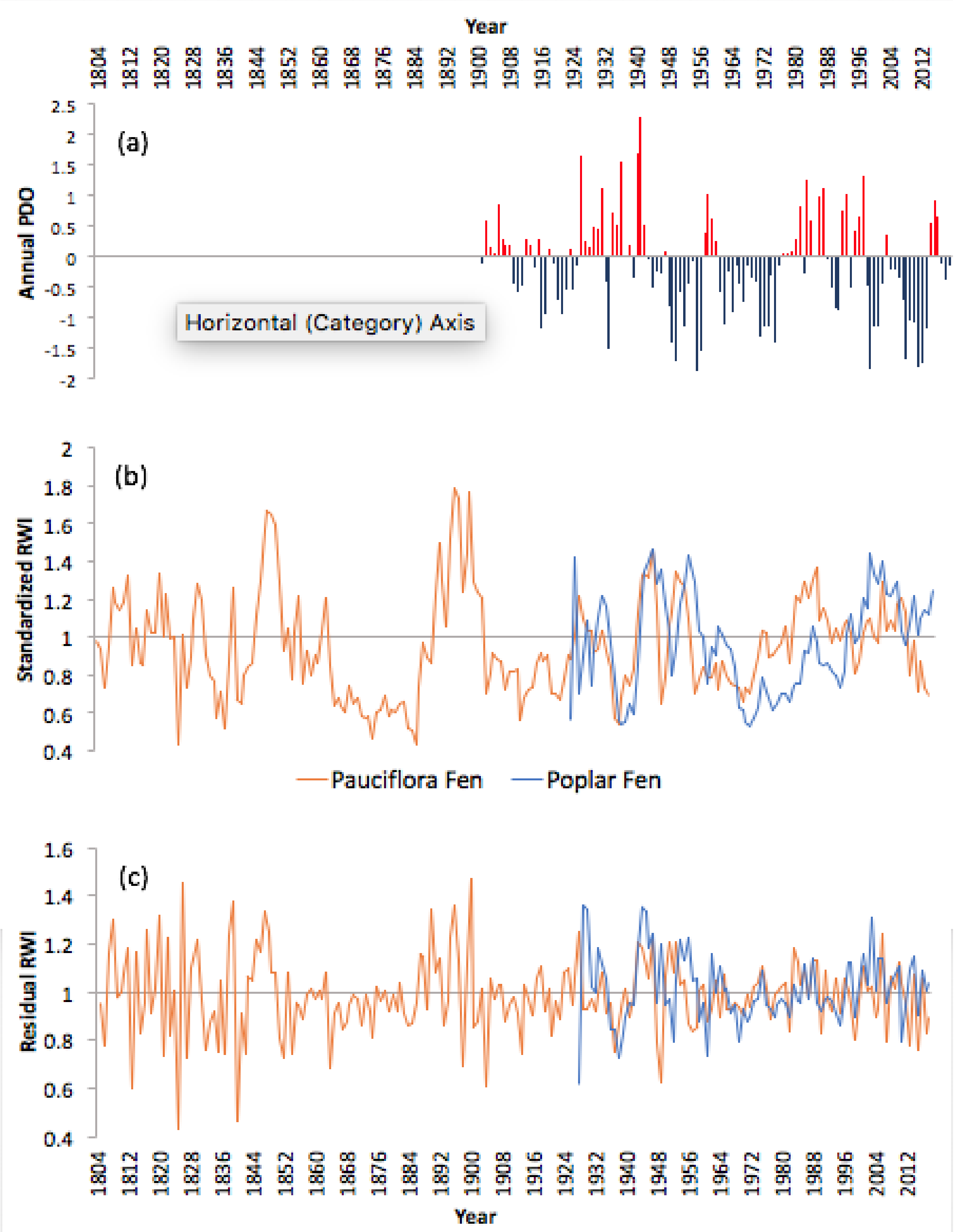


Figure 2-6. (a) Annual Pacific Decadal Oscillation values (1901-2019; Japanese Meteorological Agency, 2020) expressing warm (red) and cool (blue) phases; (b) standardized and (c) residual ring width indices (RWI) of both Pauciflora Fen (1804-2019) and Poplar Fen (1926-2019), Fort McMurray, Alberta, Canada.

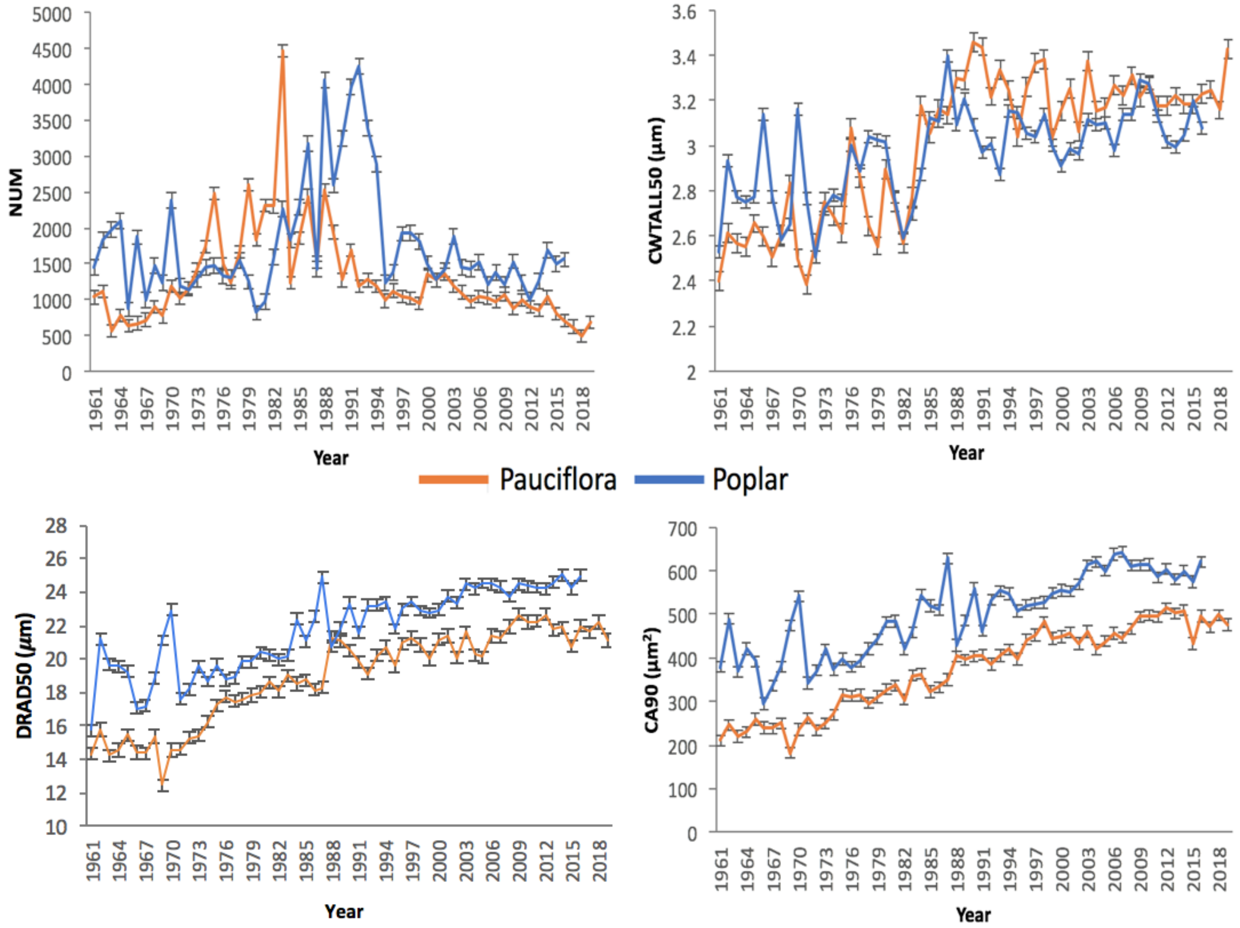


Figure 2-7. Anatomical feature comparisons of (a) cell number (NUM), (b) cell wall thickness (CWTALL50), radial diameter (DRAD50), and (d) cell area (CA90) measurements of Pauciflora Fen and Poplar Fen earlywood cells, Fort McMurray, Alberta, Canada (1961-2019).
Note: Poplar Fen tree series spans 1961-2016 only.

2.4.5 Anatomical features, ring width and climate relationships

The number of cells (NUM), cell area (CA90), radial diameter (DRAD50), and lumen diameter (LD90) chronologies of the EW cells at Pauciflora Fen were negatively correlated to T_{max} in the previous year's July and positively correlated to the previous year's October (Figure 2-8a). The NUM and DRAD50 chronologies of the LW cells were negatively correlated to T_{max} in the previous year's August. At Poplar Fen, CA90 and LD90 of EW cells were negatively correlated to T_{max} in previous year's September and

DRAD50 of EW cells negatively correlated with T_{max} in previous year’s June, July and September, as well as current year’s April and May (Figure 2-8a). CWTALL50 EW cells demonstrated a correlation with T_{max} in the previous year’s December and current year’s January and March, at Pauciflora. Few weak correlations were observed between CWTALL50 and both T_{max} and T_{min} at Poplar Fen.

T_{min} had fewer and weaker correlations with the anatomical features of both Pauciflora Fen and Poplar Fen trees (Figure 2-8b). However, there was a strong positive correlation between CWTALL50 and T_{min} in the EW cells of Pauciflora trees in the current year’s March and beginning of April. EW cell correlations, for features related to cell size (i.e. CA90, DRAD50, and LD90), found in the current year’s July and following months were not considered as EW cells grow primarily in early to late spring (May and June).

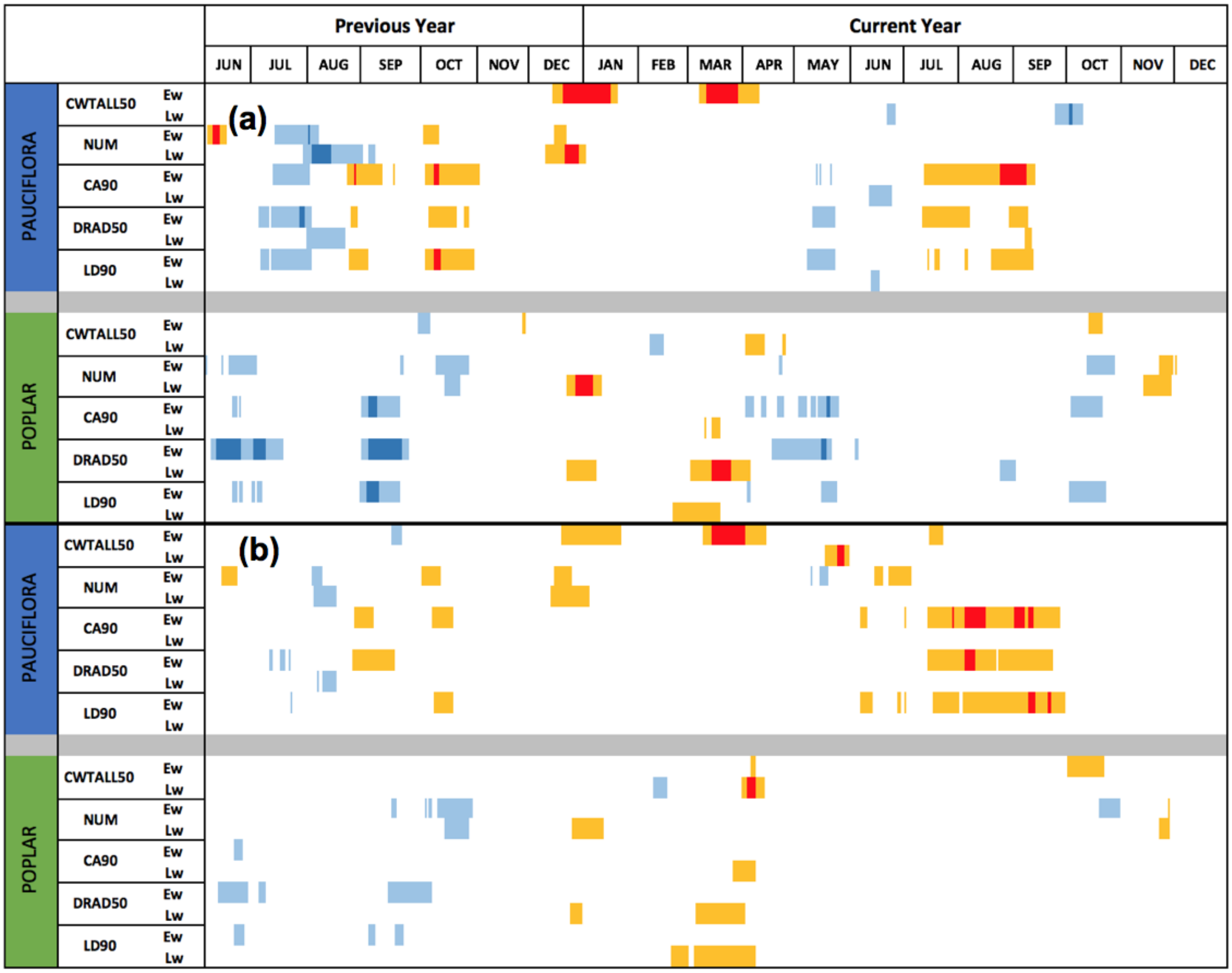


Figure 2-8. Site-specific correlations of cell wall thickness (CWTALL50), number of cells (NUM), cell area (CA90), cell radial diameter (DRAD50), and cell lumen diameter (LD90) and average maximum temperature (a) and minimum temperature (b), at Pauciflora Fen and Poplar Fen, Fort McMurray, Alberta, Canada. Climate data were organized in 30-day windows, centered to the end of the window, moving with a 1-day step from the previous year's June to the current year's December (1961 – 2019). Bar colours are related to the partial correlation coefficient ($p < 0.05$) and bar length is related to the period of significant correlation. Key: Positive correlation (yellow), strong positive correlation (red); negative correlation (light blue), strong negative correlation (dark blue).

The anatomical features of Pauciflora trees demonstrated few, weak correlations to daily P values (Figure 2-9) compared to Poplar Fen. The CWTALL50 of EW and LW cells in Poplar Fen trees were positively correlated to P for the current year's (mid) January, February, and beginning of March. Both the NUM and DRAD50 of EW cells at Poplar Fen were positively correlated to P in the current year's April and May. The CA90 and LD90 of LW cells at Poplar Fen were negatively correlated to current year's early (May, June) and late (September) growing season.

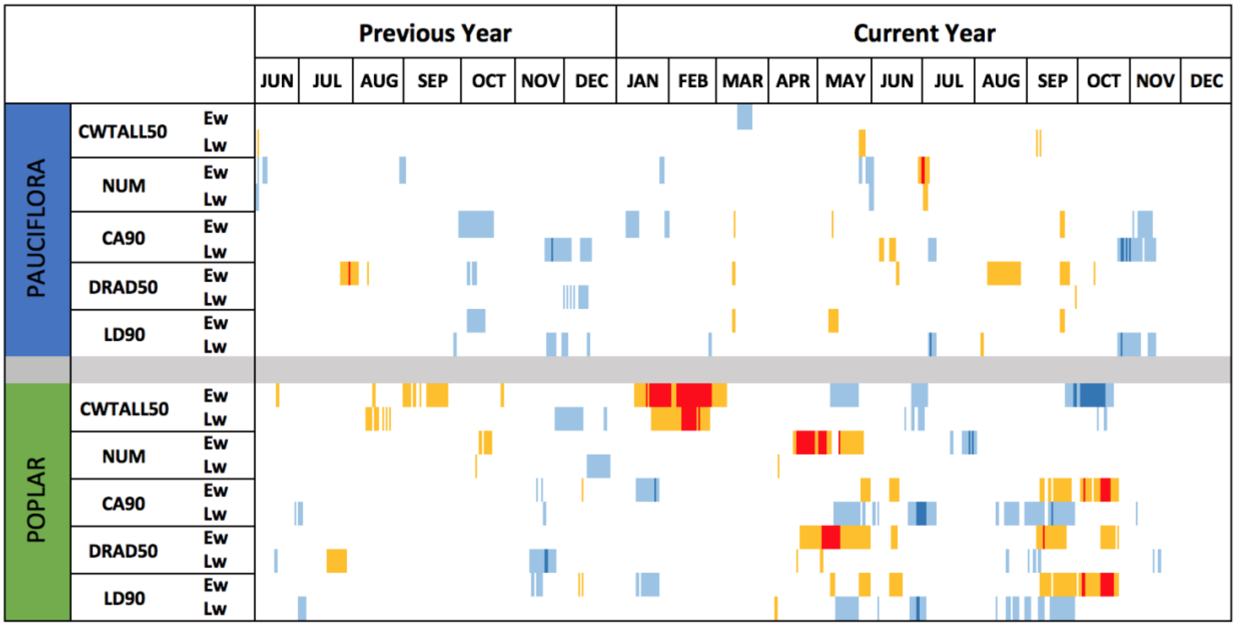


Figure 2-9. Site-specific correlations between CWTALL50, NUM, CA90, DRAD50, and LD90 earlywood (Ew) and latewood (Lw) cells and precipitation at Pauciflora and Poplar Fens, Fort McMurray, Alberta, Canada. Correlations are for the period of 1961 – 2019 at Pauciflora Fen and 1961-2016 at Poplar Fen, inclusive. Climate data were organized in 30-day windows, centered to the end of the window, moving with a 1-day step from the previous year's June to the current year's December. Bar colours are related to the partial correlation coefficient ($p < 0.05$) and bar length is related to the duration of significant correlation. Key: Positive correlation (yellow), strong positive correlation (red); negative correlation (light blue), strong negative correlation (dark blue).

2.5 Discussion

2.5.1 The influence of large-scale atmospheric patterns on tree growth

The PDO is a phenomenon that originates from changes in sea surface temperature of the northeast and tropical Pacific Ocean. The cause of these changes remains largely disputed. Fluctuations in the PDO are categorized into "cool" and "warm" phases based on ocean surface topography data and typically oscillate every 20-30 years. A shift in sea surface temperature ultimately impacts the hydroclimate of terrestrial landscapes, such as northwestern Canada, via the jet stream. The low frequency, positive phases of the

PDO and high frequency El Niño-Southern Oscillation (ENSO) cycles have brought drier summers and thus, controlled annual growth rates in northwestern Canada (Pisaric, St-Onge, & Kokelj, 2009). Tree-ring width has been previously linked to high and low frequency large-scale atmospheric patterns in Asia (Wang et al., 2019; Zhou, Fang, Zhang, & Dong, 2020), Mexico (Cleaveland et al., 2003; Pompa-García, & Jurado, 2014), United States of America (Gedalof, Peterson, & Mantua, 2004; Starheim, Smith, & Prowse, 2013), and Canada (Dinis et al., 2019; Hart et al., 2010). Ultimately, these results suggest that the PDO could have played a role in black spruce annual ring growth in the AOSR (Figure 2-6), specifically in time periods where high correlation coefficients were observed. But the observation of multi-decadal hydroclimatic patterns was limited by the temporal scale of this project. The future of large-scale, low frequency oscillations, such as the PDO, in a changing climate is also largely unknown. Determining the impact of large-scale atmospheric cycles on dominant northern plant species, such as black spruce, could be crucial for understanding ecosystem function in a changing climate. Tree species often require specific environmental conditions in order to be productive. If the intensity and patterns of the PDO change with climate warming, it is likely that regional hydroclimates of terrestrial landscapes will respond accordingly. A shift in environmental conditions (i.e. T_a, P) could affect vital water and carbon cycling for a number of plant species. Therefore, understanding the future behaviour of large atmospheric patterns is crucial for ecosystem conservation.

2.5.2 Hydroclimatic controls on xylem anatomy features

Cell lumen size (CA90, LD90) of Poplar Fen black spruce were consistently larger than that of black spruce at Pauciflora Fen (Figure 2-7). For the majority of the study period, NUM of Poplar Fen black spruce exceeded that of black spruce at Pauciflora Fen but CWTALL50 of both study areas were comparable. The cell wall thickness of *Pinus sylvestris L.* (Scots Pine) in a Southern Alpine peat bog were smaller than that of mineral soil pine, perhaps due to reduced carbon accumulation during moisture deficits and inundated conditions (Dinella et al., 2021). The contrast between Poplar and Pauciflora Fen cell size was likely the result of the difference in tree height (Figure 2-7; Soriano et al., 2020) and should be considered in future analyses. Cell lumen size of vascular plants, increases from apex to base to maintain a constant hydraulic conductance and prevent cavitation (Lechthaler et al., 2019; Soriano et al., 2020). That is, taller trees have larger conduits at the stem base (longer distance from the apex) compared to shorter trees. Interestingly, despite the relatively larger mean cell area at Poplar Fen, both study areas demonstrated comparable cell wall thickness, suggesting Poplar Fen trees may be less resistant to cavitation (Rosner et al., 2018) and thus, more vulnerable to tree mortality relative to the cooler and wetter climate of Pauciflora Fen. Although, several cell traits are known to influence resistance to cavitation (Venturas, Sperry, & Hacke, 2017).

The localized flow system of Poplar Fen, generated in the surrounding uplands, often flows vertically from the underlying outwash aquifer. Interestingly, Poplar fen can be subject to flow reversals unlike Pauciflora Fen, a recharge zone, where flow is predominantly downward. Flow reversals and the high hydrological connectivity present at Poplar Fen (Elmes et al., 2019) demonstrates a level of resilience to dry periods compared to Pauciflora Fen. Greater sensitivity to the growing season hydroclimate was observed for both sites. This result was recorded in Danella et al. (2021) with peatland Scots pine and was attributed to the limiting hydrogeological regimes.

2.5.3 Impacts of temperature on tree growth

T_a was a greater influence on black spruce xylem formation at Pauciflora Fen compared to that of Poplar Fen (Figure 2-8), confirming this study's initial hypothesis. This result is similar to the *Picea abies* in the Italian Alps (Castagneri et al., 2015). Cell production (main determinant of ring width; Dufour & Morin, 2013), as well as cell enlargement, was limited by high T_{max} in the previous year's summer (Figure 2-8), but positively correlated in previous year's fall at Pauciflora Fen. The influence of the previous year's summer T_a on cell number has been observed in other peatland sites (Danella et al., 2021). Cell enlargement at Poplar Fen was limited by high T_{max} in the previous year's mid- to late-growing season. This contradicts the initial hypothesis of high spring and summer T_a positively impacting cell number at the low elevation site but upholds the hypothesis suggesting high summer temperatures negatively impact cell size. Although, the negative relationship between cell size and summer temperature was observed at both sites. Negative effects of previous year's summer T_a on radial growth (tree-ring width) were observed in previous studies on black spruce in Canada (Hofgaard, Tardif, & Bergeron, 1999), but have not been documented for xylem anatomical traits. It is suggested that high summer temperatures in the previous growth year do not allow for sufficient water storage for the following growth year and thus, hinder cell expansion. Warmer winter temperatures had a positive effect on cell wall thickness of EW cells at Pauciflora Fen, but not at Poplar Fen. Therefore, warming at northern latitudes and higher altitudes should increase cell wall thickness. Indeed, cell size was negatively affected by previous year's summer temperature, but positively by current summer temperature. Given the cooler annual temperature of Pauciflora Fen (Figure 2-2), it is likely that higher summer temperatures of the current growth year allow for high productivity rates. The observed positive relationship between EW cell size and current year's summer T_{max} and T_{min} at Pauciflora Fen (Figure 2-8) was in contrast to the largely negative relationship found in eastern Quebec black spruce (Puchi et al., 2020). The hydrological regimes of Pauciflora and Poplar Fens (Figure 2-5) could be a key factor in these observed differences. These conflicting results further illustrate the key role local environmental conditions play in tree growth and the importance of site-specific research.

2.5.4 Impacts of precipitation on tree growth

Black spruce anatomical features were more affected by P at Poplar Fen compared to Pauciflora Fen (Figure 2-9), confirming this study's hypothesis. These results are consistent with relationships reported on *Picea abies* by Castagneri et al. (2015). However, the complex groundwater and surface water interactions at Poplar Fen, due to a localized groundwater connection (Elmes & Price., 2019), likely has a strong influence on tree growth, as vertical flow reversals are detected during periods of below average P. Lower water tables limit black spruce growth and increase drought sensitivity (Walker & Johnstone, 2015). Seasonal water deficits were shown to counteract the benefits of the lengthening of growing seasons in northern ecosystems (Buermann et al., 2018), but the moisture content of northern peatland fen systems may help mitigate ecosystem degradation due to drought (Kettridge & Waddington, 2013). In particular, EW cell number and size were positively affected by high P in spring and summer, as observed in black spruce in Quebec forests (Puchi et al., 2020), confirming the dependency of EW cell enlargement on water availability in boreal forests (Belokopytova et al., 2020). LW cell size showed the opposite relationship with radial growth and number of cells positively correlated to spring and early summer daily P at Poplar Fen (Figure 2-9), highlighting the importance of water availability for LW cell production. This outcome was expected given moisture deficits are commonly observed in the Spring time of the AOSR. In contrast, the lack of a relationship between cell size and P identified a difference in water constraint effects on cell production (NUM) and cell enlargement (CA). This disparity was also reported in Castagneri et al. (2015). The low and scattered relationships between P and anatomical parameters of black spruce at Pauciflora Fen (Figure 2-9) were likely related to the consistently higher soil water availability compared to Poplar Fen, suggesting that P variability scarcely affected black spruce anatomical features at this site.

2.6 Conclusions

Incorporating two study areas into this research facilitated exploration of historical black spruce xylem response to varying external conditions. Determining past environmental controls on black spruce growth allowed for inferences regarding xylem and ecohydrological responses to future warming. This study demonstrated that xylem cell production is governed primarily by T_a in cooler, wetter conditions and P in warmer, drier conditions of the same geographical region. In both hydroclimates, increased summer T_a of previous years seemed to inhibit xylem production and enlargement, whereas an extended previous growing season, as a result of higher fall T_a, likely enhanced growth, specifically at Pauciflora Fen. Seasonal water deficits may counteract the benefits of the lengthening of growing seasons in northern ecosystems, but the moisture content of northern peatland fen systems may help mitigate ecosystem degradation due to drought. Enhanced previous summer T_a at both study sites could reduce lumen size, impede water transport to the tree apex (Castagneri et al., 2015; Hentschel et al., 2014; Heres et al., 2014), and thus, diminish black spruce productivity. The potential loss of peatland black spruce stands and the indirect loss of water storage due to consistently high summer temperatures could result in a vegetation shift toward more dry-tolerant species (i.e. trembling aspen). However, higher winter T_a at high altitudes and greater winter P at lower altitudes could increase wood density and thus, mitigate potential for cavitation and/or tree mortality in reoccurring drought conditions. With the expected future increase in both frequency and magnitude of drought events in the boreal region, reduced Spring P may hinder cell production and cell enlargement of black spruce of warmer, drier hydroclimates. The role large-scale atmospheric patterns play in continental hydroclimates and tree-ring growth has been previously defined however, the future of this relationship under global warming scenarios remains uncertain. This study demonstrated a potential, but variable, link between boreal black spruce ring width and the PDO and should be further explored across differing hydroclimatic zones. This study speculates that black spruce xylem response under a warming climate through the examination of past limiting factors for black spruce anatomical feature variability. Ultimately, results demonstrate the complexity of black spruce anatomical features and thus, further investigation is needed.

Chapter 3: Manuscript 2: The impact of road disturbance on xylem anatomy traits of *Picea mariana* in a boreal treed swamp, northeastern Alberta, Canada

Abstract

In the Athabasca Oil Sands Region (AOSR), wetlands dominate 55500 km^2 (54%) of the natural boreal landscape. Peat-forming AOSR wetlands (peatlands) of the AOSR are heavily disturbed due to intensive oil and gas activity. These disturbances have amplified habitat fragmentation and shifts in regional peatland regimes. Roughly 80% of boreal anthropogenic disturbances in northeastern Alberta are attributed to linear disturbances, (i.e. unpaved roads). Despite this, the influence of these disturbances on the growth and resilience of peatland conifer tree species remains unclear. Past findings based on [annual] tree-ring width analysis suggests unpaved roads bear certain hydrological and ecological implications for underlying peatland ecosystems. Ongoing studies at a cell anatomical level will further help determine intra-seasonal conifer tree responses to hydrological disturbance, within the context of baseline climatic variability. Quantitative wood anatomy, the study of xylem anatomical traits, can for example identify which external variables affected intra-ring growth. To this end, we correlate long-term, intra-annual level wood anatomical parameters (i.e. cell size, cell wall thickness, number of cells) of 20 *Picea* mariana (black spruce) across four subgroups in a disturbed treed swamp peatland (320 m a.s.l) with daily temperature and precipitation prior to (1961 - 1978) and following road construction (1980 - 2019). Water table depth was measured throughout the growing season of 2019 on opposing sides (east and west) of the road while fugitive dust load was measured at varying distances away from the unpaved road

to infer its influence on black spruce development. There was no evident shift in climatic influence on tree anatomy for any of the four sample subgroups following road disturbance. Although site-level ring width indices indicate a potential influence of large-scale atmospheric patterns on regional hydroclimatic variability throughout the period of interest and should be explored further. Water table depth on opposing sides of the road showed similar temporal trends, suggesting minimal impediment of groundwater flow despite disturbance. Fugitive dust load was highest 2 m west of the road (4.01 $gm^{-2}day^{-1}$) and exhibited an exponential decline away from the road. Interestingly, cell size and cell wall thickness of the trees in subgroups west of the road increased ($p < 0.05$) following road construction indicating a potential shift in water availability rather than fertilization via dust deposition. Nevertheless, intense human activity surrounding the treed swamp at the time of road construction prevents a definitive conclusion. Future research in the AOSR might consider disturbed peatland systems with long-term instrumental and land-use change records.

3.1 Introduction

The Athabasca Oil Sands Region (AOSR) occupies over 93000 km^2 of the Western Boreal Plains (WBP) in northern Alberta (ABMI, 2017). Approximately 54% of the AOSR landscape is classified as wetlands (Alberta Environment and Parks, 2018), despite its sub-humid climate where precipitation (P) is often less than potential evapotranspiration (PET). These boreal wetland landscapes (i.e. fens, bogs, swamps, marshlands) differ significantly due to the region’s spatially variant climate, topography, and surficial and bedrock geology (Devito et al., 2005; Halsey et al., 1998; Vitt et al., 1996). About 5%, or 4750 km^2, of the AOSR is suitable for open-pit mining activities (ABMI, 2017), with 895 km^2 (~1%) already having been mined (Government of Alberta, 2017). Following completion of mining, oil sands mine closure plans suggest that ~295 km^2 of peatlands will not be restored back to their original function prior to mining operations (Rooney et al., 2012). An estimated loss of 11 to 47.3 million metric tonnes of carbon storage is expected because of these activities (Rooney et al., 2012). However, a significant portion of the landscape may also be impacted by other indirect features of oil sands development, posing a more persistent threat to the services by, and ecohydrological functions of these wetlands. Other oil sands-related development, such as permanent access roads and urbanization, occupies over 2100 km^2 of the region (ABMI, 2017) and may hold direct implications for peatland hydrological regimes, ecological processes, and vulnerability to natural disturbances (Rooney et al., 2012; Thompson et al., 2017; Waddington et al., 2015). Research in non-peatland systems observed negative impacts, both directly and indirectly, as a result of unpaved roads. Chemical and physiological implications for plant foliage such as reduced photosynthetic processes (Sarma et al., 2017), increased leaf temperature (Eller, 1970; Zia-Khan et al., 2014), and altered water-use efficiency (Sharifi et al., 1997) were associated with fugitive dust deposition. These impacts are directly related to plant yield and productivity (Fischer et al., 1998; Sarma et al., 2017). Matsuki et al. (2016) proposed the temporal variability of dust load was linked to rainfall variation, indicating that potential dust impacts are largely governed by local environmental conditions and could regionally differ. Bocking et al. (2017) observed peatland black spruce dieback because of long-term inundation caused by beaver damming at a culvert in an unpaved road. Resulting tree mortality demonstrated the importance of hydrological regimes to tree health and development. However, few studies have examined the role unpaved roads play in local tree development of swamp peatlands in the AOSR.

Conifer-dominated swamp wetlands are characterized by gentle sloping topography, shallow peat depth, and tall, dense canopies (Locky et al., 2005). Ecological surveys have characterized boreal swamps as biodiversity hotspots, in part due to their fire resilience, as well as the abundance of rare and threatened species (Hörnberg et al., 1998; Segerström, 1997). In the AOSR, swamps occupy approximately 11570 km^2 (12%), with more than half of swamps being conifer-dominated (AESRD, 2015), namely *Picea mariana* (black spruce) (Jeglum, 1991). Despite their prevalence, black spruce swamps in the AOSR have been overlooked. With the observed challenges climate change and anthropogenic disturbance (Bocking et al., 2017; Elmes et al., 2021; Strack et al., 2018; Turetsky et al., 2002) bring to other boreal wetland types, it is important to characterize and quantify the environmental factors that limit dominant vegetation development in swamps. Schneider et al. (2016) suggest wetlands, such as swamps, which exist at the peatland-forest interface, will be more susceptible to external forces in future due to their low relative water table and peat thickness. In drier conditions, swamps may no longer be able to sustain their limited peat stock and certain drought-sensitive vegetation (Schneider et al., 2016) if limiting factors, such as hydrologic connectivity and nutrient sources (Page et al., 1999), are altered. Ultimately, warming conditions and disturbance events may have substantial consequences for local microclimates (i.e. evapotranspiration rates) and carbon storage capacity of conifer swamps.

Black spruce tree growth in swamp systems have not been considered in retrospective, long-term research in the AOSR. Retrospective dendrochronology studies only consider year to year variability in tree growth despite the influence of intra-annual factors on wood formation and structure (and therefore, ring width). Quantitative wood anatomy (QWA) characterizes plant xylem anatomical features (i.e. cell wall thickness, cell lumen dimensions) that are relevant to plant functioning and development, and their external environment (von Arx et al., 2016). These anatomical features offer structural support to the plant, as well as define the transport and storage of water, nutrients, carbohydrates, and hormones (von Arx et al., 2016). Annual xylem formation and structure is influenced by both internal and external factors (Fonti et al., 2010; Carrer et al., 2015; Castagneri et al., 2015) and thus, can retroactively define intra-annual plant-environment relationships at multi-decadal time scales.

Quantifying the influence of climate change and disturbance on boreal black spruce swamps is important due to their prevalence and thus, influence on the regional water balance in the AOSR. A black spruce swamp intersected by an unpaved road was selected for this study due to: (1) the potential susceptibility of swamps to future climate change scenarios (Page et al., 1999; Schneider et al., 2016; Wösten et al., 2008); and (2) the lingering uncertainties around the effects of anthropogenic disturbance on boreal swamp hydrological and ecological regimes (Cole et al., 2015).

The objectives of this paper were to quantify the influence of road construction on swamp black spruce anatomical features (growth) by evaluating: (a) dust deposition from road traffic; and (b) potential flow impediment through the swamp as a result of road development. This paper therefore hypothesizes:

(i) Shifts in black spruce growth as a result of atmospheric dust deposition from unpaved roads is poorly understood. However, past research suggests a negative impact on plant yield and productivity (Fischer et al., 1998; Sarma et al., 2017). Thus, we hypothesize that dust deposition due to road traffic will have a negative impact on black spruce development, particularly for trees close to the road.

(ii) Dominant groundwater flow pathway of the swamp moves northeast, perpendicular to the road, and drains into the adjacent fen system. The lack of flow through the road culvert suggests an obstruction of flow. Thus, following road construction, precipitation events will positively influence anatomical feature development to the east due to reduced water availability.

(iii) The relationship between cell size and water availability is well-known (Puchi et al., 2020), with cell enlargement being recorded as the most vulnerable to drought. Due to the impediment of subsurface flow from road construction, it is hypothesized that site-wide cell size will have decreased in trees to the east of the road.

3.2 Study Site

Tree samples were taken from a treed swamp in the AOSR of the WBP. The study area (56º96’ N, 111º56’ W), hereafter referred to as *Heaven Swamp* is a working component of the greater Heaven Fen, a 415 hectare moderately-rich wetland-upland system. Heaven Swamp is 29 hectares, sitting at ~320 m a.s.l and approximately 28 km north of Fort McMurray, Alberta (Figure 3-1).

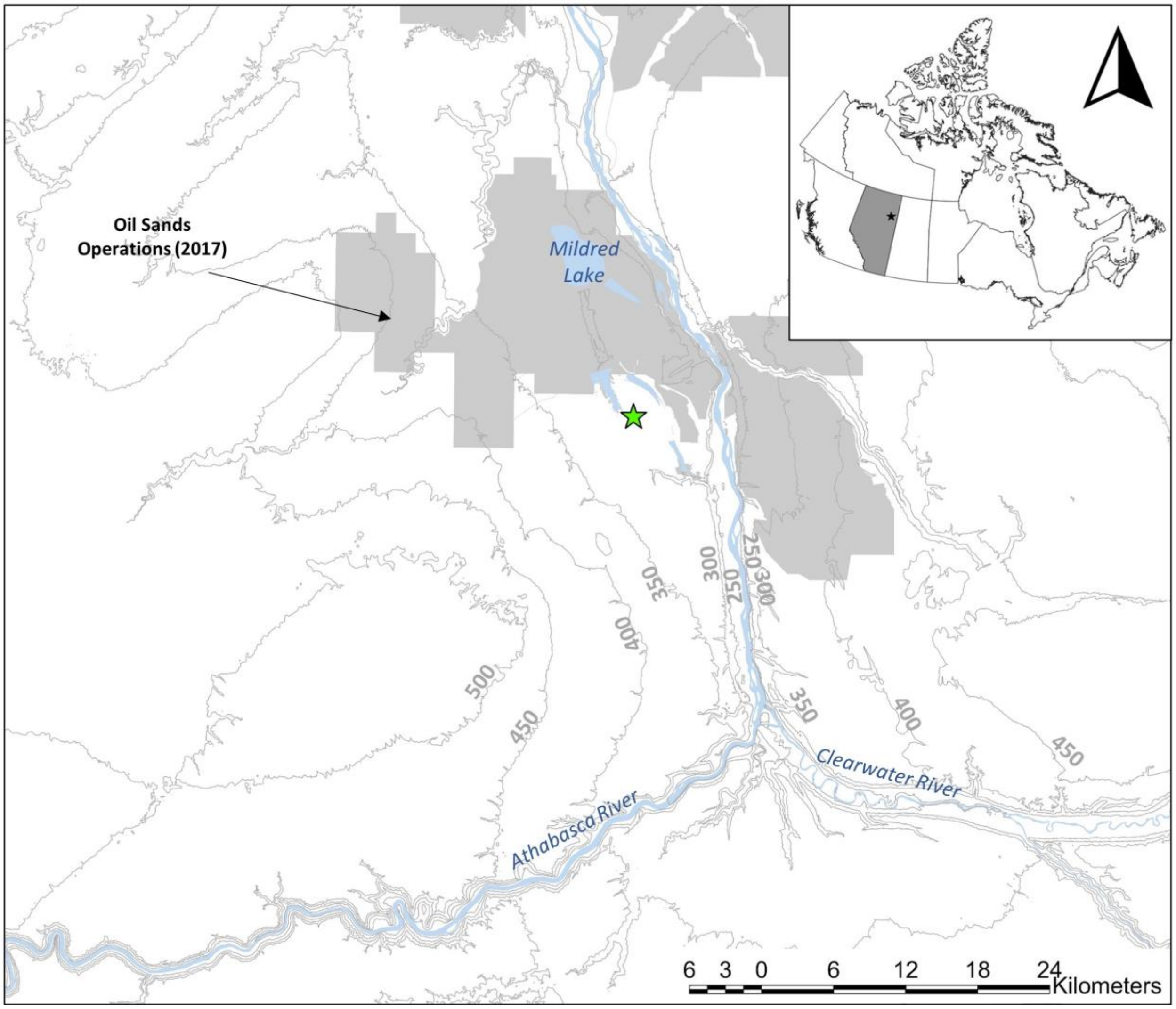


Figure 3-1. Map of the study area, Heaven Swamp (green), and oil sands operations (as of 2017) of the Fort McMurray region, Alberta, Canada.

Heaven Swamp is characterized as a medium to high density treed wetland consisting of mature black spruce and *Larix laricina* (tamarack) species. Understory vegetation includes immature *Populus balsamifera,* bush species (*Salix spp, Rhododendron groenlandicum),* as well as ground mosses (predominantly *Sphagnum*). The AOSR is characterized by a sub-humid climate with cold winters and cool summers (Volik et al., 2017), and a growing season from May through September. Within the period of interest (1961 – 2019), the average annual air temperature (T_a) at Heaven Swamp was 0.6^oC, peaking in the month of July (Figure 3-2; Alberta Agriculture and Forestry, 2020). Average annual precipitation (falling as both rain and snow) is estimated at 433 mm with the majority falling as rain in the growing season months and peaking in July (Figure 3-2; Alberta Agriculture and Forestry, 2020).

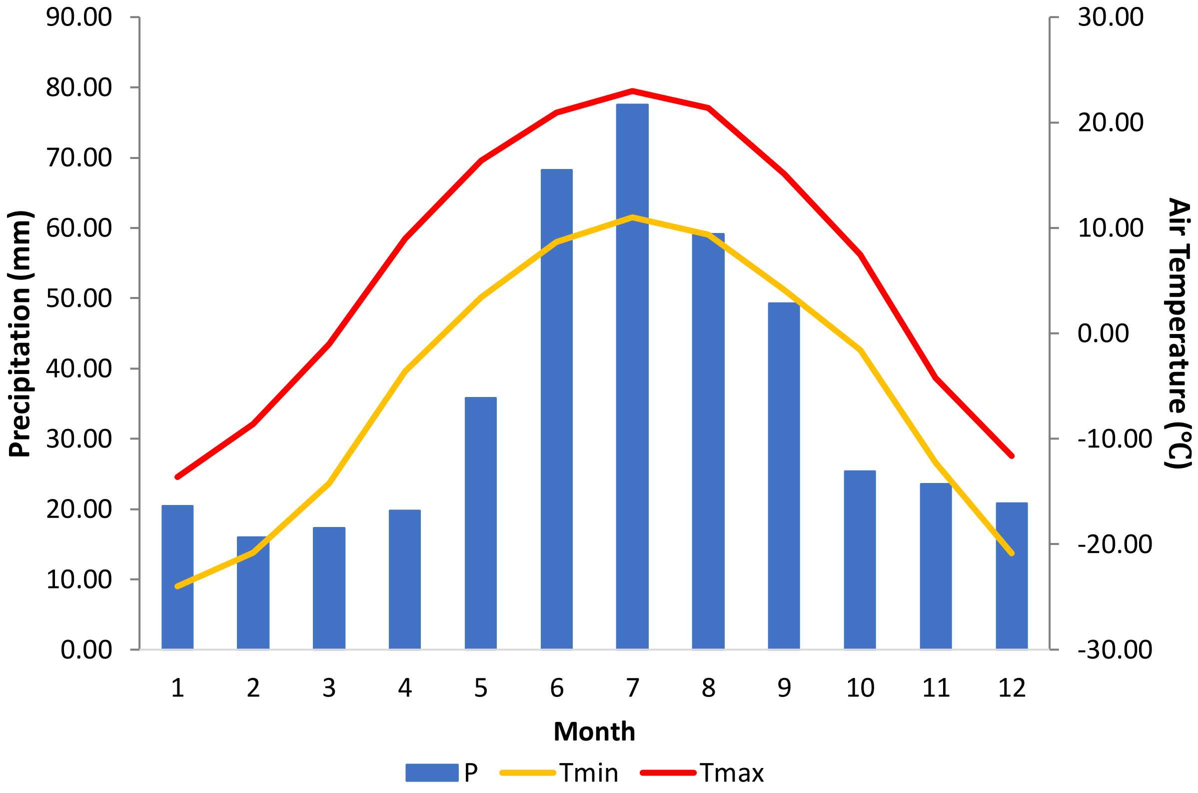


Figure 3-2. Regional monthly average air temperature (T_a; °C) and monthly total precipitation (P; mm) collected by Alberta Climate and Information Service (1961 - 2019), Fort McMurray, Alberta, Canada.

The development of an unnamed, unpaved road that runs northeast through the treed swamp began in 1978 (Figure 3-4). Prior to 1978, the unpaved road existed only as a winter road for exploration and extraction purposes. The road was elevated above the natural ground surface by approximately 1 m relative to the east and 0.5 m to the west and sits at an elevational high within the study area (Hu, unpublished). A culvert was installed at the northern end of the road to allow for water movement from one side to the other (Figure 3-3). Water pools year-round on both sides of the culvert and does not tend to flow via the culvert during the growing season. Along the east side of the road, a clearing the length of the study area and approximately 20 m wide was made to accommodate power lines. The tree line begins just beyond this clearing. A sparse line of bush species (*Salix spp*, *Betula pumila*) and *P balsamifera* occupy the edge of the road on either side.

3.3 Materials and Methods

3.3.1 Climate Data

Daily meteorological data was obtained through the Alberta Climate and Information Service (ACIS) for Heaven Swamp during the period of interest (1961 - 2019) (Alberta Agriculture and Forestry, 2019). ACIS classifies land area by township and approximates regional weather data using interpolation and inverse distance weighting (IDW) methods. Daily maximum and minimum temperature values for Heaven Swamp (township: T092R10W4) were estimated using a linear IDW procedure, with the 8 closest stations or stations within a 200 km radius (Alberta Agriculture and Forestry, 2019). Daily precipitation values were estimated using a hybrid IDW approach and the closest 8 stations or those within a 60 km radius. If there was no station within the given radii, the nearest neighbor was used (Alberta Agriculture and Forestry, 2019). 29 February and 31 December were removed from the analysis to reduce inter-annual inconsistencies and missing regional climate data.

Site-level meteorological data was collected at Heaven Swamp in 2018 to record meteorological variables at 30-minute intervals during the growing season (May through September). Air temperature (°C) was measured at 1 and 6 m above the surface at

Heaven Swamp (HOBO U23 Pro v2, Onset Computer Corporation, Bourne, MA). Precipitation (P; mm) was measured nearby using a tipping bucket rain gauge (HOBO U23 Pro v2, Onset Computer Corporation, Bourne, MA). Site-specific meteorological data was collected in the growing season for 2018 and 2019. Site-level air temperature and precipitation were regressed with historical IDW data collected from the Alberta Climate Information Service (ACIS) to verify an accurate representation of site conditions from 1961 - 2019.

3.3.2 Hydrology

A water monitoring well was installed on both the east and west sides of the unnamed road at Heaven Swamp (Figure 3-3) in the growing season of 2019. Wells were measured bi-weekly during the growing season to establish the fluctuations in water table depth (WTD) relative to seasonal precipitation and assess if a disparity existed between opposing sides of the road.

3.3.3 Vegetation

Tree density surveys were conducted at both the disturbed (n = 6) and reference (n = 2) subgroups in the late growing season. Tree saplings (< 1.3 m in height) and/or trees with a DBH of < 1 cm were removed from analysis due to little relative impact on overall density and competition. Survey plots were 10 x 10 m and randomly selected within the defined subgroup areas. Dead, fallen, and severely leaning trees were removed from analysis. Total number of trees, height, and DBH were taken of each tree that was >1 m in height and > 1 cm in DBH. Trees above 5 m in height were measured using a clinometer and those below were measured using a measuring stick.

3.3.4 Atmospheric deposition

Three dust collectors were constructed for each of the four subgroups at Heaven Swamp for a total of 12. One grouping of collectors was approximately 1-2 m from the road to the west, 20 m away the east, and 100 m away on both the east and west sides. Collectors were positioned within each subgroup of nearby sampled trees, as well as in more open areas to minimize organic debris collection from the surrounding canopy (Figure 3-3). All collectors were approximately 1.6 m above the ground and installed for 30 days within the mid-growing season. Reusable round drain pans (8.3 L) were used to collect and store both wet (rain) and dry deposition. A thick double layer of chicken wire was used to hold a layer of glass marbles above the bottom of the pan to allow for dust collection. The marbles and chicken wire layers minimize the loss of atmospheric dust deposition due to wind and rain events. This method did not account for the removal of dust from foliage due to rain or wind events, rather all dust deposition over the 30-day period of collected. Therefore, total dust load per day could be overestimated.

Figure 3-3. Images of atmospheric dust collectors used in August of 2019 to capture dust deposition from the nearby, unpaved road, Heaven Swamp, Fort McMurray, Alberta, Canada.

Due to frequent and heavy rainstorms in the mid-growing season, dust collectors were emptied of collected water/dust mixture at the two-week mark and stored in sealed 18.9 L buckets. This was done to minimize loss of dust collection due to overflowing of rainwater. At 30-days, collectors were taken down and filtered into their corresponding buckets. Marbles, chicken wire, and any visible organic debris (twigs, leaves, needles) were removed from the water/dust mixture. Buckets were then left to settle and excess water was decanted. 0.45 µm filter papers were weighed with an analytical scale and then used with vacuum filtration to filter the remaining mixture. % LOI analysis was adapted from Heiri, Lotter, & Lemcke (2001) and Dean (1974). Used filter papers, along with the collected dust, were placed in a convection oven for 48 hours at 60°C to remove any remaining water. All dry samples ("dry weight") were weighed using an analytical scale.

Dust-filled filter papers were then placed into 12 crucibles placed in a muffle furnace at 550 ^{o}C for 2 hours and left to cool overnight. Crucibles were then weighed again ("ash weight") for % loss of ignition (% LOI), or % total of organic content in the sample, and calculated using:

$$\% \text{ LOI} = ((\text{dry weight} - \text{ash weight})/\text{dry weight}) * 100\% \quad [1]$$

Although % LOI is not relevant to the scope of this study, the final weight of the dust sample clarified the relative proportion of atmospheric dust deposition at varying distances away from the road.

The final weight of dust was categorized based on distance from the road (2, 20, 100 m), reference and road subgroups, and east and west sides of the road. An ANOVA test was run for each sample category using the R package Stats (R Core Team, 2013) to determine the variance between groupings.

3.3.5 Dendrochronology Techniques

Field work was conducted in order to understand the influence of the unpaved road on black spruce anatomical traits. A "disturbed" and an "undisturbed" subgroup on either side of the road, making four subgroups in total (2 disturbed, 2 reference), were established. However, due to the extent of human activity and ecosystem disturbance in the AOSR it is presumed that the "Reference" groups are indeed disturbed, but to a much lesser degree. The disturbed subgroup to the east of the road, hereafter referred to as Rd E, sits approximately 20 m from the road (Figure 3-4). The disturbed subgroup to the west, herein referred to as Rd W, is situated ~2 m from the road. Both the reference subgroups to the east and west, hereafter referred to as Ref E and Ref W, respectively, are at an approximate distance of 100 m. Tree cores and stem discs were collected from mature black spruce within the study area. 10 trees were sampled from both disturbed subgroups (n = 20) and 20 trees from each reference subgroup (n = 40). A total of 40 trees were sampled from the reference groups to develop a robust site master chronology. Deformed, young, leaning, and dead trees were avoided. Mature trees were targeted to ensure that it covered the period of interest (1961-2019), which is constrained by available climate data. Stem discs were taken from trees with a DBH < 10 cm using a circular saw. Tree cores were taken using a 5.1 mm diameter Haglöf increment borer (Haglöf, Långsele, Sweden). In the scenario where sampling from tilting trees was unavoidable, tree cores were taken perpendicular to leaning direction to avoid compression/expansion in xylem. Both stem discs and tree cores were collected at breast height (approximately 1.3 m). Tree samples were then air-dried for 48 hours.

Stem discs were sanded using a belt sander at progressively finer grit (P100, P220, and P320). Tree cores were hand sanded using P400 and P600 grit. Annual ring boundaries for both stem discs and tree cores were counted and dotted based on the dot notation system beginning at the outermost ring (2019). Stem discs were scanned using the flatbed Epson Perfection 4990 Photo scanner (Hillsboro, Oregon, USA) at 2400 dpi. Disc ring boundaries were automatically measured (in mm) and dated using the CooRecorder (v9.4) dendrochronology program and configured as a master chronology through the CDendro software (v9.4). Tree cores were manually measured using the Velmex (New York, USA) and Measure J2X systems (in mm). Both stem disc and core ring width measurement files were compiled and run through the COFECHA statistical program (Holmes, 1983). COFECHA is a dendrochronology program that primarily determines the accuracy of cross-dating and ring width measurements of a tree-ring series (Grissino-Mayer, 2001). COFECHA assesses inter-series correlation and sensitivity values of a tree record against a master chronology (Grissino-Mayer, 2001; Holmes, 1983). A series inter-correlation value is measured using

$$r_{xy} = \frac{\sum_{t=1}^{t=n}(x_t - m_x)(y_t - m_y)}{(n-1)S_x S_y} \qquad [2]$$

where x_t is the core's index value at year t, y_t is the master chronology index value at year t, m_x is the mean index value for the core, m_y is the mean index value for the master chronology, n is the number of years of interest, S_x is the standard deviation for the core, and S_y is the standard deviation for the master. Typically, an inter-series correlation value > 0.4 is ideal for dendrochronology (Speer, 2010). Each measured tree series was standardized using the R package dplR (Bunn, 2008), to remove age-related growth influence, and subsequently combined using a robust bi-weight mean to create a standardized RWI chronology. Chronologies were standardized by dividing annual ring width values by a best-fit negative exponential or linear regression function. This technique preserves low-frequency climate and disturbance signals present in a tree ring series. Pacific Decadal Oscillation (PDO) values were collected from Japan Meteorological Agency (2020) to assess the influence of large-scale atmospheric patterns on local hydroclimates and thus, black sprue tree growth. Pearson correlation coefficients were calculated for standardized RWI throughout the period of interest (1961-2019) and annual PDO values.

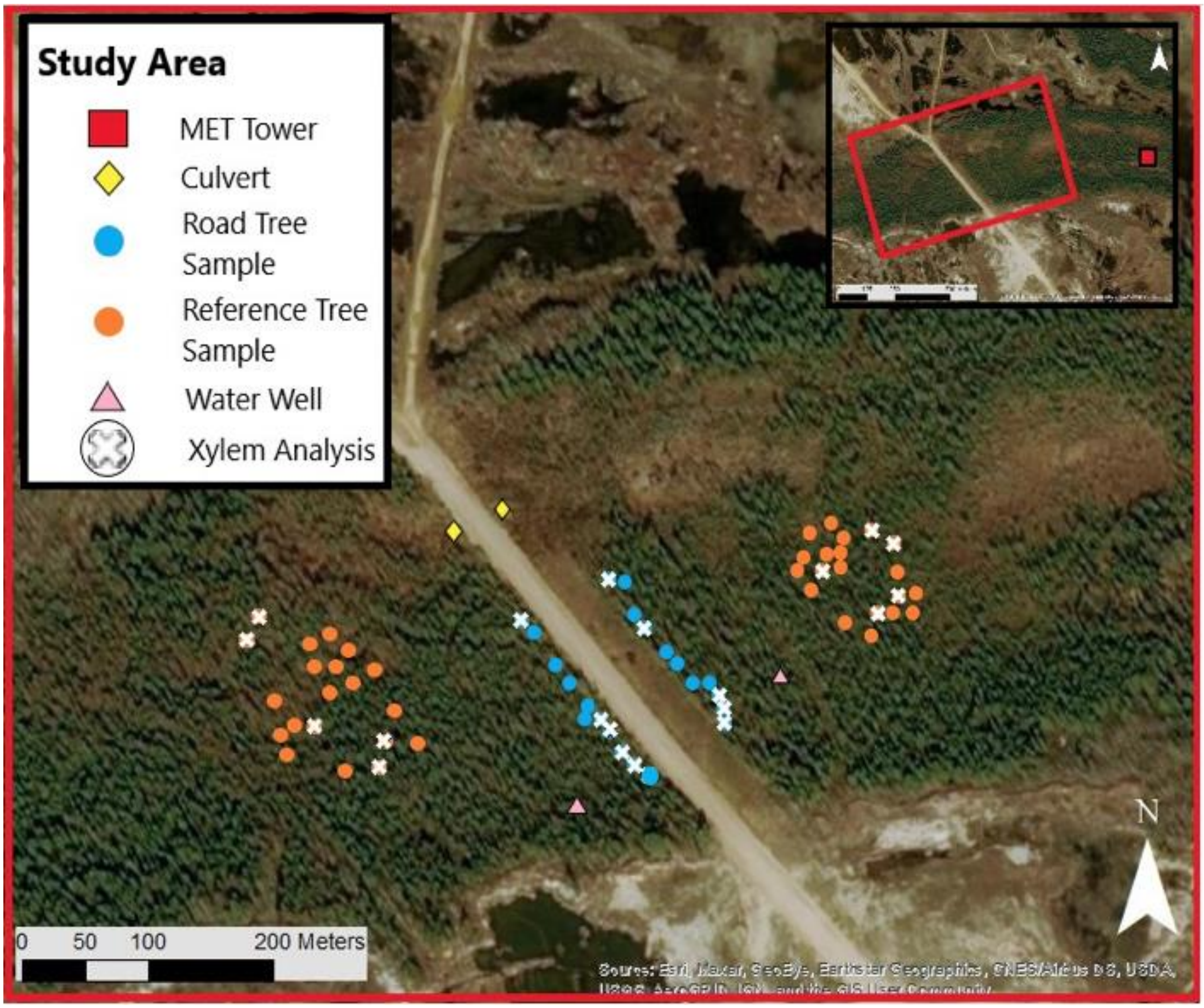


Figure 3-4. Site map of Heaven Swamp, showing the location of tree core sampling, the unnamed road and culvert, sampled monitoring water wells, and site-level meteorological tower (MET tower).

3.3.6 Quantitative Wood Anatomy

Five records from each subgroup (n = 20) were selected for xylem anatomy analysis (Figure 3-4) based on age, quality of sample, and adequate COFECHA inter-correlation value (>0.4). Stem discs were subsequently cut into 2.5 cm thick cross-sections from bark to pith. Tree cores and the 2.5 cm cross-sections were subsequently divided into 4-5 cm long pieces and transversely sliced at 12 μm thickness using a rotary microtome (Leica, Heidelberg, Germany). Feather N35 blades (Feather Safety Razor Co., Ltd, Osaka, Japan) were used to slice the transverse cross-sections. Standard procedures were used in preparation and slicing of cores (Castagneri et al., 2017; von Arx et al., 2016). Transverse sections were mounted on microscope slides and stained with safranin (1% distilled water) and Astrablue (0.5%) dye and rinsed in diluted ethanol solution (70, 95, and 100%). Samples were then fixed to the slide using Eukitt (BiOptica, Milan, Italy) and dried in a convection oven at 60ºC for 48 hours. The dried slides were digitally scanned by the Zeiss Axio Scan.Z1 (Zeiss, Oberkochen, Germany) at 100x magnification. These cross-sections were automatically analyzed within ROXAS (version 2.0) (von Arx & Carrer, 2014), an image analysis software that detects and measures anatomical parameters (i.e. cell area, cell wall thickness, number of cells), as well as annual ring boundaries within a tree record. Ring widths measured in ROXAS are cross-dated against manual measurements made using the Velmex and CooRecorder to assign a calendar year to detected ring boundaries. Annual rings that are ripped, damaged (due to frost, resin ducts), and/or variation from external variables besides climate were removed from analysis. The plyr R package (Wickham, 2011) defines the raw annual earlywood (EW) and latewood (LW) cells for each tree series. Tree anatomical traits demonstrate long-term trends (Carrer, von Arx, Castagneri, & Petit, 2015; Castagneri et al., 2017) therefore, a cubic spline with 50% frequency cut-off of 32 years was fitted to each parameter series (Cook & Kairiukstis, 1990). The detrended series, created using the R package dlpR (Bunn, 2008), was used to calculate the robust mean and subsequently, build the EW and LW standardized chronologies for each anatomical trait in all four subgroups (Martin-Benito, Beeckman, & Cañellas, 2013). These anatomical traits include cell wall thickness (CWTALL50), number of cells per section (NUM), cell area (CA90), lumen diameter

(LD90) and cell radial diameter (DRAD50). The CWTALL50 and DRAD50 anatomical chronologies were compiled using measured values in the top 50th percentile and CA90 and LD90 values in the top 90th percentile. Anatomical analysis was limited to available meteorological data spanning 1961 - 2019.

3.3.7 Climate-anatomy Relationships

The role climate conditions play in the radial growth and xylem anatomical characteristics was examined using Pearson correlation analysis at an intra-annual timescale. Pearson correlations were calculated for anatomical mean chronologies and daily precipitation, maximum temperature, and minimum temperature over 30-day time-windows (centered to the end of the window), moving with a 1-day step. Pearson correlations were calculated for 10, 14, 20, 30, and 40-day moving windows. However, the 30-day window provided a more robust result and will be focused on in the Results section. Correlations were established for the previous year's June through to the current year's December for the period of 1961 – 2019.

3.4 Results

3.4.1 Historical Climatic Conditions

Mean annual air temperature and precipitation (P; mm) for Heaven Swamp was 0.63 °C and 433 mm, respectively, during the period of interest (1961 - 2019). P fell as snow in the winter months and peaked in the month of July (77 mm), along with average monthly maximum (T_{max}; 22.9°C) air temperature (Figure 3-2). Annual average minimum (T_{min}) temperature and T_{max} illustrated an increasing trend over the period of interest (Appendix 2, Figure A2-1), whereas P demonstrated a decreasing trend. However, the decreasing trend in mean annual P (slope = -2.5) was visibly greater than the increasing trend of average annual T_{max} (slope = 0.04) and T_{min} (slope = 0.07).

Historical climate data collected from the Alberta Climate Information Service (ACIS) was analogous to site-level meteorological data collected from 2018 - 2019. There was an R^2 value of 0.97 between regional and site-level daily average air temperature (T_a) values and an R^2 value of 0.92 (Appendix 2, Figure A2-2) between estimated monthly regional and measured site-level monthly average P.

Annual ring width index values for black spruce at both study sites were correlated to annual PDO index values (Japanese Meteorological Agency, 2020) based on the defined “warm” and “cool” phases of the PDO during the study period. This was because site RWI appeared to follow the inter-annual trends of the PDO (Figure 3-7). While in the negative phase of 1961-1976 and the positive phase of 1977-1998, the PDO and site-level RWI had a low Pearson correlation of -0.03 and 0.02, respectively. The site-level RWI of Heaven Swamp between 1999-2019 however, was well-aligned (r = 0.58).

3.4.2 Hydrology

Both east and west sides of the unnamed road demonstrated similar trends in WTD in 2019 (Figure 3-5). Input from adjacent uplands may have been a contributing factor to maintaining water table trends on both sides of the road (Hu, unpublished). WTD fluctuated with rainfall events and increased with cumulative precipitation throughout the 2019 growing season (Figure 3-5).

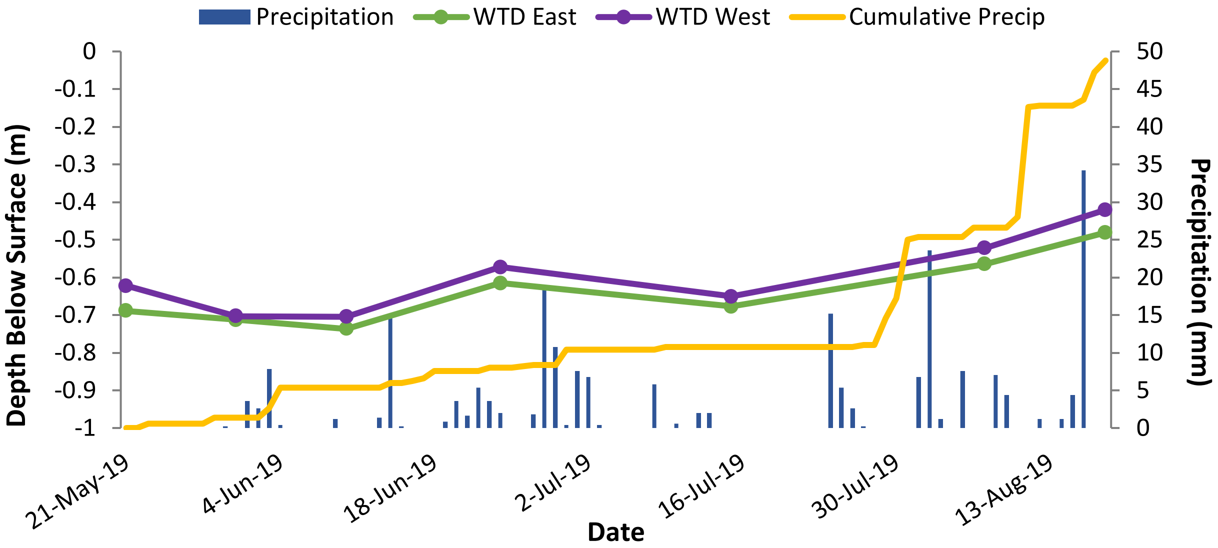


Figure 3-5. Daily total precipitation (mm) and cumulative precipitation (mm) for Heaven Swamp, as well as point measurements of water table depth (mm) on the east and west side of the unnamed road during the growing season of 2019.

3.4.3 Vegetation Composition

The difference in mean tree height and DBH of reference subgroups compared to those in road subgroups was statistically significant ($p < 0.05$), with the smallest average DBH and tree height in the Rd W subgroup closest to the road (2 m) (Table 3-1). Both reference plots consisted of exclusively *Picea mariana* and *Larix laricina*, unlike the road plots which had relatively small proportions of *Betula pumila, Salix spp.,* and *Populus balsamifera.* Both reference and road plots were denser to the west of the road (Table 3-1).

Table 3-1. Diameter at breast height (cm), tree height (m), species proportion (%), and tree density (trees per ha) at Heaven Swamp, Fort McMurray, Alberta, Canada.

Plot	DBH (cm)	Tree Height (m)	Species Proportion (%)	Tree Density (per ha)
Ref E*	6.17 ±1.6	5.92 ±2.3	*P mariana (60.4), L laricina (39.6)*	5300 ±0
Rd E**	5.57 ±1.1	5.05 ±1.2	*P mariana* (64.77), *L laricina* (30), *B pumila* (3.97), *P balsamifera* (1.22)	6300 ±1900
Rd W***	5.29 ±1.3	5.23 ±1.1	*P mariana (*60.2), *L laricina* (26.5), *Salix spp* (9.07), *P balsamifera* (4.23)	9000 ±1600
Ref W*	6.85 ±0.1	6.97 ±1.1	*P mariana (55), L laricina (45)*	8000 ±0

Values are the mean ± standard deviation.
*100 m from road; **20 m from road; ***2 m from road
Note: Both east and west reference plots demonstrate a standard deviation = 0, as one tree survey was conducted at each.

3.4.4 Atmospheric Dust Deposition

Fugitive dust deposition at the four sampled subgroups showed an exponential decline moving away from the road (Figure 3-6). Approximately 2 m west of Heaven Swamp road, fugitive dust deposition averaged 4.01 g m^{-2} day^{-1} (n = 3); 20 m east of Heaven Swamp road averaged 0.99 g m^{-2} day^{-1} (n = 3); and 100 m both east and west of the road exhibited an average of 0.62 g m^{-2} day^{-1} (n = 6) over 30 deposition days. Dust load (g) was significantly different (p = 0.035) between reference and road subgroups but not between east and west sides of the road (p = 0.076).

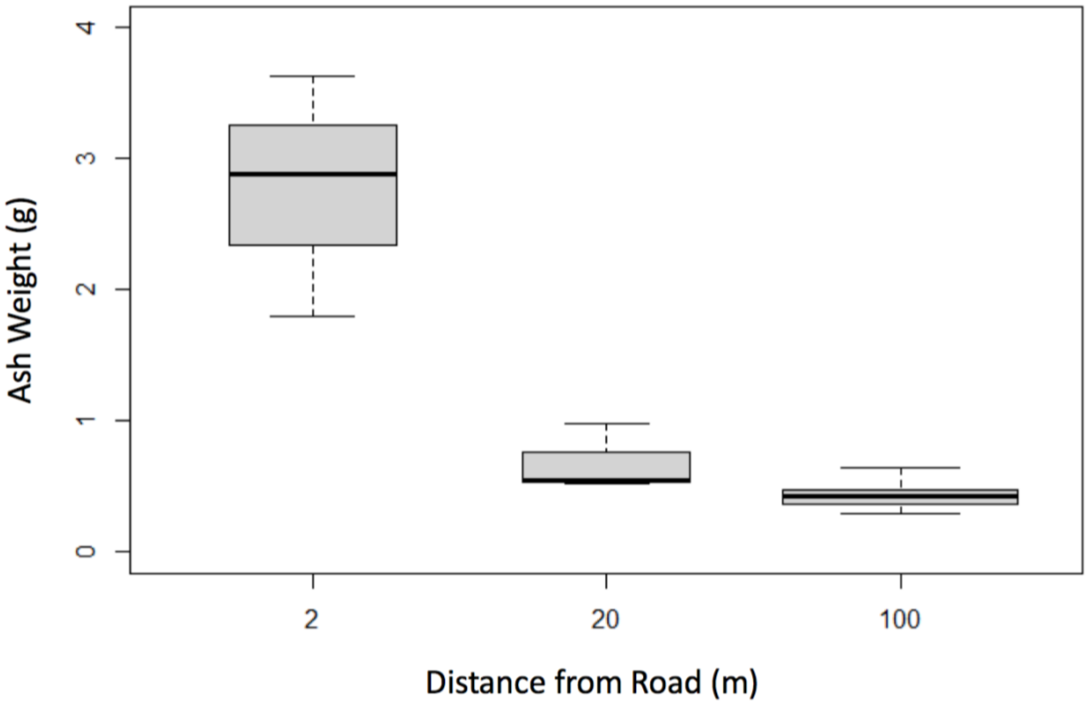


Figure 3-6. Total ash weight (g) collected from the east and west sides and varying distances away from the road, Heaven Swamp, Fort McMurray, Alberta, Canada. 2 m west from the road (n = 3) at Rd W subgroup (left); 20 m west from the road (n = 3) at Rd E subgroup (centre); 100 m east and west from the road (n = 6) at both Ref E and Ref W subgroups (right).

3.4.5 Site Master Chronology and Tree Ring Widths

Rd E and Ref W subgroups had the longest (91 years) and shortest (58 years) chronology, respectively (Table 3-2). Ref W subgroup showed the largest average ring width (1.71 mm; Table 3-2), which corresponded well with average tree height and DBH observed in tree survey plots (Table 3-1).

Table 3-2. Descriptive statistics of ring-width series of the trees selected for anatomical analysis, Heaven Swamp, Fort McMurray, Alberta, Canada**.**

Subgroup	Total Period	# of Trees	Ring Width (mm)	Inter-series Correlation
Ref E	1939-2019	5	1.08 ±0.22	0.467
Rd E	1927-2019	5	1.09 ±0.31	0.538
Rd W	1937-2019	5	1.08 ±0.25	0.472
Ref W	1960-2019	5	1.71 ±0.29	0.509

*Ring width values are mean ± standard deviation.
**Inter-series correlation values were calculated using COFECHA software.

Standardized RWI of Rd E, Rd W, Ref E, and Ref W subgroups and the site master chronology demonstrated two potential shifts in RWI trends throughout the period of interest that align with the oscillations of the annual PDO index (Figure 3-7). The annual PDO index shifted from cool to warm phase in 1977 and 2014 and from warm to cool in 1999. Specifically, from 1999-2019 the PDO experienced high variability and shorter warm and cool phases. Average RWI of the three divided periods (based on observed trends) was: 1961 - 1976 (0.99 mm), 1977 - 1998 period (0.87 mm) and 1999 - 2019 (1.08 mm). Marker years were identified in 1975 and 2011 due to high and low P totals, respectively.

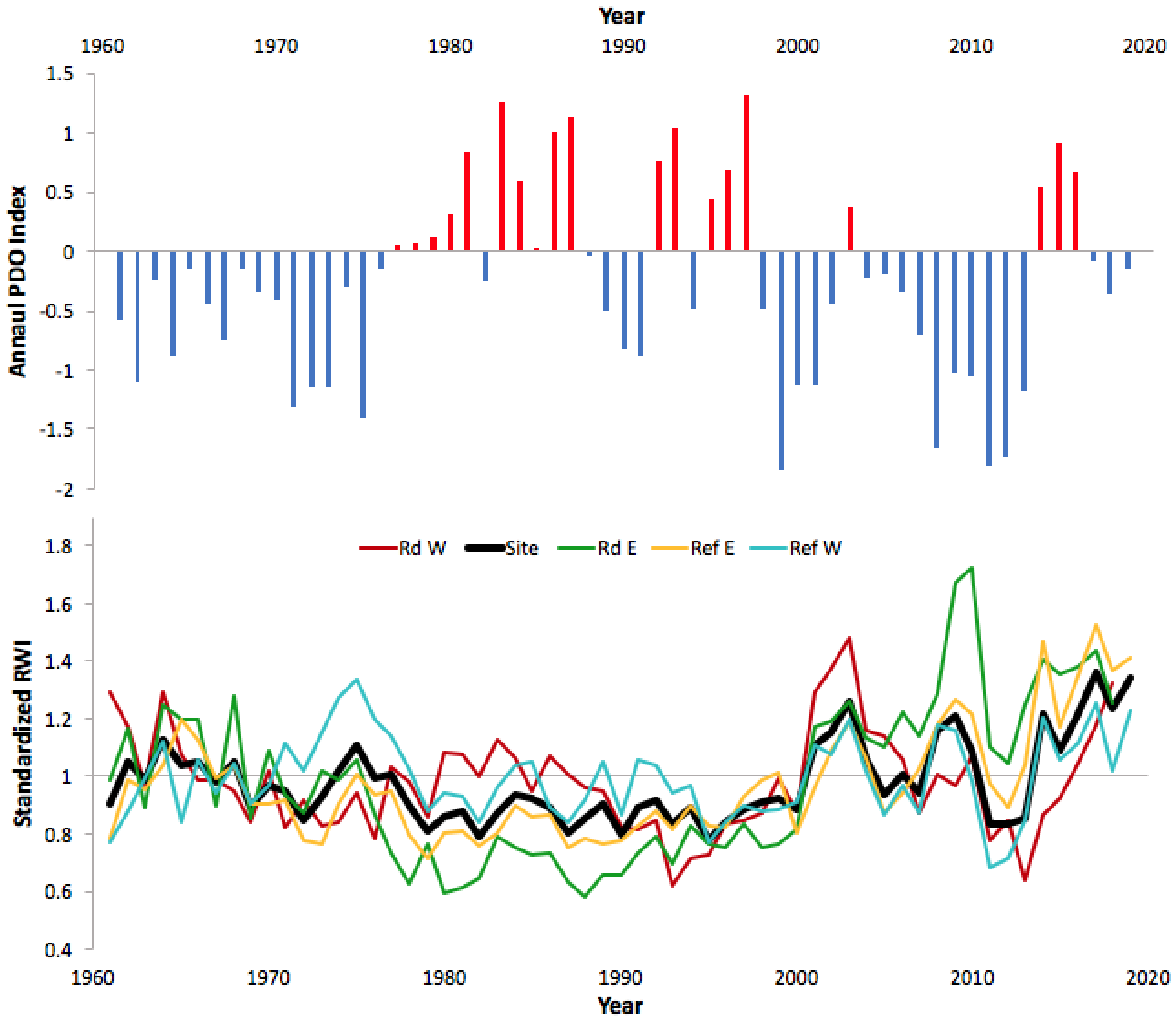


Figure 3-7. Annual Pacific Decadal Oscillation index values for the period of interest; warm (red) and cool (blue) phases are shown (above). Standardized ring width indices for Rd E (green; n = 7), Rd W (red; n = 7), Ref E (yellow; n = 13), and Ref W (blue; n = 15) subgroups as well as the combined site-wide master chronology (n = 42) of Heaven Swamp, Fort McMurray, Alberta, Canada (below)**.**

3.4.6 Anatomical Comparisons Between Subgroups

20 m and 100 m east of the unpaved road showed little significant difference in anatomy before (1974-1978) and after (1981-1985) road construction with the exception of the number of cells (Figure 3-8), where average annual cell numbers decreased.

Interestingly, significant differences ($p < 0.05$) were observed for all anatomical features before and after road construction, with the exception of the number of cells, 2 m from the road at Rd W (Figure 3-8). Cell size and cell wall thickness increased following road construction at 2 m from the road. The shifts observed for all anatomical features were statistically significant ($p < 0.05$) before and after road construction at Ref W. Measurements increased after road construction, rather than decreased, at Rd W. The reference subgroups, 100 m from the road, had divergent results (Figure 3-8) despite similarities in dust deposition load. Growing season T_a and P before (1974-1978) and after (1981-1985) the road were not significantly different ($p > 0.05$), indicating that seasonal climate conditions had little to no effect on the variation of xylem traits.

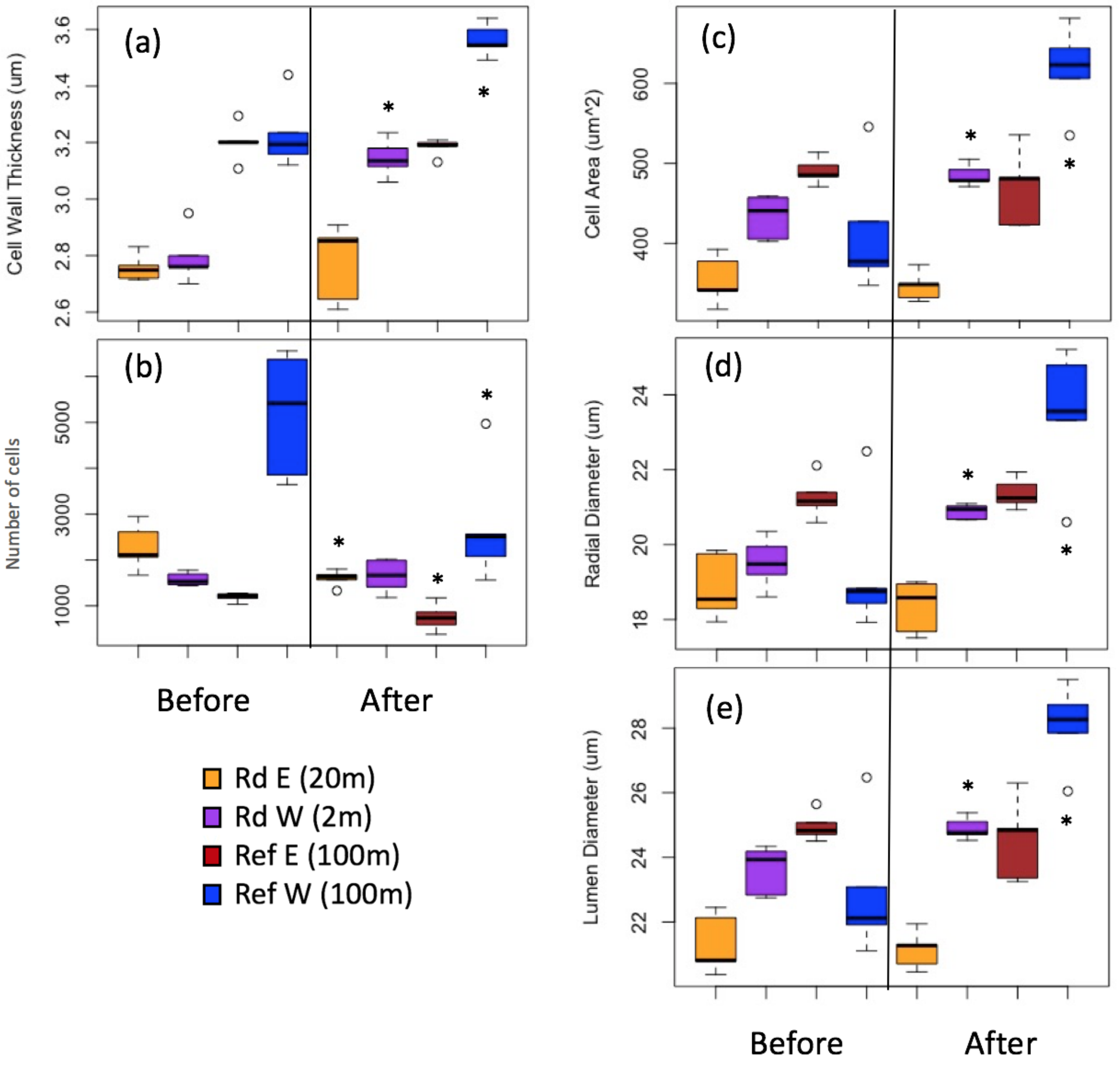


Figure 3-8. Comparison of anatomical feature earlywood chronologies before and after road construction for all subgroups at Heaven Swamp, Fort McMurray, Alberta, Canada. (a) Cell wall thickness; (b) Number of cells; (c) Cell area; (d) Radial diameter; and (e) lumen diameter. An asterisk denotes statistical significance ($p < 0.05$).

3.4.7 Anatomical Feature-Climate Analysis

Fewer and weaker significant correlations exist in the time period after road construction (AR; 1980 - 2019) for all subgroups and daily P compared to before road construction (BR; 1962 - 1978) (Figure 3-9). Both Rd E and Ref E subgroups exhibited few significant correlations with P in the BR period. However, a brief positive relationship existed between NUM, CA90, and LD90 and precipitation in the previous year's December in the Ew cells. Additionally, there was a negative relationship between Lw cell size and precipitation in the previous year's December. The anatomical features of Rd W had, by far, the greatest number of significant correlations compared to other subgroups within the BR period. The CWTALL50, CA90, and LD90 of Lw cells were positively correlated to the previous year's late growing season and current year's June. CA90 and LD90 of Ew cells in the Rd W subgroup were positively correlated to the previous year's October and December. DRAD50 of Ew cells at Rd W showed a positive relationship with the current year's May. The REF W subgroup demonstrated few, weak negative correlations in the BR period.

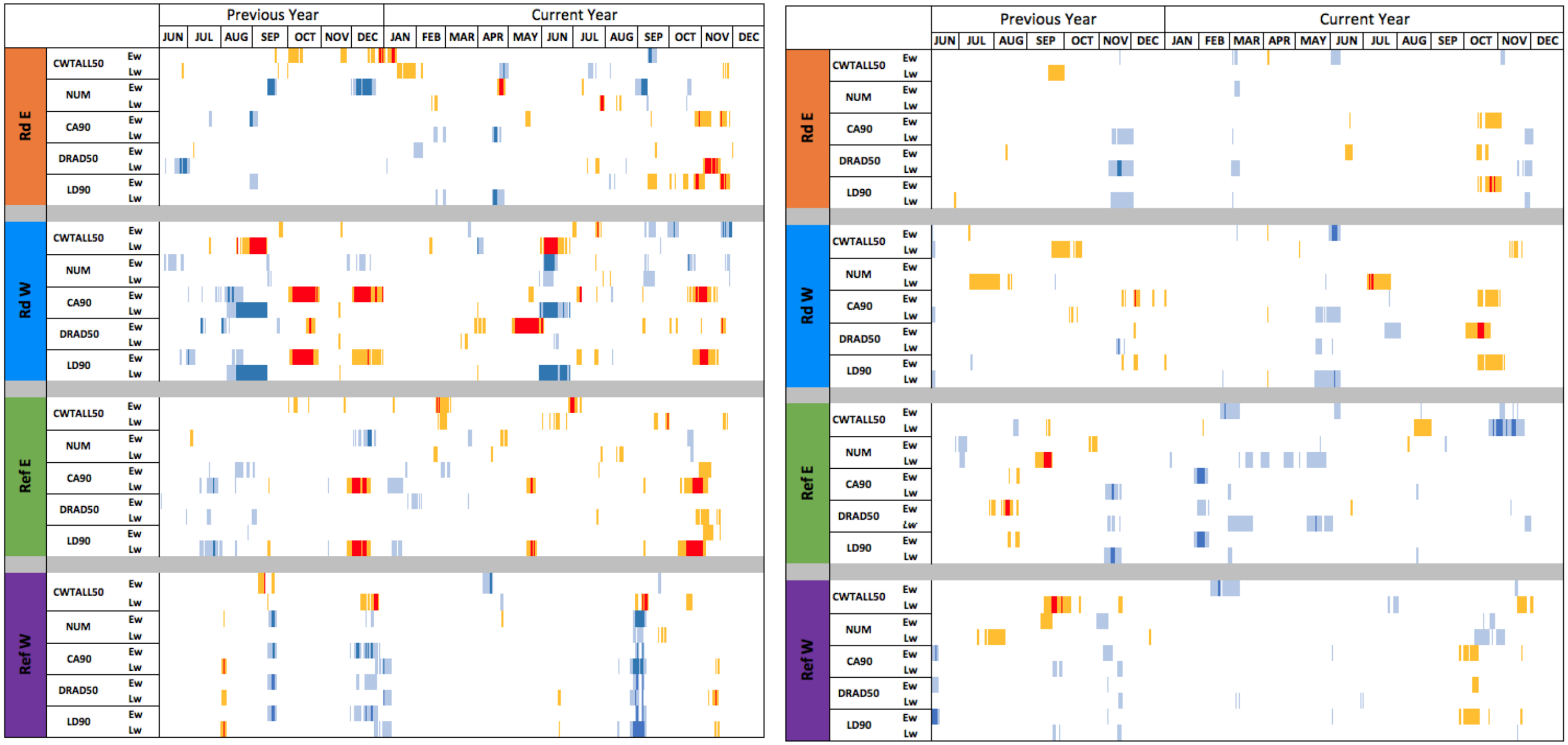


Figure 3-9. Significant correlations between precipitation (mm) and the anatomical features (CWTALL50, NUM, CA90, DRAD50, LD90) of the EW and LW cells for trees sampled in the four subgroups (Rd E, Rd W, Ref E, Ref W) at Heaven Swamp. Climate data were organized in 30-day windows, centered to the end of the window, moving with a 1-day step from the previous year's June to the current year's December. Correlations are for the previous and current growing years prior to road construction (left; 1961 - 1978) and after road construction (right; 1980-2019) and are statistically significant ($p < 0.05$). Left figure key: strong positive correlation (red; $x > 0.618$), positive correlation (yellow; $0.497 > x > 0.618$), strong negative correlation (dark blue; $x < -0.618$), negative correlation (light blue; $-0.497 > x > -0.618$). Right figure key: strong positive correlation (red; $x > 0.437$), positive correlation (yellow; $0.316 > x > 0.437$), strong negative correlation (dark blue; $x < -0.437$), negative correlation (light blue; $-0.316 > x > -0.437$).

Xylem features of trees in all four subgroups showed few significant correlations with T_{max} in both the BR and AR periods (Figure 3-10). Existing correlations appeared primarily in the previous year's months for all subgroups, with the exception of Rd E in the BR period. However, Rd E subgroup demonstrated a weaker but significant positive correlation between the NUM of EW cells and T_{max} in the previous year's July. In the current growth year, the CWTALL50 of the EW cells showed a short but strong positive correlation with July, while the LW demonstrated a similar correlation in May. The CA90 and LD90 of LW cells of Rd E exhibited weak negative correlations in the current year's June and September. Contrastingly, in the AR period the CWTALL50 of EW cells, as well as the CA, DRAD50, and LD90 of LW cells at Rd E, were negatively correlated to the previous year's August and September. In the BR period, the CWTALL50 of EW cells at Rd W were negatively correlated with the previous July. The NUM of LW cells were positively correlated to the previous year's June and July. The DRAD50 of EW cells were positively and negatively correlated to the previous year's July/August and September, respectively. Rd W in the AR period is dissimilar to that of the BR period. The CA90, DRAD50, and LD90 of LW cells were negatively correlated to the previous year's end of August, beginning of September. The Ref E subgroup demonstrated weak and scattered correlations in both the BR and AR periods. Correlations seen in the Ref W subgroup during the BR period were not similar to those in the AR period. The CWTALL50 of both EW and LW cells were negatively correlated to the previous year's June. The NUM, CA90, DRAD50, and LD90 of EW cells showed weak positive correlations in the previous year's July.

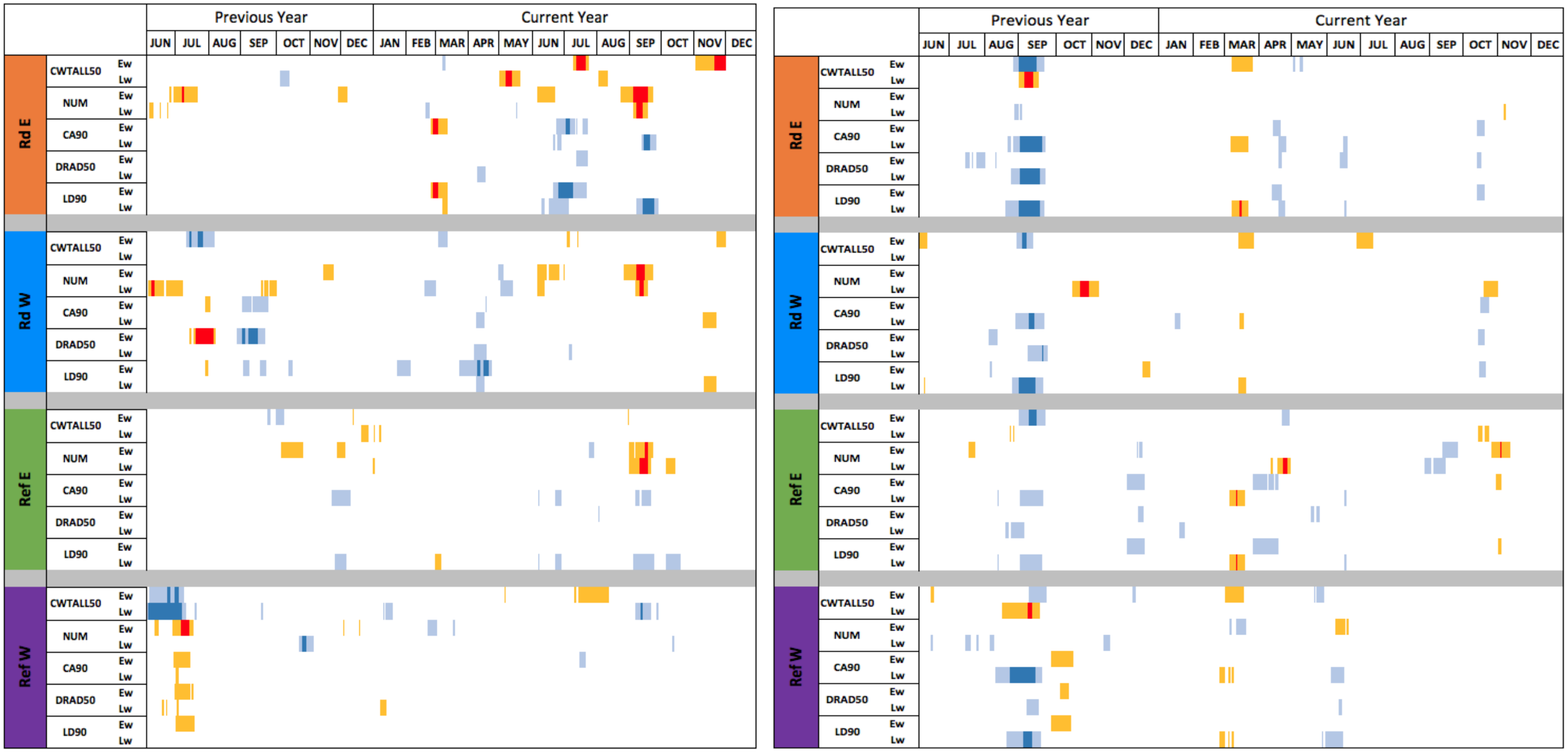


Figure 3-10. Significant correlations between maximum air temperature (T_{max}) and the anatomical features (CWTALL50, NUM, CA90, DRAD50, LD90) of the EW and LW cells for trees sampled in the four subgroups (Rd E, Rd W, Ref E, Ref W) at Heaven Swamp. Climate data were organized in 30-day windows, centered to the end of the window, moving with a 1-day step from the previous year's June to the current year's December. Correlations are for the previous and current growing years prior to road construction (left; 1961 - 1978) and after road construction (right; 1980-2019) and are statistically significant ($p < 0.05$). Left figure key: strong positive correlation (red; $x > 0.618$), positive correlation (yellow; $0.497 > x > 0.618$), strong negative correlation (dark blue; $x < -0.618$), negative correlation (light blue; $-0.497 > x > -0.618$). Right figure key: strong positive correlation (red; $x > 0.437$), positive correlation (yellow; $0.316 > x > 0.437$), strong negative correlation (dark blue; $x < -0.437$), negative correlation (light blue; $-0.316 > x > -0.437$).

Sampled trees in all four subgroups displayed fewer and weaker correlations to daily T_{min} in the BR period compared to AR (Appendix 2, Figure A2-3). In general, T_{min} correlations exhibited similar trends to T_{max}. However, Ref W correlations were comparatively stronger with T_{min} values versus T_{max} in the AR period.

3.5 Discussion

3.5.1 The role of fugitive dust in local tree growth

Results of this study show a statistically significant difference for dust load (g) between road and reference subgroups ($p < 0.05$; Figure 3-6), indicating a potential for greater influence of fugitive dust on plant productivity closer to the road. Reduced photosynthetic processes (Sarma et al., 2017), increased leaf temperature (Eller, 1970; Zia-Khan et al., 2014), and altered water-use efficiency (Sharifi et al., 1997) were recorded to be chemical and physiological impacts of dust deposition on plant foliage. These impacts have been directly related to plant yield and productivity (Fischer et al., 1998; Sarma et al., 2017). Although, observed negative implications for vegetation productivity have often been observed in semi-arid environments (i.e. Matsuki et al., 2016; Sharifi et al., 1997) and the Arctic tundra (Myers-Smith, Arnesen, Thompson, & Chapin, 2006) where rainfall is scarce. Matsuki et al. (2016) proposed the temporal variability of dust load on plant foliage was linked to rainfall frequency, indicating that potential dust impacts were largely governed by local environmental conditions. Thus, fugitive dust effects may differ widely between semi-arid environments and sub-humid northern boreal peatlands. Dust levels measured 2 m from the road (4.01 g/m^2; Figure 3-6) were above the average daily deposition rate reported in previous studies (0.67 – 2.3 g/m^2, Matsuki et al., 2016; 2.8 g/m^2, McGranahan & Poling, 2021; 2 g/m^2, Thompson et al., 1984), suggesting that known negative effects of dust deposition could be a factor for black spruce anatomical traits at Heaven Swamp, specifically 2 m west of the road. However, cell size and cell wall thickness increased following road construction (Figure 3-8) at both Rd W and Ref W therefore, contradicting this study's hypothesis. The data limitations of this study prevented further clarification of relative dust load effects on black spruce xylem traits. Given that P peaked in the growing season within the period of interest and annual anatomical means demonstrated an increase following road construction, it's likely dust was not a limiting factor for black spruce growth. The review of dust impacts on vegetation by Farmer et al. (1993) highlights variability in fugitive dust implications as a result of factors including dust particle size, total dust load, dust source, prevailing winds, and vegetation type. Further research should consider wind direction, as well as chemical composition, particle size, and deposition rate in tandem to properly characterize dust load impacts on black spruce species.

3.5.2 Impacts of road construction on wood anatomy

WTD trends of both east and west sides of the road, in the growing season of 2019, indicate stark similarities despite road disturbance (Figure 3-5). Heaven Swamp road was built on an elevational high, suggesting impediment of flow was negligible. Primarily, groundwater flow moved outward from the road on either side (Hu & Elmes, personal communication) thus, minimizing impacts on local hydrological regimes. However, most anatomical feature measurements in both the west subgroups were significantly different ($p < 0.05$) and increased after road construction (Figure 3-8). This suggests that road disturbance likely played a larger role in anatomical development to the west of the road but not as a result of dust deposition unless to catalyze a fertilization effect as observed in moss species (Walker & Everett, 1987). However, dust deposition has primarily been recorded to negatively influence plant yield and productivity (Fischer et al., 1998; Sarma et al., 2017). Wood anatomy research indicates a positive relationship between water availability and cell size (Puchi et al., 2020). The increase in cell features related to cell size (CA90, LD90, DRAD50; Figure 3-8) following road construction, points to an increase in water availability for trees in the west subgroups. However, the relative role the road played in water table change is indeterminate due to a number of compounding regional disturbances during that time period. For example, Heaven Swamp road gave access to gravel pit mining and logging operations. Contrastingly, east of the road, subgroups showed only statistically different anatomical chronologies for NUM pre- and post-road construction (Figure 3-8) indicating a relatively minimal influence of road disturbance on anatomical development. It is important to note sample size was limited for anatomical comparisons and results should be interpreted with caution.

3.5.3 Influence of climate on wood anatomical features and ring width prior to and following road construction

Inter-annual trends in site-level RWI (Figure 3-7) at Heaven Swamp were presumed to be regional given similarities observed in Tyler (Chapter 2, p.30). Kershaw (2013) demonstrated declining growth trends in the year 2000 for *Picea glauca* (white spruce) species, which was considered the result of a substantial increase in pollutant accumulation from upwind oil sands operations. This notable intensification of oil sands activity in the year 2000 could explain the distinct trend at Heaven Swamp from 2000 to 2019 (Figure 3-7). However, large-scale, low-frequency atmospheric patterns such as the PDO have also been recorded as a determinant for climatic patterns in Canada (Hart, Smith, & Clague, 2010; Pisaric, St-Onge, & Kokelj, 2009), suggesting potential implications for black spruce in northern Alberta. Dendrochronology has been previously used to study the effects of teleconnections on continental hydroclimates around the world (i.e. Cleaveland et al., 2003 [Mexico]; Gedalof, Peterson, & Mantua, 2004 [USA]; Pisaric et al., 2009 [Canada]; Wang et al., 2019 [Asia]). However, little is understood about the influence of these large-scale atmospheric patterns on black spruce anatomy traits in peatland systems. Site-level RWI relationship with the PDO was highest between 1999-2019 and lowest from 1977-1998 (Figure 3-7). Ultimately, the PDO could have played a larger role in black spruce annual ring growth compared to high-frequency climate patterns but a robust analysis of multi-decadal hydroclimatic influence was hindered by the temporal scale of this study and the construction of the road (compounded disturbance). Variability and instability of the PDO signal over the past 200 years (MacDonald & Case, 2005) was another source of uncertainty in this study's analysis. Defining the relative impact of large-scale atmospheric phases on dominant northern tree species, such as black spruce, may be crucial for understanding ecosystem function in disturbed landscapes and should be explored further.

No clear relationship existed between cell enlargement and daily P within subgroups furthest from the road, and both within and between the two identified periods of interest (1961 - 1978, 1980 – 2019; Figure 3-9). Peatland systems have been observed as resilient to short-term climate fluctuations (Webb et al., 1993) but less so to extreme and prolonged events, which alter WTD (Wilmking & Myers-Smith, 2008). Additionally, tree growth at Poplar Fen demonstrated greater dependence on precipitation than black spruce of Pauciflora Fen (Castagneri et al., 2015; Tyler, manuscript 1, p.34). Contrastingly, all subgroups at Heaven Swamp demonstrated few, scattered correlations with P both before and after the road (Figure 3-9), which could be attributed to localized conditions such as WTD. Rd W illustrated the largest change in correlation intensity relative to the other subgroups. The shift in frequency and magnitude of correlations between Rd W and P pre- and post-road construction was likely an indirect result of disturbance via water table change. However, this shift in Rd W correlations could not be definitively linked to road construction due to land-use change of nearby landscapes within a similar time period.

Unlike P, daily T_{max} (Figure 3-10) and T_{min} (Figure A2-3) revealed relatively stronger and more frequent correlations with anatomical traits in the period following road construction. Negative relationships between Canadian boreal black spruce ring width and temperature was previously studied (Bocking, 2017; Brooks et al., 1998; Juday & Alix, 2012; Drobyshev et al., 2013; Walker & Johnstone, 2014). Although peatland trees have been less likely to be influenced by extreme temperature events (i.e. droughts) if there was high soil moisture content in the rooting zone (Pepin et al., 2002). This, as well as the relatively minimal relationship between temperature and warmer, drier hydroclimates (Chapter 2, p.33), explained the overall limited relationship observed between black spruce and temperature at Heaven Swamp. The size of LW cells in Rd E and Ref W exhibited a stronger correlation to T_{max} and T_{min} in the previous year’s late growing season post-road construction only (Figure 3-10). This indicates that with increasing previous summer temperature LW cell size may have been more negatively impacted, specifically following disturbance.

3.6 Conclusions

This is the first study to assess the influence of a road on peatland black spruce anatomical features in the AOSR. Contrary to this study’s hypotheses, there was no clear effect of fugitive dust from the unpaved road on black spruce anatomical features. Though the increase in cell size following road construction may be, in part, attributed to a fertilization effect from fugitive dust and should be explored further in future research. There was no apparent impact of road disturbance on anatomical feature response to climatic conditions, highlighting the complexity of northern peatland black spruce growth. The lack of relationship between black spruce anatomical features and both daily temperature and precipitation indicated other limiting factors are at play, such as water table change. Differences in anatomical features across sites have often been related to localized conditions however, tree ring-width in this study demonstrated a potential link to large-scale atmospheric patterns such as the PDO and should be considered in future tree-ring anatomy studies of the AOSR. The increase in cell size following road construction to the west points to a potential link to water table fluctuations due to the established relationship between cell size and water availability, as well as the importance of water table depth for peatland black spruce growth. The similarities in water table trends on opposing sides of the road observed in 2019 could suggest that hydrological regimes can evolve or recover over time. Unfortunately, the relative role of the road in black spruce anatomical trends was not definitive due to the complexity of black spruce growth and compounding human disturbance of nearby landscapes. It is recommended that the relationship between water table depth and tree-ring anatomy be further examined in disturbed peatland landscapes.

4.0 Summary, Limitations, and Future Research

4.1 Summary

This study examined the role of environmental conditions (i.e. hydroclimates) and anthropogenic disturbance in black spruce anatomical characteristics. Characterizing these influences allow for better predictions of xylem response to future warming and the intensification of human activity in the Athabasca Oil Sands Region (AOSR). This study demonstrated that black spruce cell features are governed primarily by temperature in cooler, wetter hydroclimates and precipitation in warmer, drier hydroclimates of the same region. Enhanced previous summer temperature at both study sites could reduce lumen size, impede water transport to the tree apex and subsequently, lower black spruce productivity. However, higher winter temperatures at Pauciflora Fen and greater winter precipitation at Poplar Fen could increase wood density and thus, mitigate potential for cavitation and/or tree mortality in reoccurring drought conditions. As drought events increase in both duration and intensity in northern Alberta (Kettridge & Waddington, 2013), reduced spring precipitation may hinder cell production and cell enlargement of black spruce stands in warmer, drier hydroclimates.

This is the first study to evaluate the influence of a road on peatland black spruce anatomical features in the AOSR. Despite the volume of fugitive dust collected adjacent to the road in 2019, there was no clear effect of fugitive dust on black spruce anatomical features. Future studies may examine a potential positive impact of road dust on black spruce growth due to the observed increase in cell size following road construction. Further characterization of the dust-anatomy relationship should consider dust particle size, chemical composition, rain variability, and wind direction. Given the established relationship between cell size and water availability and the observed increase in cell size to the west of the road ($p < 0.05$) following road construction, it is assumed the water table shifted as a result. However, the complex nature of water table variation was not able to be captured using a single well with bi-weekly measurements. The similarities in water table depth on opposing sides of the road in 2019 could be an example of a peatland's ability to recover and stabilize following disturbance. Northern peatland landscapes with long-term records of water table depth measurements should be prioritized for future wood anatomy studies. Additionally, there was no evident shift in anatomical feature response to daily climatic conditions after road construction. The placement of the road, sitting at an elevational high relative to the swamp area (Hu & Elmes, personal communication), likely mitigated road-related impacts on black spruce anatomy.

Large-scale atmospheric patterns, such as the Pacific Decadal Oscillation (PDO), have influenced tree-ring growth in the northern reaches of North America. Regional ring-width trends within this study presented a potential connection to the PDO, specifically between 2000-2019 for black spruce at Poplar Fen and Heaven Swamp. Unfortunately, the duration and data limitations of this study did not allow for a comprehensive analysis of the PDO influence on black spruce growth of the AOSR.

The compounding effects of a warming climate and the escalation of anthropogenic disturbance on peatland black spruce growth in the AOSR is still relatively uncertain mainly due to complex localized conditions. However, this study has successfully taken steps to understanding future black spruce survival and productivity within the AOSR. Nevertheless, this study highlighted key determinants for northern peatland black spruce growth that require further investigation.

4.2 Limitations and Future Research

Assessing climate-anatomy correlations at a large temporal scale was limited by the available meteorological data for Pauciflora Fen and Poplar Fen. Tree core quality and characteristics were also limiting factors for both the master chronology development as well as the anatomical analysis for all three study sites. Thus, instances in which older samples (more rings) were forfeited due to quality and replaced with younger samples (less rings) of higher quality. Additionally, further analysis of the Pacifica Decadal Oscillation influence on black spruce growth was limited by instrumental records and tree-ring data.

Black spruce sample size at all three study sites was the minimum suggested *n* for quantitative wood anatomy (QWA). This was a result of the allotted time and scope of the studies. Sample size for all three sites were further reduced for anatomical feature comparisons between sites/subgroups because of tree height. It is recommended that future QWA studies in northwestern Canada target trees of similar height and increase total sample size and sample area where possible.

Determining the long-term effects of water table trends at all three study sites was difficult given the lack of available data. Given the observed significance of water table depth on wetland tree growth (Bocking et al., 2017), future research should consider wetland sites with long-term water level records. The vapour pressure deficit (VPD) of an area implies to what extent water may be extracted from terrestrial ecosystems and holds implications for tree water use. The observed link between upland black spruce anatomy and VPD (Puchi et al., 2020) should be considered for future black spruce research in wetlands of northwestern Canada.

The fugitive dust collectors at Heaven Swamp measured the total dust load at varying distances away from the road for 30 days in the growing season of 2019. However, other factors, such as particle size, chemical composition, wind direction (Farmer, 1993), and rainfall (Matsuki et al., 2016), determine the relative impact of fugitive dust on tree growth and health. The aforementioned variables should be considered, in future, when examining the relationship of fugitive dust from roads and black spruce growth in the Athabasca Oil Sands Region.

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Appendix 1

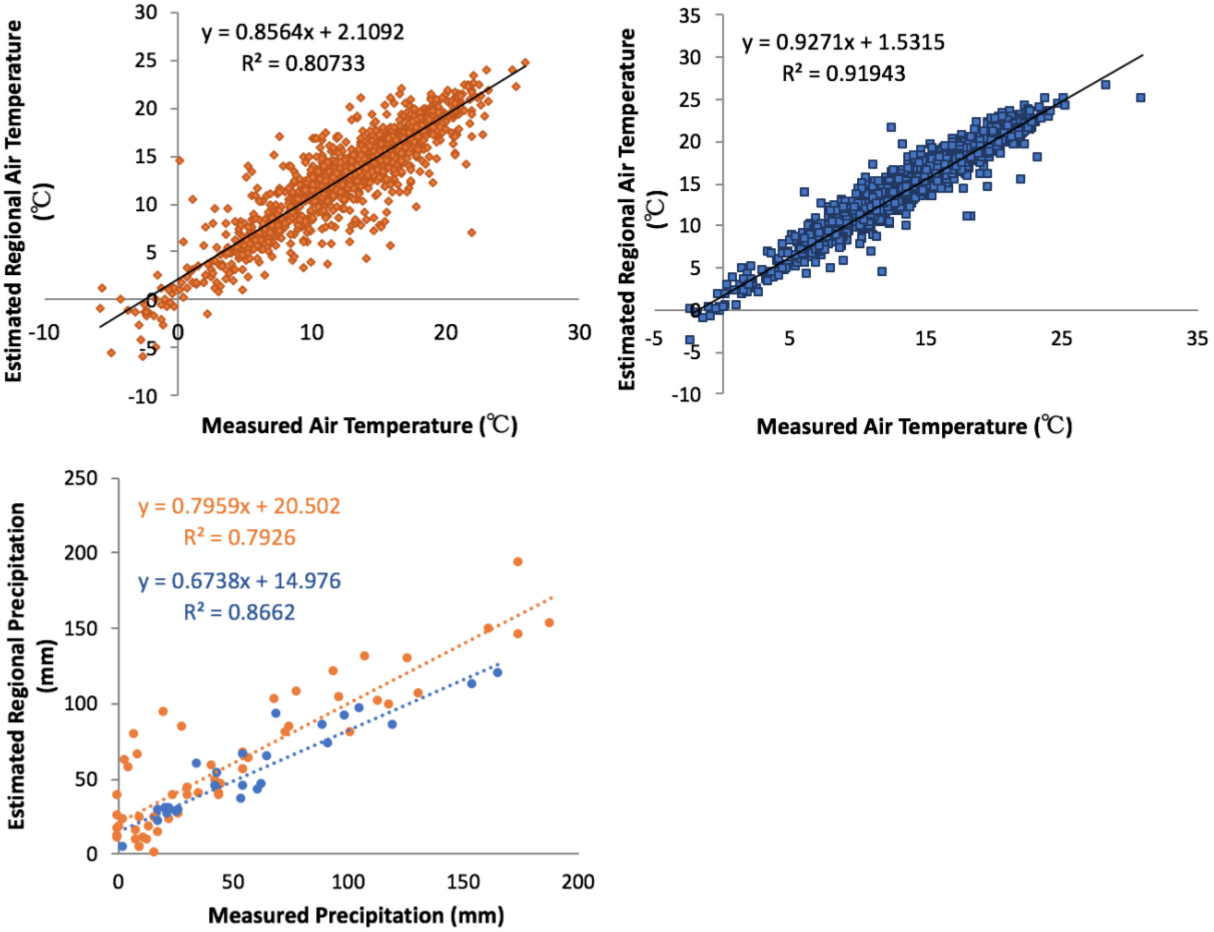

Figure A-1. A comparison of estimated regional daily air temperature and measured site-level air temperature from 1961-2019 at Pauciflora Fen (top left) and Poplar Fen (top right). Monthly measured precipitation against estimated regional precipitation (mm) from 1961-2019 (bottom left). Pauciflora Fen (orange) and Poplar Fen (blue), Fort McMurray, Alberta, Canada. Regional daily air temperature and precipitation was collected from the ACIS (Alberta Agriculture and Forestry, 2019).

Appendix 2

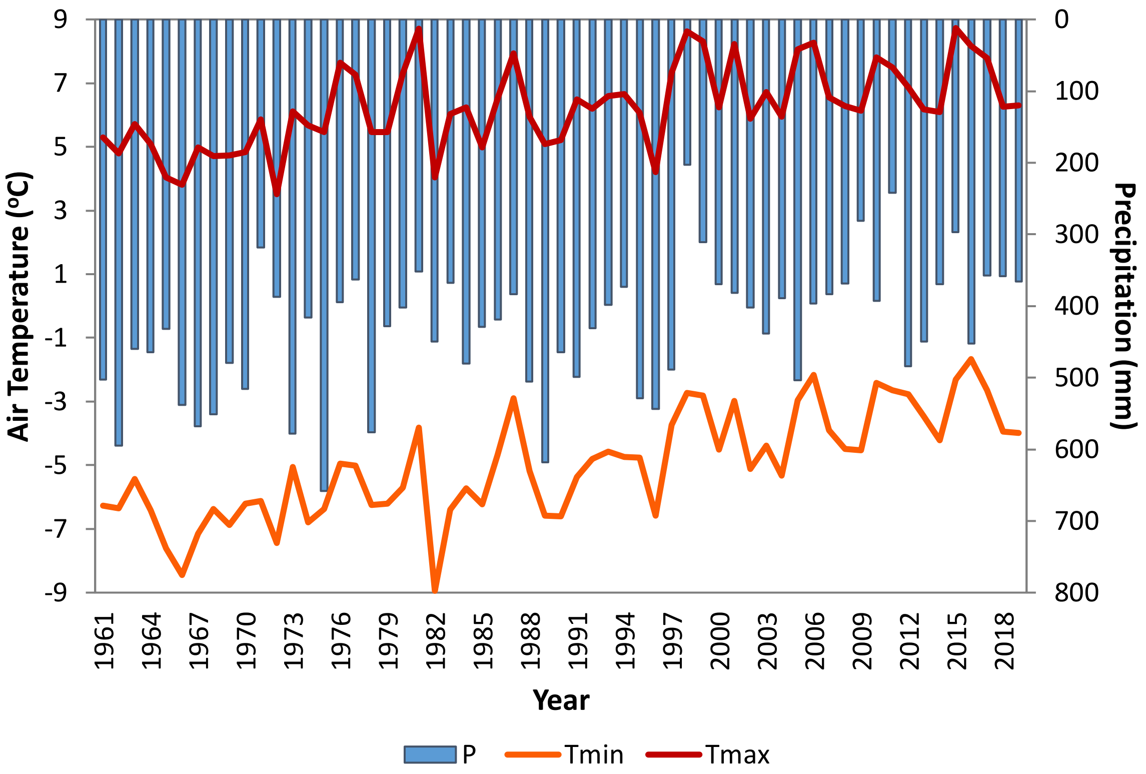

Figure A2-1. Maximum and minimum annual air temperature (°C) and annual precipitation (mm) for the period of interest (1961 - 2019), Heaven Swamp, Fort McMurray, Alberta, Canada**.**

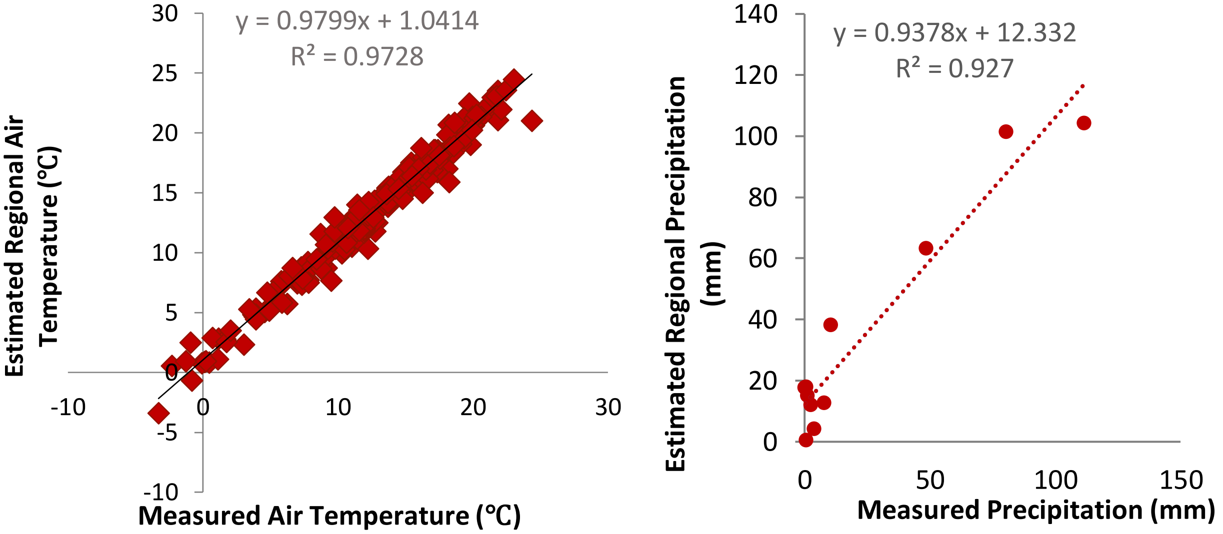

Figure A2-2. Measured site-level against estimated regional daily average air temperature (°C; left). Measured precipitation against estimated regional precipitation (mm; right), Heaven Swamp (2018-2019), Fort McMurray, Alberta, Canada.

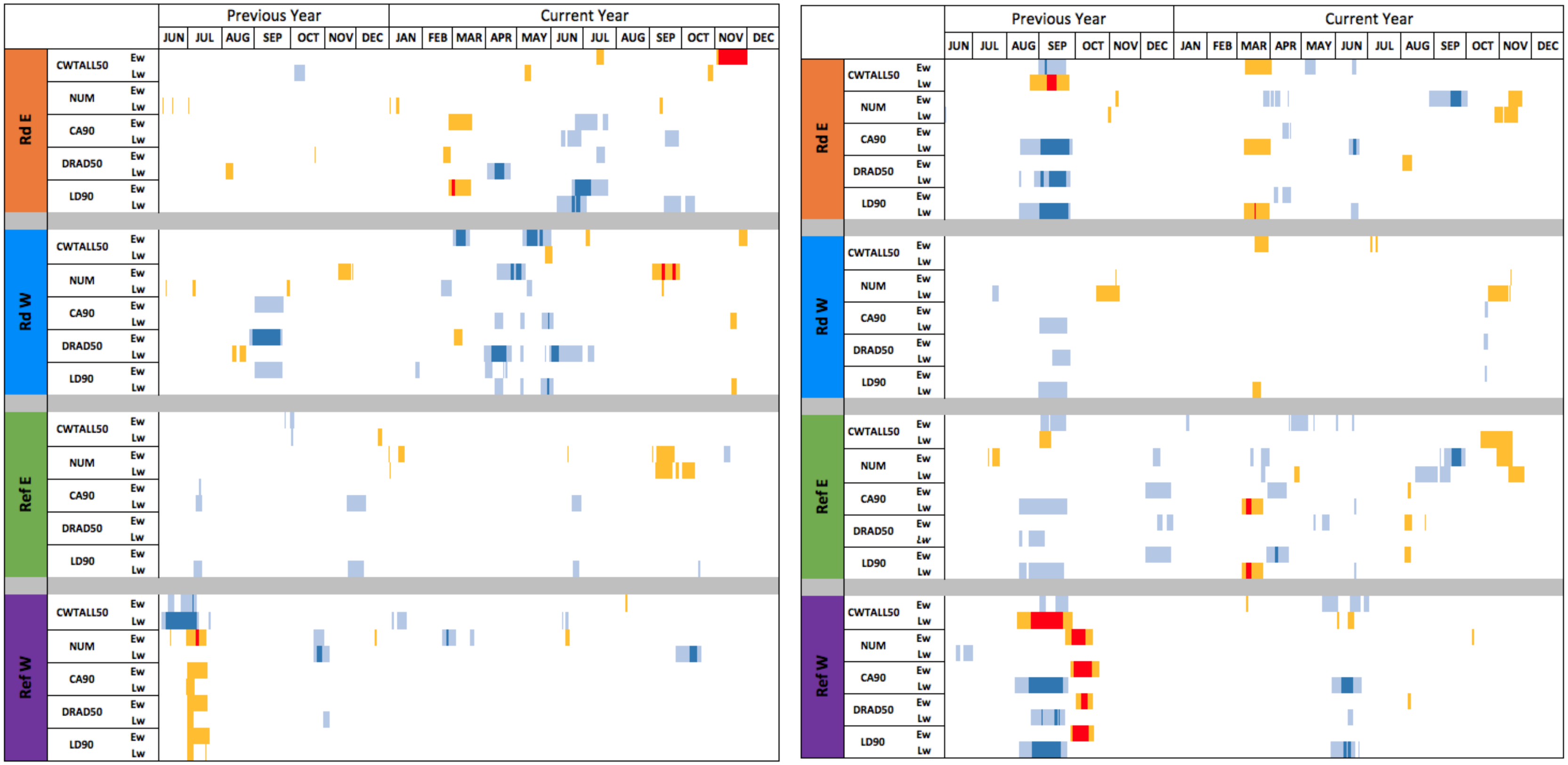

Figure A2-3. Significant correlations between maximum air temperature (T_{max}) and the anatomical features (CWTALL50, NUM, CA90, DRAD50, LD90) of the EW and LW cells for trees sampled in the four subgroups (Rd E, Rd W, Ref E, Ref W) at Heaven Swamp. Climate data were organized in 30-day windows, centered to the end of the window, moving with a 1-day step from the previous year's June to the current year's December. Correlations are for the previous and current growing years prior to road construction (left; 1961 - 1978) and after road construction (right; 1980-2019) and are statistically significant ($p < 0.05$). Left figure key: strong positive correlation (red; $x > 0.618$), positive correlation (yellow; $0.497 > x > 0.618$), strong negative correlation (dark blue; $x < -0.618$), negative correlation (light blue; $-0.497 > x > -0.618$). Right figure key: strong positive correlation (red; $x > 0.437$), positive correlation (yellow; $0.316 > x > 0.437$), strong negative correlation (dark blue; $x < -0.437$), negative correlation (light blue; $-0.316 > x > -0.437$).