THE RESPONSE OF SUBALPINE FIR (*Abies lasiocarpa* (Hook.) Nutt)) GROWTH AND RESILIENCE TO CLIMATE CHANGE IN NORTHERN ROCKIES, INTERIOR BRITISH COLUMBIA, CANADA

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Abstract

Understanding forest growth and resilience under global climate change is crucial for forest management, to maintain wood supply for future. In this research, I focused on the response and resilience of subalpine fir (*Abies lasiocarpa* (Hook.) Nut)) growth to climate variables and severe drought events at five stands located along northern slopes of the Rockies in northern BC, Canada. Results revealed that temperature (especially summer and previous fall) was the most important climate factor controlling growth of subalpine fir trees at study sites. The lower the latitude, the more summer temperature negatively effected tree growth. Also, results showed that subalpine fir trees were resilient to very dry conditions at study sites, when considering the growth recovery period to drought was between 1 to 2 years. The lower the latitude, the faster the trees recovered from drought. However, subalpine fir trees located at higher latitudes were more resistant to the effects of drought.

Table of Contents

List of Tables:

List of Figures:

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Chapter 1. General introduction

Introduction

1.1 Context

Under all emission scenarios explored by the Intergovernmental Panel on Climate Change, global average temperature and sea levels are predicted to rise. Global average temperature is projected to rise by 1.4 °C to 5.8 °C between 1990 to 2100 (IPCC 2013), and the average global temperature has already increased by 0.82 ºC during the period between 1880 and 2012 (IPCC 2014). Summers are generally predicted to be warmer and drier, while winters are likely to be warmer and wetter (Mote 2003). Climate vulnerability, in areas susceptible to disproportionately large changes in the climate system, is projected to be particularly high (Lindner et al. 2010). In this context, cold temperature ecosystems consisting of cold-adapted species are particularly sensitive to recent global warming (Körner 1999). Of all forests around the world, Canada is ranked the third largest in forested area (Canadian Forest Service 2017), and several studies have indicated that forest habitats may be at risk because of global warming (Seager et al. 2007; Candel-Pérez el al. 2012).

The impact of climate change is evident as reflected by the 2ºC increase in average annual temperatures in the boreal regions in Western Canada during the 1950-2003 period (Price et al. 2013). Forests are among the most sensitive ecosystems in the world, affected by global climate change. Boreal forests in British Columbia (BC) are among vulnerable ecosystems which have also been impacted by global climate change (Hamann and Wang 2006; Lo et al. 2010) as well as forest ecosystems of central British Columbia (Zhang et al. 1999; Wang et al. 2012). Species at the edge of their natural range or growing beyond their niche are considered to be particularly vulnerable (Handewinkel et al, 2013; Seidl et al, 2011). High-altitude forests will be specifically vulnerable if the frequency of disturbances increases considerably (Keane et al 2018). Generally, temperature is considered more important to growth of tree species than precipitation in northern interior BC (Splechtna et al. 2000; Wood and Smith 2015; Cortini et al. 2016) most probably because this region has long and cold winters (Wood and Smith 2015). Studies in the boreal forest of northwestern Canada and in the Canadian northern Rockies show that the annual-rings of these species are mostly under control of summer temperature (D'Arrigo et al. 1992; Szeicz and MacDonald 1995; Luckman et al. 1997). Adams (2014) points out that global warming is expected to initiate long-term changes in cellular wood structure and radial growth resulting in basic shifts in productivity and wood quality over vast areas. Consequently, BC forests may be in danger of tracheid degradation and/or lower wood product quality for final products like pulp and paper (Wang et al. 2012).

Fibre length is defined as the length of wood cells along the longitudinal axis, also called tracheid length in softwoods (Van Leeuwen et al. 2011). Fibre length is an important wood quality attribute for timber items considering that longer fibres result in higher wood quality for the pulp and paper industry because of the positive relationship between fibre length and paper strength (Jozsa and Middleton 1994). Furthermore, Jozsa and Middleton (1994) found that trees generally produce large diameter, thin-walled fibres during the early part of the growing season, and smaller diameter, thick-walled fibres in the late summer and end of growing season, both of which are also fibre characteristics used in wood quality determination. Recently, expanded timber harvesting of spruce (*Picea* sp.) alongside different species like *Pinus* sp., has diminished spruce supplies in some lower-elevation habitats in the northern Rockies (Kean et al. 2018). Furthermore, the convergence of invasive pests including mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*), and expanded rapidly spreading wildfires which are for the most part climatically driven (Abatzoglou and Williams 2016) recently in interior BC. Therefore, the wood supplies tied with high wood quality needed by the wood factories are affected, especially for future timber supply and silvicultural plans. Thus, the forest and wood products industries are being forced to consider higher elevation forested zones and other species, such as subalpine fir (*Abies lasicarpa*) for timber supplies.

1.2 Background

Subalpine fir is a broadly dispersed North American fir which territory range stretches out from 32° 52′ N latitude in Arizona and New Mexico to 64° 30′ N in the Yukon Region, Canada (Alexander 1990). This species is one of the fundamental timber yield species in the boreal district of British Columbia (Splechtna et al. 2000), of significance both economically and environmentally. Subalpine fir is a shade tolerant species and in the lower elevations of the Engelmann Spruce – Subalpine Fir (ESSF) biogeoclimatic classification zone; it is the most abundant in the understory. However, at high elevations of this zone and in some wetter areas, subalpine fir frequently dominates the forest canopy (Coupe et al. 1991). In the Rocky Mountains of British Columbia and Alberta south of the Peace River, subalpine fir grows between 914 to 2134 m (3,000 to 7,000 ft), but it is more abundant above 1524 m (5,000 ft) (Alexander et al. 1984). From ecological aspects, subalpine fir habitat is restricted to cold, humid habitats. Subalpine fir can be sensitive to some types of climate change, for example, it has low tolerance to high temperatures (Alexander et al. 1990).

Subalpine fir can be a climate sensitive species (Zhang et al. 1999). Due to accumulation of snowpack in subalpine fir stands, growth of this species is limited to a short growing season (Peterson et al. 2002). Zhang (1999) showed that growth of subalpine fir is limited by June temperature and July precipitation. However, fall temperature positively correlated with subalpine fir growth in northwestern US (Peterson et al. 2002). Generally, at higher latitudes and on northern slopes where soil is wetter, subalpine fir growth is limited by late snowpack melting and as a result shorter growing season because of delay in start of growing season (Peterson et al 2002). At lower latitudes and warmer sites, summer temperature could be more detrimental to growth of subalpine fir (Ettl and Peterson 1995).

Some wood anatomical traits, including density and microfibril angle, are among the most important determinants for wood stiffness and strength and therefore, wood quality (Zhang et al. 2020). Microfibril angle (MFA) is a measurement attributed to the angle of cellulose microfibrils located in the secondary cell wall of fibres to the tracheid axis (Barnett and Bonham 2004). MFA affects strength and elasticity of wood (e.g. shrinkage behavior), which influences wood quality (Huang et al. 2003; Donaldson 2008). The decrease in microfibril angle from the pith outwards to the bark produces higher strength mature wood in comparison to juvenile wood (Mansfield et al. 2009). Mature wood compared with juvenile wood has smaller microfibril angle and higher wood density (Zhang et al. 2020). Therefore, wood quality can be related to rate of tree growth and proportion of mature and juvenile wood within a stem. The higher the density, the higher the quality of wood (Zhang et al. 2020) and strength (machinability) (Josza and Middleton 1994). Some wood anatomical traits including proportion of earlywood and latewood, and ring width are mostly controlled by environmental factors rather than genetic traits (Lenz et al. 2010). Wood density can be calculated through the ratio of latewood proportion to earlywood proportion (Van Leeuwen et al. 2011); Juvenile wood and earlywood generally have lower density values (Mansfield et al. 2009). Radial growth rate which influences on wood quality (Zhang et al. 2020) is both genetic and climatically controlled of which environmental parameters generally have been shown to be more important than genetic parameters (Downes and Drew 2008). Latewood contains dense cells attributed to the slower growth periods in the end of growing season (late summer).

Conversely, earlywood includes less dense cells which form in the periods of faster growth in first months of the growing season (early summer). Generally, it can be inferred that earlywood cells form when climate parameters including the most influential ones (temperature and precipitation) are optimum (first months of growing seasons) and latewood cells forms when reduction starts in amount of precipitation and temperature at the end of growing season (Sun et al. 2016). Looking deeper into wood properties may clarify intra-annual wood property variation, which forms within months of the year that are probably more sensitive to climate variations than tree-ring width, which forms annually.

The resilience of forest ecosystems has recently received increased attention in response to growing concerns about climate change, and has been proposed as an important factor in addressing future uncertainties in ecosystem management (Biggs et al. 2012; Seidl 2014). Meanwhile, wide-ranging changes in climate and disturbance regimes, including prolonged drought and increased wildfire size and frequency, have raised concerns about forest resilience to environmental climatic change (Abatzoglou and Williams 2016; Seidle et al. 2016).

Flexibility or resilience can be extensively described as a system's capacity to deal with perturbance and to endure in the face of it (Carpenter et al. 2001) or potential ability of an ecosystem to be able to return to the preconditions including physiological condition, composition and structures, after disturbance (Holling 1973). Hence, a forest’s resistance to climatic stressors depends on the trees’ ability to restore and survive (Hanklin et al. 2018). It should be considered that stand level variables may have stronger influences on forest resilience than climate. For instance, Seidl et al. (2017) showed that the role of forest age in forest resilience was highlighted where old forests and overstock conditions have especially low resilience to perturbations. Furthermore, in those stands that trees have already experienced several drought events in recent past years, resilience to future disturbances may decreases (Gutschick and BassiriRad 2003; Seidl et al. 2017). It usually takes a few years (2 to 4 years on average) for the trees to recover after perturbance even when climate conditions return to the normal (Anderegg et al. 2015).

1.3 Research gap

Few studies have focused on the relationships between growth and climate variations in subalpine fir in northern BC. Furthermore, most previous studies have focused on tree-ring width, and the number of articles focusing on anatomical traits including fibre/cell wall thickness (FWT), ring density (RD), fibre width (FW), and MFA of subalpine fir is small. Also, there is a lack of information on the relationship between climate and forest tree resilience and study of legacy effects in subalpine fir forests of northern interior BC, as these kinds of studies are fairly new and were only initiated in recent years.

1.4 Research Questions and Objectives

1- How do climate variations (temperature and precipitation) affect wood anatomy (RW, EW, LW, MXD, MND, RD, FL, MFA, FWT, FW) of subalpine fir at five geographically different stands in northern interior BC?

Objectives:

- Determine if there are any statistically significant relationships between climate variations and radial growth of subalpine fir in northern British Columbia, and, if so, determine and compare variation in subalpine fir's wood properties with temperature and precipitation at study sites.
- Evaluate whether intra-annual wood characteristics show stronger relationships with climate than do annual-ring widths, through correlation analysis.

2- Do relationships between radial growth and climate show evidence of resilience to drought, in subalpine fir stands in interior BC? If so, do these relationships show differences in drought resilience with changes in latitude in northern interior British Columbia?

Objectives:

- Evaluate patterns in deviations from the average in wood measurements as indicators of resistance, resilience or recovery after severe climate (e.g., drought) in subalpine fir forests. Compare measurements and trends at five study sites with different latitudes.
- Evaluate how long (years) it takes to subalpine fir recover after severe drought (legacy effects) in the five study sites of the Rocky Mountains, British Columbia, Canada.

This thesis contains two data chapters that address the above questions, and a concluding chapter in which data chapters are synthesized. Chapter 2 explores wood properties including RW, EW, LW, RD, MXD, MND and FL, FWT, FW, MFA at five natural and unmanaged stands near Prince George along high elevations of the Rocky Mountains in BC, Canada in relation to climate. Chapter 3 examines resilience of subalpine fir (study of legacy effects) at five study sites with severe drought and identifies recovery durations after severe drought in subalpine fir.

In this research, I chose to focus on latitude for this particular study, while keeping elevation and aspect consistent. I acknowledge that significant variation also exists in tree growth based on elevation and different aspects as well, but these were outside of the scope of this study.

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Chapter 2: Relationship between climate and wood anatomical properties of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt)) located in the Rocky Mountains of northern interior British Columbia, Canada

2.1 Abstract

Understanding the response of boreal forests to climate change is critical for proper forest management and for sustainable wood supply. In this study I focused on climate change impacts on wood anatomy (ring width, earlywood, latewood, ring density and fibre properties) of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.)) at five forest stands located along the northern aspects of the Rocky Mountains in northern BC, Canada. Results revealed that intra-annual wood characteristics showed stronger statistical correlations with climate indices than did simple tree-ring width orders. Growth of subalpine fir, measured by ring widths, densities, fibre lengths, and fibre widths was influenced largely by summer temperature, previous fall temperature, and to a less extent September precipitation. The lower the latitude, the greater the negative effect of summer temperatures on radial growth at study stands. Generally, temperature was the most important climatic factor in controlling growth of subalpine fir at study sites.

2.2 INTRODUCTION

2.2.1 Context

Global average temperature is projected to rise by 1.4 °C to 5.8 °C between 1990 to 2100 (IPCC 2013). Meanwhile, northern latitude ecosystems seem to be more sensitive to global climate change that may have dramatic consequences in boreal ecosystems (IPCC 2013). Over the past decades, British Columbia, Canada (49°-60° north latitude) has experienced a warming trend that approximately matches climate change predictions from general circulation models discussed in the mid 1990s (Johns et al. 1997, Mote 2003). Although same general models predict climate to be warmer and wetter in pacific Northwest of north America (Lo et al. 2010; Fleming and Whitfield 2010), and forests of boreal regions are expected to benefit from global climate change by enhancing their primary and secondary growth by 2100 (Moring el al. 2009), regions of British Columbia may experience warmer and drier years along with increased drought stresses (Lo et al. 2010; Jiang et al. 2016). A growing number of studies suggests that global climate warming affects a wide range of species and ecosystems (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003).

One of the characteristics of determining the quality of wood is the density of the wood. Boreal forests, which compose 25% of all forests on earth, yield almost 33% of lumber products and 25% of pulp and paper exports (Burton et al. 2010). Generally, the mature wood portion of a tree's profile is made with dense, longer fibres or tracheids fibre length (FL), thicker fibre walls (FWT) and lower micro fibril angel (MFA) when compared to juvenile wood (Zhang et al. 2020). These characteristics are usually associated with higher wood quality (Plomion et al. 2001; Huang et al. 2003). Wood anatomy is controlled by both environmental and genetic traits (Downes and Drew 2008; Downes et al. 2009). Past studies demonstrate that wood anatomical traits are affected by changing climate (Wood and Smith 2012; Pitman and Smith 2013; Watson and Luckman 2016). Furthermore, some traits like earlywood width (EWW) or (EW) and latewood width (LWW) or (LW) are shown to be more affected by environmental and climatic factors than genetic factors (Lenz et al. 2010). Therefore, understanding the impacts of climate change on wood anatomical traits including annual-ring-with (RW), earlywood width (EWW), and latewood width (LWW), earlywood density (EWD), latewood density (LWD), maximum density (MXD), minimum density (MND), and ring density (RD) is crucial to understand tree stability in changing climates. EW is among those anatomical parameters that are directly controlled by climate variations (Nabeshima et al. 2015)

2.2.2 Background:

EW and LW are defined as the portion of the ring in which wood density is respectively below or above the mean wood density of the ring (Drew et al. 2013). EW forms during the first months of the growing season when temperature and precipitation are optimal. In warmer years, the proportion of EW in a tree-ring is higher than LW, especially at higher elevations (Wang et al. 2002; Deslauriers et al. 2003), and on south-facing, warmer slopes (Huang et al.2011). Generally, production of large, thin-walled EW cells occurs at the onset of the growing period (Barnett and Jeronimidis 2003). The relative production of EW can be attributed to the previous growing season's energy reserves. Optimal EW production occurs in June and July when photoperiod is at highest points (Rossi et al. 2006). Conversely, LW forms at the end of the growing season when precipitation and temperature decline. Onset and termination of LW formation in boreal forests may range from the end of June to mid-August, depending on both species and location (Huang et al. 2011; Zhai et al. 2012). Furthermore, that when summer is cold, formation of LW starts earlier, and as a result the proportion of LW to EW in tree-ring width is higher (Huang et al. 2011). Huang et al (2011) also found that on north-facing slopes, the proportion and formation of LW was higher than, on south-facing slopes, likely due to colder temperatures characteristic of north-facing slopes. LW is very sensitive to temperature and water availability since its formation is contingent upon carbohydrate accumulation produced by photosynthesis (Sun et al. 2016). Several studies report a negative relationship between RW and RD at higher elevations (Lindström et al. 1996; Dutilleul et al. 1998) which may strengthen the idea of formation of denser wood at slower-grown higher elevations.

Wood density is defined as a wood substance for a given volume of wood (Zobel and Van Buijtenen 1989). Together, wood density, tracheid size, and wall thickness, are the most important wood characteristics in determining wood quality. Some indicators of wood quality such as stiffness, machinability and strength are directly determined by wood density (Wimmer et al. 2002b). Wood density changes within a tree from juvenile to mature, and from EW to LW, and generally, lower wood density is found in juvenile and EW (Mansfield et al. 2009). It can be inferred that juvenile trees with fast growing traits produce larger volumes of wood and consequently lower wood density. However, mature trees and species grown in dry or cold climate situations have slower growth rates and produce denser wood (Camarero and Gutierrez 2017).

There are some studies worked on cell size and cell wall thickness under impact of climate change (Larson et al. 2001; Rossi et al. 2008; Rossi et al. 2011; Rossi et al. 2014). The wood production or xylogenesis process begins in early spring with the formation of the first row of xylem cells, which these cells have thin walls and an increase in their number and cell division usually continues until mid-summer (Rossi et al. 2014). Later in summer and near end of the growing season, the number of produced cells no longer changes, but cell wall thickening increase until cell become mature and then the process of lignification has been finished (Rossi et al. 2014).

Therefore, cells formed in the early part of the growing season display larger radial diameter, thinner cell walls with a larger lumen and relatively lower density (earlywood) when compared to cells formed later in the growing season which have a smaller radial diameter, thicker cell walls with a small lumen and higher density (Panshin and de Zeeuw 1980).

Fibre length (FL), known as tracheid length in conifers, is defined as the length of wood cells along the longitudinal axis (Van Leeuwen et al. 2011). The longer the fibre, the better the quality of wood and the stronger the paper as a final product (Jozsa and Middleton 1994). Climate variations, especially temperature, affect FL (Zhang et al. 2020). Generally, in conifers, tracheids are responsible for water transportation within the plant (Badel et al. 2015), as well as providing mechanical support (Vaganov et al. 2006). Tracheid size is positively related with water availability when cells are forming (Vieira et al. 2009).

Micro fibril angle (MFA) is angle of cellulose microfibrils in the secondary cell wall of tracheid (Wimmer et al. 2002b). These microfibril's function to provide wood elasticity and wood strength; higher wood quality is usually associated with lower microfibril angles (angles more parallel to the tracheid axis) (Huang et al. 2003). In conifers, MFA changes from bark to pith with smaller angles found towards the bark (in mature wood) and larger angles toward the pith (juvenile wood) (Van Leeuwen et al. 2011). The smaller the MFA, the higher the elasticity and the strength of the wood (Donaldson 2008). MFA is controlled both genetically (Donaldson 2008) and environmentally (Drew et al. 2013) and it seems that among environmental factors, temperature and water availability have the strongest effect on MFA. Drew et al. (2013) also showed that smaller MFA was attributed to summer temperature while larger MFA was correlated with spring temperature, and MFA increased with rainfall and decreased with drought and water stresses.

2.2.3 Relationships between RW, EW, LW, and climate

Radial growth is the diametric growth of trees represented by annual-rings, which is controlled by both genetic and environmental factors. However, radial growth is generally thought to be more controlled by climatic factors than by genetic parameters (Downes and Drew 2008; Lenz et al. 2010); climate parameters showed higher correlation with radial growth, EW, and LW than genetic influences did in white spruce (*Picea glauca*) (Lenz et al. 2010). Ring growth is shown to be affected by both current growing season and previous growing season climate characteristics (Fritts 1976).

The boreal forests in northern BC are limited in growth by temperature and long, cool winters (Wood and Smith 2015). Hence, small changes in temperature in these regions could have large proportional impact on wood properties. For examples, subalpine forests, adapted to cold temperatures and large snowpack, may experience diminishing proportion of snowpack, accelerated spring snowmelt, and expanding growth period leading to significant changes in radial development (Wood and Smith 2015). In British Columbia in particular, fewer studies have been conducted on relationships between climate variations as limiting factors and radial growth. According to a study by Bouriaud et al. (2005), climate may have different impacts on tree-ring traits including RW, EW, LW and density depending on species and stand conditions. In interior central BC Wood et al. (2016) reported that temperature in early summer showed higher correlation with RW formation of spruce stands than late summer temperature. Spletchtna et al. (2000) found that radial growth of subalpine fir at higher elevations in BC was more impacted by temperature than precipitation. they found that in general, impact of the temperature on radial growth is more than that of precipitation. They also pointed out that tree-ring characteristics of subalpine fir at high elevations were mostly correlated with summer temperature of current growing season and with July temperature of current years as well as fall temperature of the previous year. Brook et al. (1998), in a study on tree-ring characteristics of Black spruce (*Picea mariana* (Mill.)) and Jack pine (*Pinus banksiana* Lamb.) in central Canadian boreal forests, found that cool and wet climate is favorable for black spruce while high summer temperatures and spring precipitation were favorable for jack pine. From different studies done on climate impact and forest growth responses it can be inferred that response of tree anatomical traits to climate variables depends on the species and site conditions.

2.2.4 Intra-annual wood characteristics vs annual-ring width

Intra-annual wood anatomical traits are generally more sensitive to change in climate variations than tree-ring width. The higher correlations with climate records are particularly clear in wood density and fibre properties (e.g., fibre length and microfibril angle) (Drew et al. 2013; Liang et al. 2013). In stands where development is reliably limited by few climatic parameters, variation in tree-ring widths is connected to these climatic restricting variables (Fritts 1976). However, in many applications, RW estimations just give a growing season or annual portrayal of climatic information not specific and/or short duration intervals like the beginning or end of growing seasons (D'Arrigo et al. 1993). Furthermore, trees regularly do not grow at their upper edge limit for examining climate impacts through RW. To measure and understand exact ecological changes, even in small periods of time under changes in climate, intra-annually measured wood properties including cell size (cell divider thickness, cell number), FL and FWT demonstrate higher correlations to climatic variables than do RW orders (Wimmer and Grabner 2000; Davi et al. 2002). Considering that wood density is a significant component for anticipating end-use qualities of wood, it is important to understand how wood density of timber species shifts with environmental elements. For instance, in comparison to RW, MXD distinctively shows more sensitivity (Davi et al. 2002) and is known to give altogether better intermediary records of growing season conditions (D'Arrigo et al. 1992). These significant wood density-climate correlations are credited to an increasingly conspicuous similarity between wood density and climate from year to year.

2.2.5 Wood quality and need for switching to alternative species in BC

One of the essential requirements for sustainable timber management in Canada's future is comprehension of the varieties and options in forests production across various locales and zones. One zone could be the Engelmann Spruce-Subalpine Fir (ESSF) zone which has high timber, watershed, wildlife, and recreational resource values (Hamann and Wang 2006). In interior British Columbia, the ESSF zone represents a large and important timber supply (Hamann and Wang 2006). In this zone, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.)) along with Engelmann spruce (*Picea glauca* x Engelmannii) are prevalent and dominant tree species in the continental, Rocky Mountains of British Columbia, Canada (Meidinger and Pojar 1991). However, recently expanded timber harvesting of spruce wood logging alongside other species like pine (*Pinus* sp.) as well as expanded wildfires have diminished mature spruce availability in some lower-elevation habitats in the Northern Rockies (Keane et al, 2018). Furthermore, because of the convergence of invasive pests including mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*) (Abatzoglou and Williams 2016), the wood supplies needed by the wood product manufacturers are declining in interior BC. Therefore, forest managers need to think about some alternative tree species to replace the above-mentioned species, and to guarantee sustainable forest resources for future timber supply and silvicultural plans. It seems subalpine fir can be a proper option. At higher elevation in the ESSF zone and more wetter areas, subalpine fir becomes the dominant species (Alldritt-McDowell 1998). Along montane forest, central and subalpine forests of British Columbia, subalpine fir, for example, is a major merchantable species (Splechtna et al.

2000). Of about four native fir species grown in Canada, subalpine fir has the widest growth range in British Columbia (Jozsa 1991). Subalpine fir's wood is odorless, light-weight, soft, and low in bending and compressive strength which is easy to work, glues well, and holds nails and screws fairly well (Alexander 1984). Its wood is primarily used for products such as lumber for home construction and for prefabricated wood products having excellent pulping properties (Alexander 1984). Its long fibres and light color permit subalpine fir to be pulped well (Anderson 1956; Alexander 1987). Overall, subalpine fir seems to be a good option to meet the wood demand of British Columbia in the future, considering its adaptation to cold climates specially at higher elevations.

2.2.6 Research Gap

This study aims at filling the gaps in knowledge on variation in subalpine fir wood anatomical traits (EW, LW, RD, FL, FWT, MFA) under varying climate. Specifically, this study identifies the regional interannual growth and development of subalpine fir at five latitudinally different study sites and the relationship between growth and climate in these environments over time. Although some dendroclimatic studies have been done to study subalpine fir wood properties in central and southern BC (Klinka et al. 1992; Chen and Klinka 2000; Splechtna et al. 2000), still very few studies have been completed studying subalpine fir's wood anatomy responses to climate parameters in northern BC (Zhang et al. 1999).

2.2.7 Objectives

This study aims to investigate how climate variables affect wood anatomy and growth of subalpine fir at five stands along northern slopes of the Rocky Mountains in northern interior BC. The objectives of this study are to: i) determine whether there are any statistically significant relationships between climate variation and RW, EW, LW, MXD, MND, RD, FL MFA, FWT, and if so, compare variation in subalpine fir's wood properties to temperature and precipitation at five geographically different sites in northern British Columbia, ii) Evaluate whether intra-annual wood characteristics show stronger relationships with climate than do annual-ring widths, through correlation analysis.

Hypothesis

I expect that subalpine fir trees would be responsive to climate in targeted locations and ring density to be more sensitive to climate than ring width. Null hypothesis would be assuming there is no statistically significant relationship between wood parameters and climate. So, if *P* value is less than 0.05 then we reject the null hypothesis.

2.3 Method:

2.3.1 Site selection:

Subalpine fir trees were selected from five natural (not planted or previously harvested) sites located along northern slopes, between 60 - 150 years old, at between 1120 to 1330 m above sea level, in northern BC, Canada. Study sites selected, from northwestern most to southeastern most, separated by latitude (55° 24′ to 53° 19′ N; 122° 32′ to 120° 07′ W) were: Pine Le Moray provincial park, Mount Chingee, Mount Averil, Grizzly Den and McBride peak, respectively (Figure 2.1; Table 2.1). The study sites were within a range of 450 to 480 km around Prince George city, BC, Canada, from highest latitude site (Pine Le Moray) to the lowest one (McBride Peak) (Figure 2.1). The reasons for choosing northern slopes as well as selecting higher altitudes were because abundance of subalpine fir is higher on these site types (Keane et al. 1994), and it has been suggested that subalpine fir is more vulnerable to climate change on northern slopes of the Rocky

Mountains than the southern ones (Keane et al. 2018). Additionally, at altitude above 1100 m, subalpine trees become the dominant species (as observed) in comparison to spruce within the Engelmann Spruce Subalpine fir zone (ESSF) and at higher elevations, trees are more sensitive to climate variations, which are preferable for dendroclimatic studies.

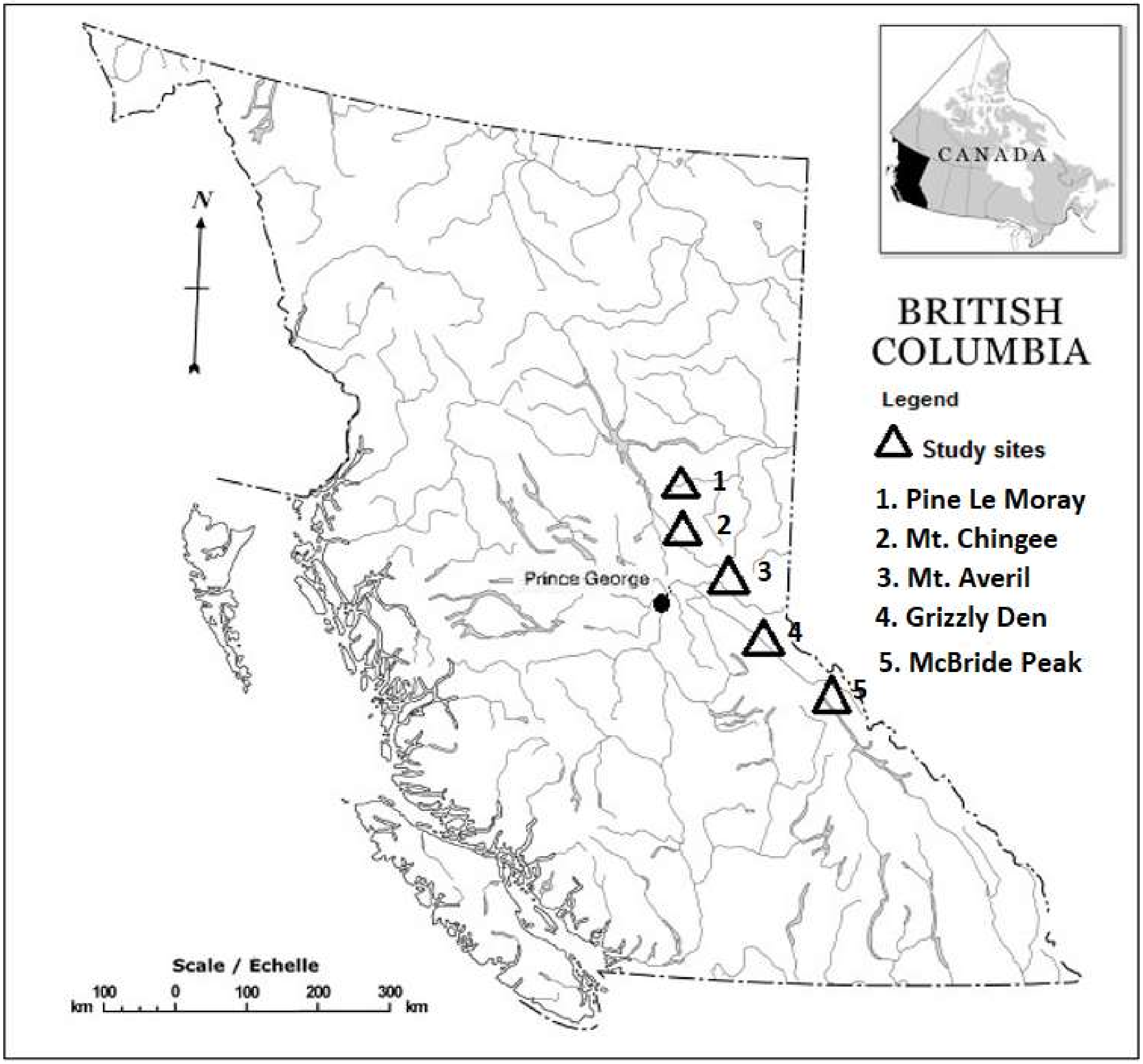

Figure 2.1. Location of sampling sites for dendroclimatic study of subalpine fir along north-facing slopes of Rocky Mountains in northern British Columbia. From top (highest latitude) to the bottom (lowest latitude): subalpine fir sampled in Pine Le Moray provincial park, Mount Chingee, Mount Averil, Grizzly Den and McBride Peak.

Table 2.1: Chronology characteristics and geographic information for subalpine fir (*Abies lasiocarpa*) at five sampling sites for dendroclimatic study along north-facing slopes of the Rocky Mountains in northern British Columbia (DeLong et al. 1993; Wang et al. 2016).

Geographic information													Tree characteristics		
Site Name	**Elevation (m)**	**Longtitude Latitude**	**Slope**	**Biogeoclimatic zone/ Subzone**	**Mean annual temperature (ºC)**	**Accumulative annual precipitation (mm)**	**Maximum teperature Month**	**Mimimum teperature Month**	**Soil texture**	**Indicator plants**	**Soil moisture regime**	**Nutrient regime**	**Core length (bark to pith) (cm)**	**Mean tree age (years)**	**Mean DBH (cm)**
Pine Le Moray	1120	-122° 32′ 55° 24′	N	ESSF Wet cold (wc3)	1.5	925	19.3 July	-15.4 January	Medium to coarse	goose berry [1] cranberry [2] devil's club [3] oak fern [4] mountain ash [5] thimble berry [6]	Sub mesic to mesic 3-4	Poor to medium B-C	21.5	90	43
Chingee	1220	-122° 53′ 55° 01′	N	ESSF Wet cool (wk2)	0	1060	16.7 July	-15.3 January	Medium to coarse	lady fern [7] gueens cup [8] black gooseberry [9] rhododendron [10] indian hellebore [11]	Mesi to sub hydric 4-5	Rich to very rich D-E	22.5	76	43
Averil	1270	-122° 25′ 54° 24′	NW	ESSF Wet cool (wk2)	1.3	1045	18 July	-13.2 December	Fine to coarse	huckleberry [12] gueens cup [8] oak fern [4] indian hellebre [11] five-leaf bramble [13]	Sub hydric 5	Poor to medium B-C	18	104	36
Grizzly Den	1250	-121° 30′ 53° 46′	N	ESSF Wet cool (wk1)	2	1085	19.3 July	-13.3 January	Fine to coarse	fireweed [14] black gooseberry [9] elderberry [15] black twinberry [16] rhododendron [10] lady fern [7]	Mesi to sub hydric 4-5	Poor to medium B-C	21	107	42
McBride Peak	1330	-120° 07′ 53° 19′	NW	ESSF Moist mild (mm1)	1.6	751	19.6 July	-12.7 December	Mid coarse	gooseberry [1] oak fern [4] fireweed [14] one-side wintergreen [17] alder [18] thimbl berry [6]	Mesic 4	Poor to medium B-C	20.5	71	41

1 Ribes uva-crispa; 2 Vaccinium subg. Oxycoccus; 3 Oplopanax horridus; 4 Gymnocarpium dryopteris; 5 Sorbus subg. Sorbus; 6 Rubus parviflorus; 7 Athyrium filix-femina; 8 Clintonia uniflora; 9 Ribes lacustre; 10 Rhododendr3on albiflorum; 11 Veratrum viride; 12 Vaccinium membranaceum; 13 Rubus pedatus; 14 Chamaenerion species; 15 Sambucus racemose; 16 Lonicera involucrate; 17 Orthilia secunda; 18 Alnus sp.

All sample sites were within the ESSF zone, found at biogeoclimatic zone above 1000 m a.sl (DeLong et al. 1993) ensuring that subalpine fir was the dominant species in study stands for dendroclimatic studies to minimize interspecies competition. Cores at sampling sites were all taken from the similar slopes (north-facing slope) to ensure sampling conditions were equal at different sites. Biogeoclimatic variant of each site was determined with review of site characteristics and Biogeoclimatic Ecosystem Classification land management handbooks (DeLong et al. 1993) (Table 2.1).

2.3.2 Sample collection and preparation

At each stand, 22 dominant mature trees were sampled for statistical robustness (Anderegg et al. 2015). Subalpine fir trees were selected to the ecosystem relatively uniformly across soil, vegetation and stand characteristic gradients, although every effort was made to minimize heterogeneity across these characteristics. All selected trees experienced similar topographic conditions (almost similar elevation and at similar slope (conditions) to ensure sample trees possess similar tree-ring patterns in each stand (Fritts 1976). High elevated forests containing tall and mature trees were selected to ensure climate was the most important factor affecting growth (Fritts 1976). Basic criteria used in selecting trees at each site included choosing healthy subalpine fir trees with open canopy (at least 5 meter in distance between two trees on the ground), and with no fire or insect damage. The minimum inter-tree spacing was used to ensure growth was not affected by competition, but mostly by climate variations (Fritts 1976). Since tree-ring characteristics typically vary also vertically along the stem (Fritts 1976), breast height (1.3 m) was used as a convenient reference height to control for this within-tree variation. Two 12 mm in diameter core samples from opposite sides of trees were extracted at breast height from each tree using increment borers. To minimize the effects of slope on tree-ring patterns, cores were extracted from the cross-slope position, avoiding compression wood. GPS locations and site related data were recorded at time of sampling. DBH was measured using core samples (by adding two samples from each tree together if both met the pith otherwise, by doubling the length of the core samples that reached the pith) at UNBC plant lab.

2.3.3 Fibre measurement

After extracting samples, tree cores were rolled in paper for transport. Once in the lab, cores were air dried. One 12 mm in diameter core of each tree was used for analyzing fibre properties including FL, FWT, MFA and FW. These cores were submerged in 95% Ethanol for 48 hours to let available water in the cores be replaced with alcohol and therefore dry faster. Since tree resins influence wood density (Lenz et al. 1976), dried core samples were placed in a Soxhlet chemical extractor acetone system which cycled acetone over each sample for 5 hours (Jensen 2007) to extract chemical compounds.

Increment cores were sanded on the radial side to make rings more visible, and core were crossdated using a dotting system. Cores were labelled with a single dot every ten years, two dots every half-century and three dots every century (Stokes and Smiley 1968); fine 600 grit sandpaper was used to identify especially narrow rings. The Yamaguchi (1991) method was implemented to determine significant marker years. Once cross-dated, twenty-two 12 mm diameter cores from each site were cut into 10-year increment sections using scalpel blade. Then 10-year sections of all trees were grouped together by year and corresponding years were analysed as an aggregate sample (Table 2.2). Bark was cut off the cores and each group of similar 10-year sections were weighed to target an optimum of 6.5 grams of biomass per 10-year interval (minimum of 5 samples) yielding composite samples A-K (Table 2.2). It worth mentioning that trees with almost similar DBH and age class were targeted at sampling sites in order to minimize the effect of differences in growth and differences in fiber size in younger trees comparing with mature trees.

Cores were then further analyzed at Canfor pulp’s head office, Burnaby, BC. Sections representing each interval were put in 80 ml beakers and acetic acid and hydrogen peroxide (60%-40%) blend were added to the beakers to completely submerge in the solution. This destructive solvent prepares samples for PulpEye analysis by chemically breaking down the core sections, called a delignification process, and turning them to cellulose bulk materials. PulpEye is a world-leading modular analysis system developed for the pulp and paper industry. Its base unit consists of a cabinet with space for three analyzer modules measuring pulp quality parameters online from one or more sampling positions. Modules are combined and connected in a system providing analysis data and control of any specific fibre property (Rahman 2018; Sundman et al. 2016).

Beakers were placed on oil bath at 70 °C leaving them for 48 hours (after the first 24 hours, core sections of each beaker were mashed and squeezed). After the second day, samples were rinsed thrice with distilled water to remove maceration solution and let air dry for 1 day in the fume hood. Oven dry (OD) weights were then determined to get a net weight of 2.5 grams of each delignified pulp sample. Samples were then rinsed in distilled water for 1 minute and poured into the PulpEye system and results for FL, FW, FWT and MFA were reported as outputs in an Excel format. Fibre property data including FL, FW, FWT and MFA were developed into chronologies by averaging the series and differencing the mean dataset of each property to remove non-stationarity (e.g., 10-year intervals and short time series) and were compared to climate variations (10-year averages), using data from meteorological records obtained through ClimateBC, and to variation in the Pacific Decadal Oscillation.

Table 2.2 Cutting, preparing, and labeling of 22 cores as aggregate, samples for further fibre analysis in Canfor Pulp Innovation Center.

Section	Year (Decade)	Chingee's core sections weight (gr)	Pine's core sections weight (gr)	Averil's core sections weight (gr)	Grizzly's core sections weight (gr)	McBride's core sections weight (gr)
A	2019-2010	6.31	8.8	6.7	6.22	7.09
B	2009-2000	6.76	5.86	8.4	8.25	6.34
C	1999-1990	6.51	6.39	9.2	6.7	7.31
D	1989-1980	6.12	5.32	9.1	6.88	6.25
E	1979-1970	6.63	5.70	5.3	6.64	6.05
F	1969-1960	6.1	6.06	6.32	6.27	6.45
G	1959-1950	7.25	6.2	6.25	6.95	7.7
H	1949-1940	5.75	6.8	6.8	6.19	9.1
I	1939-1930	---	6.7	6.27	5.8	---
J	1929-1920	---	4.7	5.8	8.91	---
K	1919-1910	---	---	---	7.46	---

2.3.4 Preparation of cores for dendrochronological and densitometric analysis

The second 12 mm in diameter core taken per tree was used for densitometry and dendrochronological analysis. Each core sample was mounted on a grooved mounting board (Stokes and Smiley 1968) using wood glue and left to dry completely. After 2 to 3 days, mounted cores were cut using a twin blade saw to obtain 2 mm laths revealing the radial surface of the core (Haygreen and Bowyer 1996) for densitometry. Since wood chemical compounds like resin affect density of wood (Grabner et al. 2005), an acetone Soxhlet apparatus was once again used to remove wood resins from 2 mm lath samples (Grabner et al. 2005) prior to densitometry measurement. Then, laths were measured using an ITRAX scanning densitometer in the Plant Lab at University of Northern BC. ITRAX densitometry scan the whole lath length from bark to pith using an X-ray laser beam. Measurements were made at 0.05 mm increments for 20 µs along each core and digital x-ray images (radiographs) were analyzed using ITRAX Windendro® version (2009) to provide maximum density (MXD) and mean density (MD) measurements.

2.3.5 Creating master chronology

I measured RW, EWW and LWW, and their boundaries using WinDendro image. Following ring measurement, series were crossdated using WinDendro software by identifying characteristics tree-ring patterns in graphical form. Visually cross-dated series were verified using COFECHA (Holmes 1983) to ensure common end-dates, and the occurrence of false and missing rings between trees were correct (Stokes and Smiley 1968). COFECHA matches individual time series to a master chronology created from cores at each site (Grissino-Mayer 2001). By comparing each core with the mean chronology of each site, the program generates the mean correlation between the series (MSI). COFECHA also takes note of individual series that may contain errors such as missed or false rings. The measurements are then validated until the remaining indicators disappear or until the MSI is well above 0.42, the minimum value of significance at the 99% confidence level (Grissino-Mayer, 2001). Cores with unique variation in ring width, not representative of the stand, were eliminated (maximum of two to three cores) from the chronologies for each site, allowing for common stand-level variation to be captured. Step standardizations including detrending and stabilizing chronologies were then conducted to extract the high frequency signal for tree RW measurements (Rossi 2003).

This process removes the non-climatic trends, such as the age-size related trends, and the effects of stand dynamics (Fritts 1976) and removes growth-frequency variation and normalizing rapid growth of young trees. I used the program ARSTAN to determine these variables, which applies statistical analysis to develop a stand-level chronologies. The detrending conducted removed growth-frequency variation attributed to tree geometry and normalized rapid growth of young trees (Cook and Peters 1981; Meko and Baisan 2001) through the application of a negative exponential curve to each series (Fritts 1976). In case it was not the best fit, then I applied Hugershoff curve to remove biological trends. Raw values of annual RW, MD, EW and LW were then transformed into dimensionless (index) values (Cook and Holmes 1999) for further analysis.

2.3.6. Comparing chronologies with climate

Climate data

Mean monthly and seasonally averaged air temperature, and mean accumulated precipitation were obtained from ClimateBC at https://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/. ClimateBC calculates seasonal and annual climate variables for specific locations based on latitude, longitude, and elevation. The program uses a combination of bilinear interpolation and elevation adjustments to predict climate data from 1900 to 2018. Seasonal averages in ClimateBC include winter (previous December, current January, and February), spring (March, April and May), summer (June, July and August), and autumn (September, October and November). The Pacific Decadal Oscillation (PDO) is often described as a long-lived El Niño-like pattern of Pacific climate variability (Zhang et al. 1997). The severe phases of the PDO have been classified as being either warm or cool. When sea level pressures are below average over the North Pacific, the PDO has a positive value and conversely, above average sea level pressures over the North Pacific, result in a negative value in PDO (Mantua 1999). PDO could affect climate regimes in western Canada during its warm and cool phases. Pacific Decadal Oscillation records were obtained from National Centers for Environmental Information or National Oceanic and Atmospheric Administration (NOAA) at https://www.ncdc.noaa.gov/teleconnections/pdo/

2.3.7. Correlation and regression analysis between climate and growth parameters

RW, EW, LW, MD and RD of all 5 sites were tested for normality using IBM SPSS version 26.

Pearson's correlation coefficients were calculated for standardized, detrended master chronologies and climate variations to determine significant correlations. Spearman's correlation coefficient was calculated for non-normal dependant variables in SPSS.

Standardized detrended fibre properties including FL, FW, FWT and MFA were compared with mean monthly, annual and seasonal air temperature, mean monthly maximum and minimum air temperature, and total annual and seasonal precipitation using a Pearson's correlation coefficient. Normality of FL, FWT, MFA and FW were tested using Shapiro-Wilk test in SPSS (because the number of data and sample size were small) before correlation analysis.

2.3.8 Regression Analysis and Comparison of Measured and Modelled Values

Regression analysis was completed where strong, significant Pearson's or Spearman's correlation coefficients were identified, above 0.4 (Wood and Smith 2012; Blanchette et al. 2015) (Tables 2.5, 2.6, 2.9). Regression models with significant correlation coefficients, and strong R^2 values (>0.25) were visually assessed against measured values to determine model accuracy over time. To obtain stronger models, multi variable model can be applied using two or more climatic variables and putting in the same model to predict better and stronger models provided that the independent variables (climatic parameters) are not statistically correlated. To find if variables were related together or not, a Durbin-Watson statistic was applied. Durbin Watson values are between 0 and 4. A value of 2.0 means that there is no autocorrelation detected in the sample. Values from 0 to less than 2 indicate positive autocorrelation and values from 2 to 4 indicate negative autocorrelation. If independent variables were autocorrelated we could potentially take an average of two independent variables and put that average in the model for prediction. For those independent climate variables that were basically different (e.g., temperature and precipitation), and needed to be combined in a model, fluctuations over time were compared visually to make sure they have same trends (See Figure A1, A2, A3, A4 in Appendix). Split verification was then used to validate the models. The latter 50% of time series was applied to calibrate the models. All predicated site-specific anatomical traits passed the verification test at 90% significance of reduction of error values (RE) compared to actual measured data.

2.4 RESULTS

2.4.1 Changes in Climate

Meteorological records for five study sites around Prince George are shown in Figures 2.2 and 2.3. Figures 2.2 - 2.3 depict mean annual temperature and total annual precipitation from 1940 to 2018. Annual precipitation has generally decreased at the Pine Le Moray and Mt. Chingee sites over time and increased at McBride Peak since 1920 (Figure 2.3 A, B, E). At the Grizzly Den and Mt. Averil sites, totals of annual precipitation generally show steady trends since 1940 (Figure 2.3 C, D).

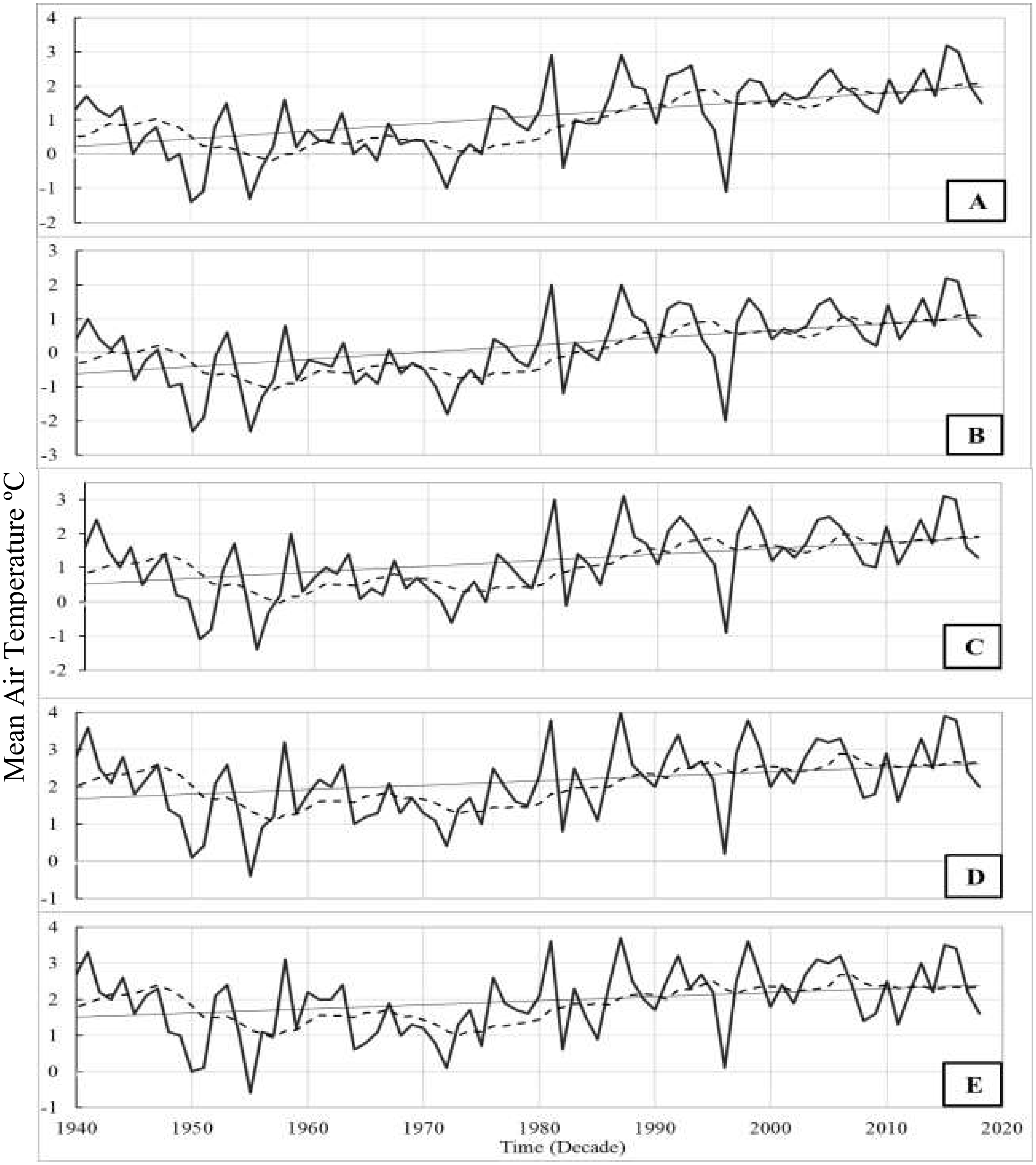

Figure 2.2 Mean annual temperature for five study sites from 1940-2018. Average temperature has generally increased at study sites over time since 1940. A= Pine Le Moray; B=Mount Chingee; C=Mount Averil; D=Grizzly Den; E=McBride Peak. The dashed average represents a 10-year moving average in temperature variation. Thin smooth lines represent trendlines during 1940- 2018 period.

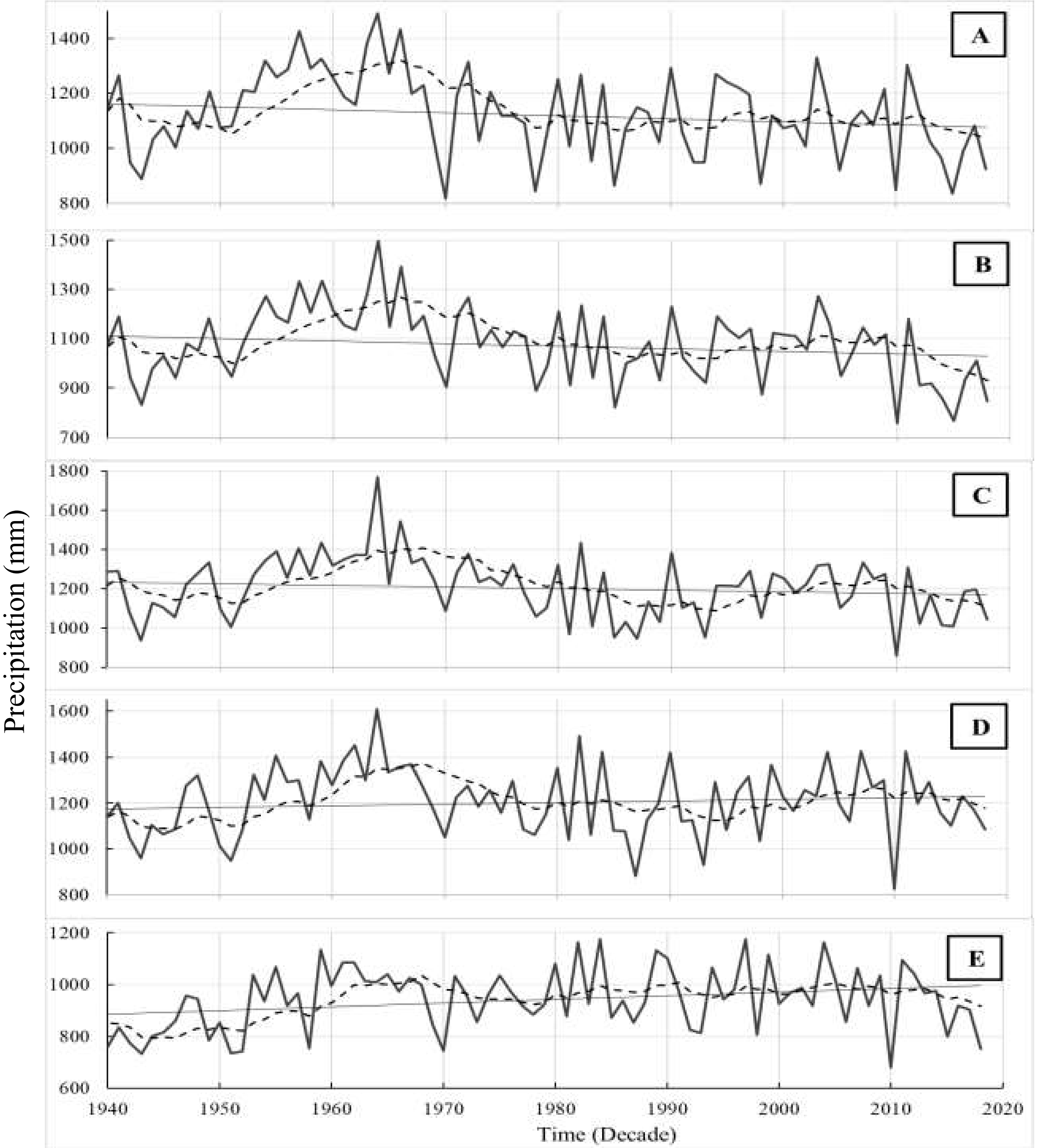

Figure 2.3 Total annual precipitation for five study sites from 1940-2018. Annual precipitation has generally decreased at the Pine Le Moray and Chingee sites (A, B) over time while increased at McBride since 1920 (E). At the Grizzly Den and Averil sites, total annual precipitation generally shows steady trends since 1940 (C, D). A= Pine Le Moray; B = Mount Chingee; C = Mount Averil; D = Grizzly Den; E = McBride Peak. A 10-year moving average line in precipitation variation is shown with dashed line. Thin smooth lines represent trendlines during 1940 – 2018 period. Note not all y-axis are the same.

2.4.2 Correlation between climate and Fibre properties

Several significant correlations ($p < 0.05$) were found between tracheid (fibre) characteristics and the previous and current monthly and seasonal temperature and precipitation records of Pine Le Moray, Mt. Chingee, Mt. Averil, Grizzly Den and McBride Peak sites (Figure 2.4 – 2.7; Table 2.5 – 2.6). FL was positively correlated with climate indices at Grizzly Den and McBride Peak sites while negatively correlated with Averil site. FWT showed positive correlations with climate variables at Pine Le Moray, Mt. Change and McBride Peak sites. MFA and FW were both positively correlated with climate parameters at Pine Le Moray and McBride Peak sites while both properties showed negative correlations with climate at Mt. Chingee site (Table 2.5). All fibre data (FL, FW, FWT and MFA) were deemed normal (Table 2.4). Durbin-Watson statistic tests showed that independent climate variables were related to each other (See Table A1 in Appendix). Therefore, we took average of corresponding variables for comparing with fibre properties and for modeling.

Table 2.3. Normality statistics for ring width (RW), earlywood density (EWD), earlywood width (EWW), latewood density LWD, latewood width (LWW), maximum density (MXD), minimum density (MND) and ring density (RD) in Pine Le Moray, Chingee, Averil, Grizzly Den and McBride sites including Skewness and Kurtosis values. Skewness and Kurtosis > +1.96 or < -1.96 were not accepted as normal data. Bold values indicate non- normal values.

Site	RW		EWD		EWW		LWD		LWW		MXD		MND		RD	
	Skewness	**Kurtosis**	**Skewness**	**Kurtosis**	**Skewness**	**Kurtosis**	**Skewness**	**Kurtosis**	**Skewness**	**Kurtosis**	**Skewness**	**Kurtosis**	**Skewness**	**Kurtosis**	**Skewness**	**Kurtosis**
Pine Le Moray	0.068	-0.777	1.299	0.834	0.393	-0.811	-0.061	-1.457	1.381	0.345	0.171	-0.248	0.896	-1.494	-0.306	0.002
Mt Chingee	0.023	-1.909	0.061	-0.787	-0.050	-1.908	0.593	-0.551	0.843	0.739	-0.441	-1.588	1.231	-0.346	0.477	-0.438
Mt Averil	**3.110**	1.196	**1.995**	0.416	**2.823**	1.103	0.040	-0.949	-1.886	-0.517	0.217	-1.100	**3.523**	**2.861**	0.003	-0.609
Grizzly Den	-0.563	-0.835	1.214	0.152	0.030	-0.177	1.214	0.152	**-2.376**	0.402	**-2.599**	-0.227	1.416	0.014	0.767	-1.164
McBride Peak	-0.410	-0.974	-0.532	-0.795	-0.696	-1.260	1.230	-1.123	0.338	-0.708	-0.717	-0.841	1.540	-0.900	-0.746	-0.892

Table 2.4. Normality statistics for fibre length (FL), fibre wall thickness (FWT), micro fibril angle (MFA) and fibre width (FW) in Pine Le Moray, Mt. Chingee, Mt. Averil, Grizzly Den and McBride Peak sites including Shapiro-Wilk test to validate normality of sites with small fibre sample sizes. P-value> +0.05 is considered as normal data.

Site	FL		FWT		MFA		FW	
	Shapiro-Wilk	**Sig (*P-value*)**	Shapiro-Wilk	**Sig (*P-value*)**	Shapiro-Wilk	**Sig (*P-value*)**	Shapiro-Wilk	**Sig (*P-value*)**
Pine Le Moray	0.888	0.23	0.943	0.64	0.915	0.39	0.935	0.56
Mt. Chingee	0.957	0.79	0.861	0.15	0.906	0.37	0.964	0.85
Mt. Averil	0.913	0.34	0.960	0.80	0.920	0.39	0.877	0.15
Grizzly Den	0.919	0.35	0.926	0.41	0.958	0.76	0.960	0.78
McBride Peak	0.821	0.07	0.925	0.51	0.866	0.17	0.848	0.12

Table 2.5. Pearson correlations between climate variations and fibre length (FL) and fibre wall thickness (FWT) for Pine Le Moray, Mt. Chingee, Mt. Averil, Grizzly Den and McBride Peak sites. Only strongest and significant correlations have been shown. Only R > 0.7 was accepted as significant correlation. "*" Values are significant at 95% (*P*<0.05) and "**" shows significance at 99% (*P*<0.01). Oct = October.

Climatic parameter	**Fiber Length**					**Fiber Wall Thickness**				
	Chingee	**Averil**	**Pine**	**McBride**	**Grizzly**	**Chingee**	**Averil**	**Pine**	**McBride**	**Grizzly**
Mean + Maximum Temperature (May)	0.511	-0.512	-0.15	0.161	0.454	0.611	-0.11	**0.757***	-0.131	0.121
Maximum Temperature (July)	0.682	-0.608	-0.32	0.571	0.044	**0.802***	-0.46	-0.131	-0.475	-0.274
Minimum Temperature (Previous_Oct)	-0.182	0.482	0.195	-0.185	0.029	-0.329	-0.29	0.273	**0.867***	0.441
Maximum Temperature (Fall + summer)	0.506	**-0.763***	-0.028	-0.089	0.131	0.371	-0.42	-0.018	-0.692	-0.202
Mean and Minimum temperature of December	0.339	0.383	0.412	-0.29	**0.713***	0.3	-0.31	0.139	-0.538	0.579
Minimum Temperature and Precipitation (Previous Fall)	-0.411	0.234	0.68	**0.883****	0.043	0.381	-0.41	0.218	0.126	0.041

Table 2.6. Correlations between climate variations and, micro fibril angle (MFA) and fibre width (FW) for Pine Le Moray, Mt. Chingee, Mt. Averil, Grizzly and McBride Peak sites. Only strongest and significant correlations (R > 0.7) are accepted as significant correlation. "*" Values are significant at 95% (*P*<0.05) and "**" show significance at 99% (*P*<0.01).

Climatic parameter	**Micro Fibril Angle**					**Fibre Width**				
	Pine Le Moray	**Chingee**	**Averil**	**Grizzly**	**McBride Peak**	**Pine Le Moray**	**Chingee**	**Averil**	**Grizzly**	**McBride Peak**
Maximum Temperature (fall)	-0.491	-0.199	0.109	0.284	0.331	0.2	0.525	-0.305	0.145	**-0.972****
Maximum Temperature (July)	-0.216	**-0.807***	0.046	0.142	0.038	0.266	0.58	-0.18	-0.14	-0.577
Minimum Temperature (August)	0.691	-0.291	-0.137	-0.175	**0.819***	0.418	-0.044	0.23	0.154	0.247
Precipitation (Previuos October)	-0.171	-0.237	0.282	-0.111	0.572	-0.251	**-0.812***	0.024	-0.093	0.028
Mean Temperature (August) and Minimum Temperature (July + August)	**0.867****	-0.217	-0.231	-0.066	0.496	0.679	0.111	0.18	0.337	-0.042
Mean Temperature (June + July) and Minimum Temperature (July)	0.697	-0.483	-0.202	-0.38	0.228	**0.85****	0.309	0.28	0.35	0.211

FL at the Mt. Averil site was significantly and negatively correlated (R = -0.763) with maximum air temperature of Fall and summer (Figure 2.4; Table 2.5), while this property at McBride Peak and Grizzly Den sites showed significant positive correlations (R = 0.883 and 0.713) with minimum temperature combined with precipitation in previous year fall season, and average temperature combined with minimum temperature of December respectively (Figure 2.4; Table 2.5).

Results showed maximum July temperature was significantly and positively (R = 0.802) related with FWT at Mt. Chingee during 1950- 2018. Maximum and average May temperature was positively correlated (R = 0.757) with FWT at Pine Le Moray during 1940- 2018. FWT was correlated (R = 0.867) with minimum temperature of the previous October at McBride Peak from 1950 to 2018 (Figure 2.5; Table 2.5).

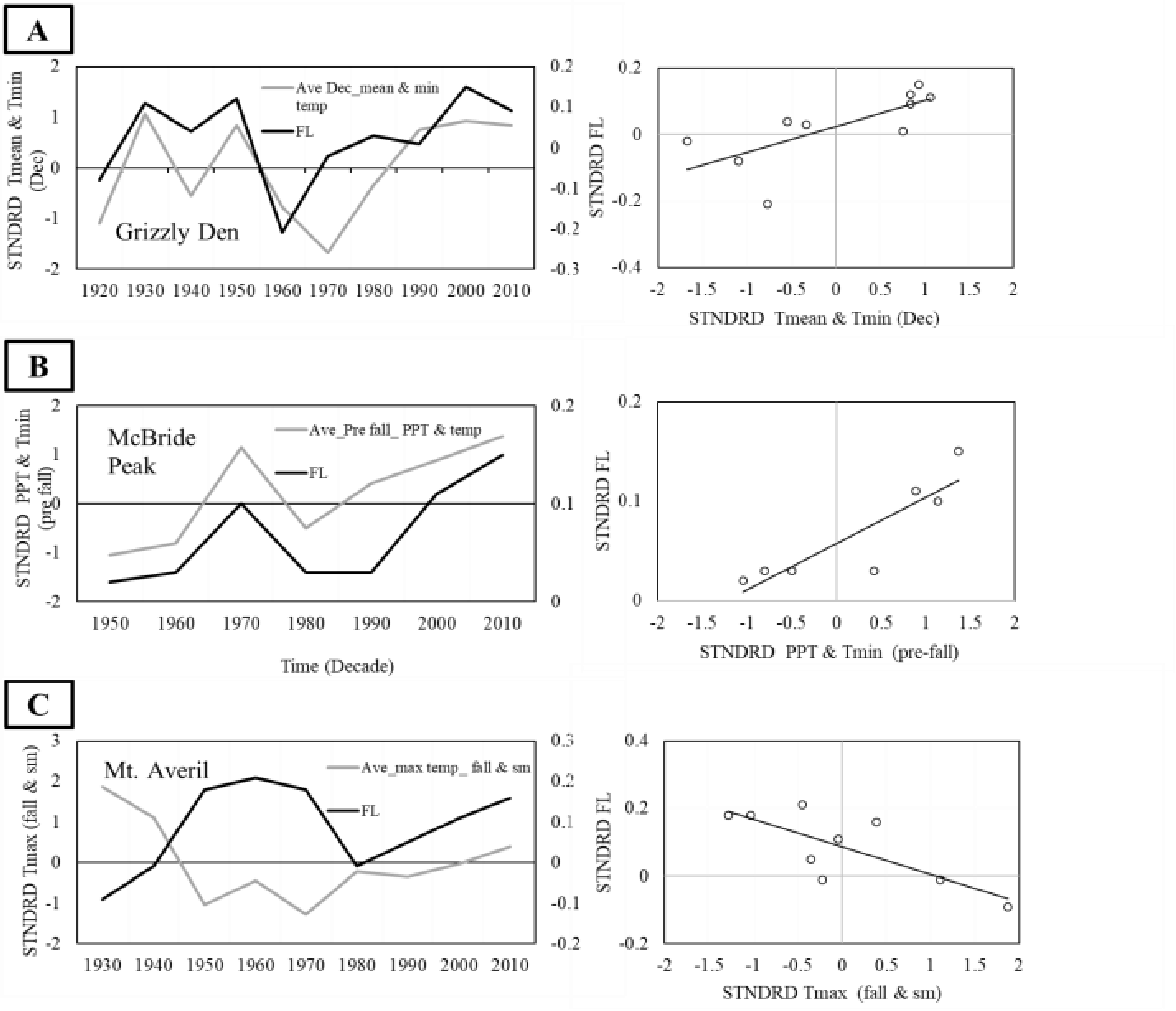

Figure 2.4 Relationships between climate variables and fibre length (FL) for Grizzly Den, McBride Peak and Averil sites during 1920 to 2018. A: Relationship between average and minimum temperature of December and FL (Left), and linear relation of average and minimum temperature of December and FL at Grizzly site during 1920-2018 (Right). B: Relationship between minimum temperature and precipitation of previous fall and FL (Left), and linear relation of minimum temperature and precipitation of previous fall and FL at McBride site during 1950-2018 (Right). C: Relationship between maximum temperature of fall and summer and FL (Left), and linear relation of maximum temperature of fall and summer and FL at Averil site during 1930- 2018 (Right). Tmean= mean temperature, Tmax= maximum temperature, Tmin= minimum temperature, Ave= average, Pre= previous, PPT= precipitation, STNDRD= standardized, sm= summer, FL= fibre length.

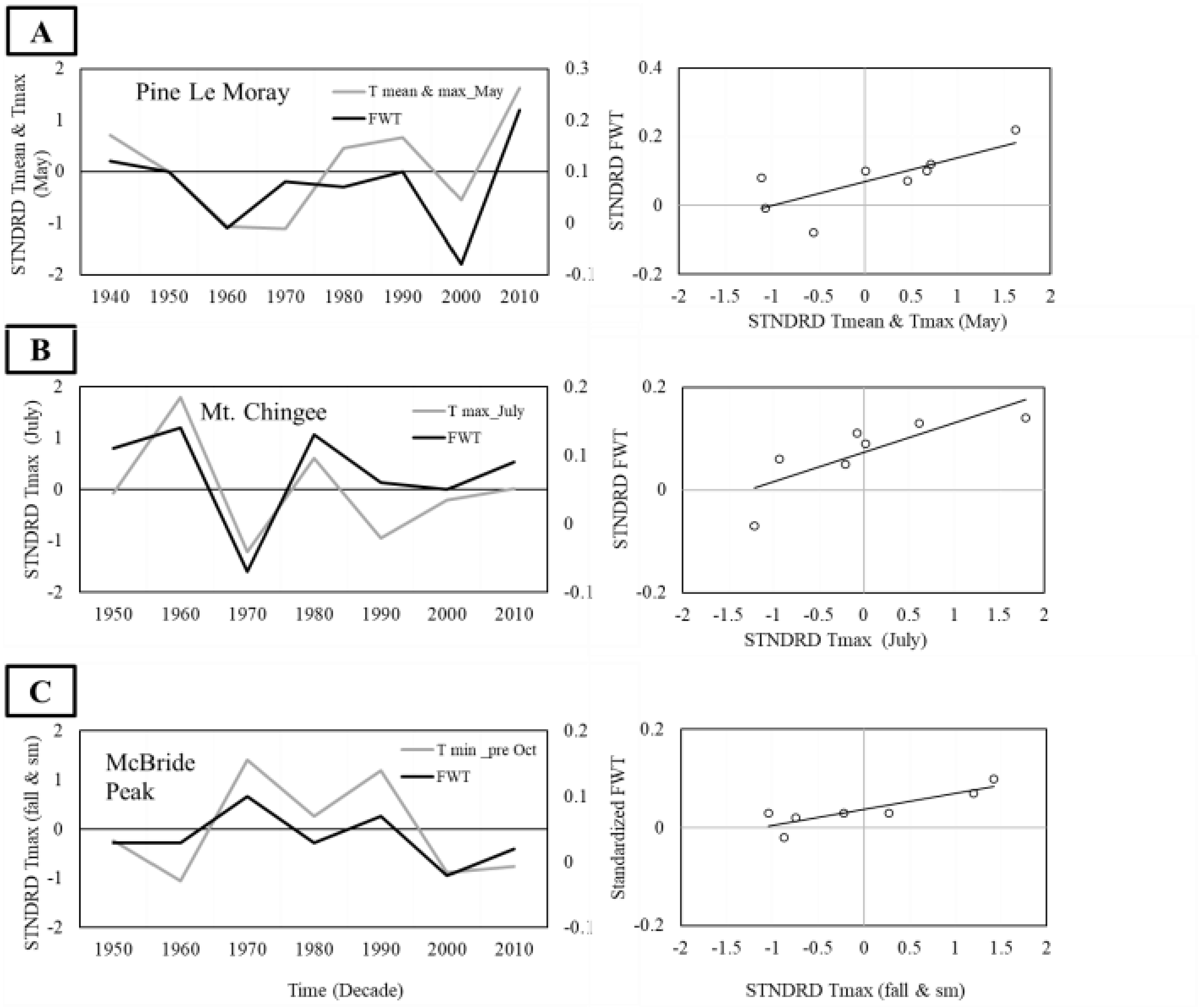

Figure 2.5 Relationships between climate variables and fibre wall thickness (FWT) at Pine Le Moray, Chingee and McBride peak sites during 1940 to 2018. A: Relationship between average and maximum temperature of May and FWT (Left), and linear relation of Average and maximum temperature of May and FWT at Pine Le Moray during 1940-2018 (Right). B: Relationship between maximum temperature of July and FWT (Left), and linear relation of maximum temperature of July and FWT at Chingee during 1950- 2018 (Right). C: Relationship between minimum temperature of previous October and FWT (Left), and linear relation of minimum temperature of previous October and FWT at McBride during 1950-2018 (Right). Tmean= mean temperature, Tmax= maximum temperature, Tmin= minimum temperature, Ave= average, Pre= previous, PPT= precipitation, STNDRD= standardized, sm= summer, Oct= October.

Some significant correlations were obtained from comparison between climate variables and MFA at study sites. Figure 2.6 shows the relationships between climate variables and MFA for Pine Le Moray, Mt. Chingee and McBride Peak from 1940 to 2018. Maximum July temperature of July was significantly and negatively (R = -0.807) correlated with MFA at Chingee. At Pine Le Moray, a combination of average temperature of August and minimum temperature of July and August were positively correlated (R = 0.867) with MFA. August minimum temperature was positively and significantly correlated with MFA at McBride site (Figure 2.6; Table 2.6).

The relationships between climate variables and fibre width at Pine Le Moray, Mt. Chingee and McBride Peak from 1940 to 2018 are shown in Figure 2.7. Previous October precipitation was negatively (R = -0.812) correlated with FW at Mt. Chingee site. Results for Pine Le Moray site showed positive correlation (R = 0.85) between average June and July temperature in combination with minimum July temperature, and FW.

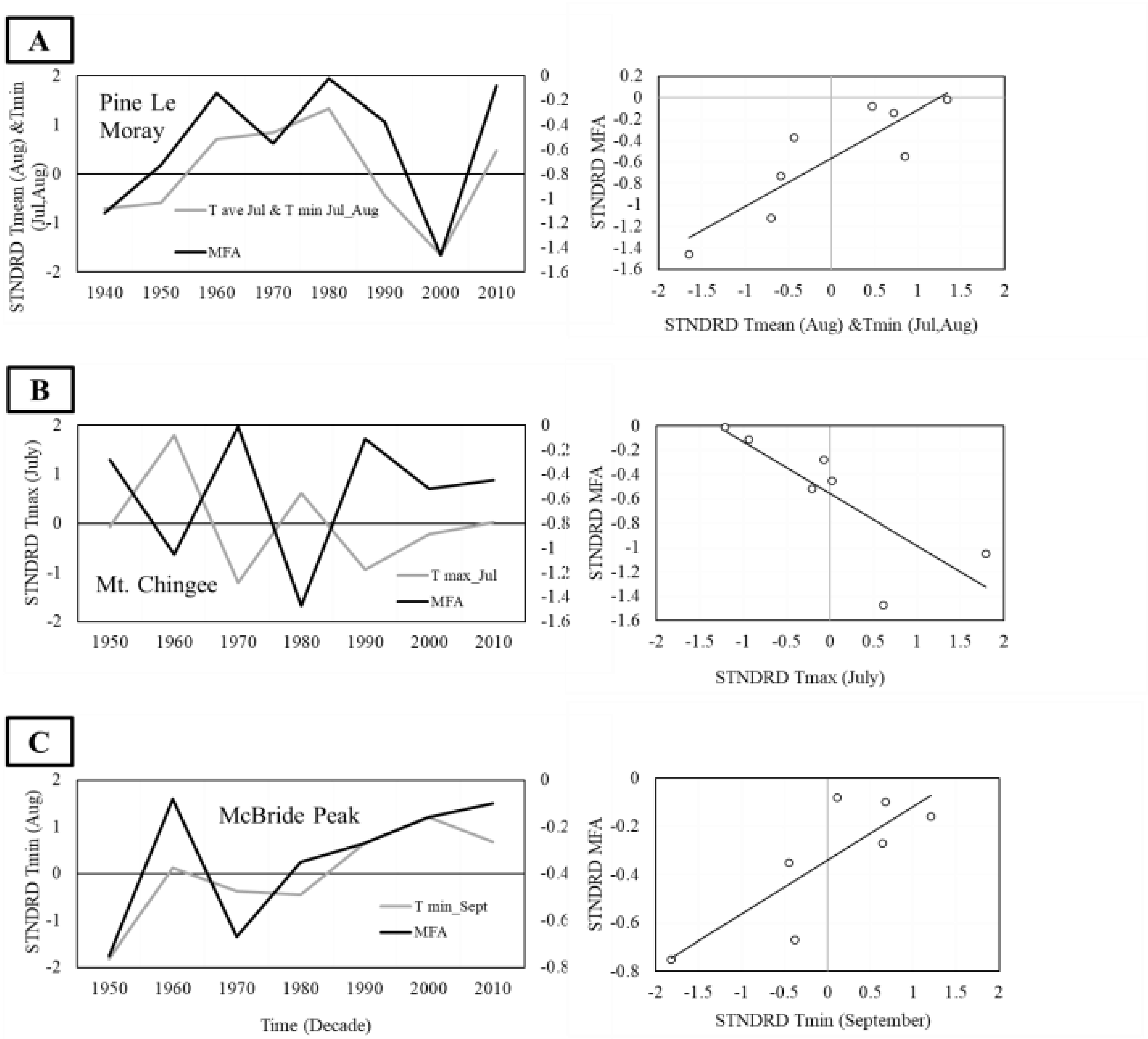

Figure 2.6 Relationship between temperature and micro fibril angle (MFA) at Pine Le Moray, Chingee and McBride Peak sites during 1940 to 2018. A: Relationship between Average temperature of August combined with minimum temperature of July and August, and MFA (Left), and linear relationship of Average temperature of August combined with minimum temperature of July and August, and MFA at Pine Le Moray during 1940-2018 (Right). B: Relationship between maximum temperature of July and MFA (Left), and linear relation of maximum temperature of July and MFA at Chingee during 1950- 2018 (Right). C: Relationship between minimum temperature of August and MFA (Left), and linear relation of minimum temperature of August and MFA at McBride Peak during 1950-2018 (Right). Tmean / ave= mean temperature, Tmax= maximum temperature, Tmin= minimum temperature, STNDRD= standardized, sm= summer, Jul = July, Aug = August, Sept = September.

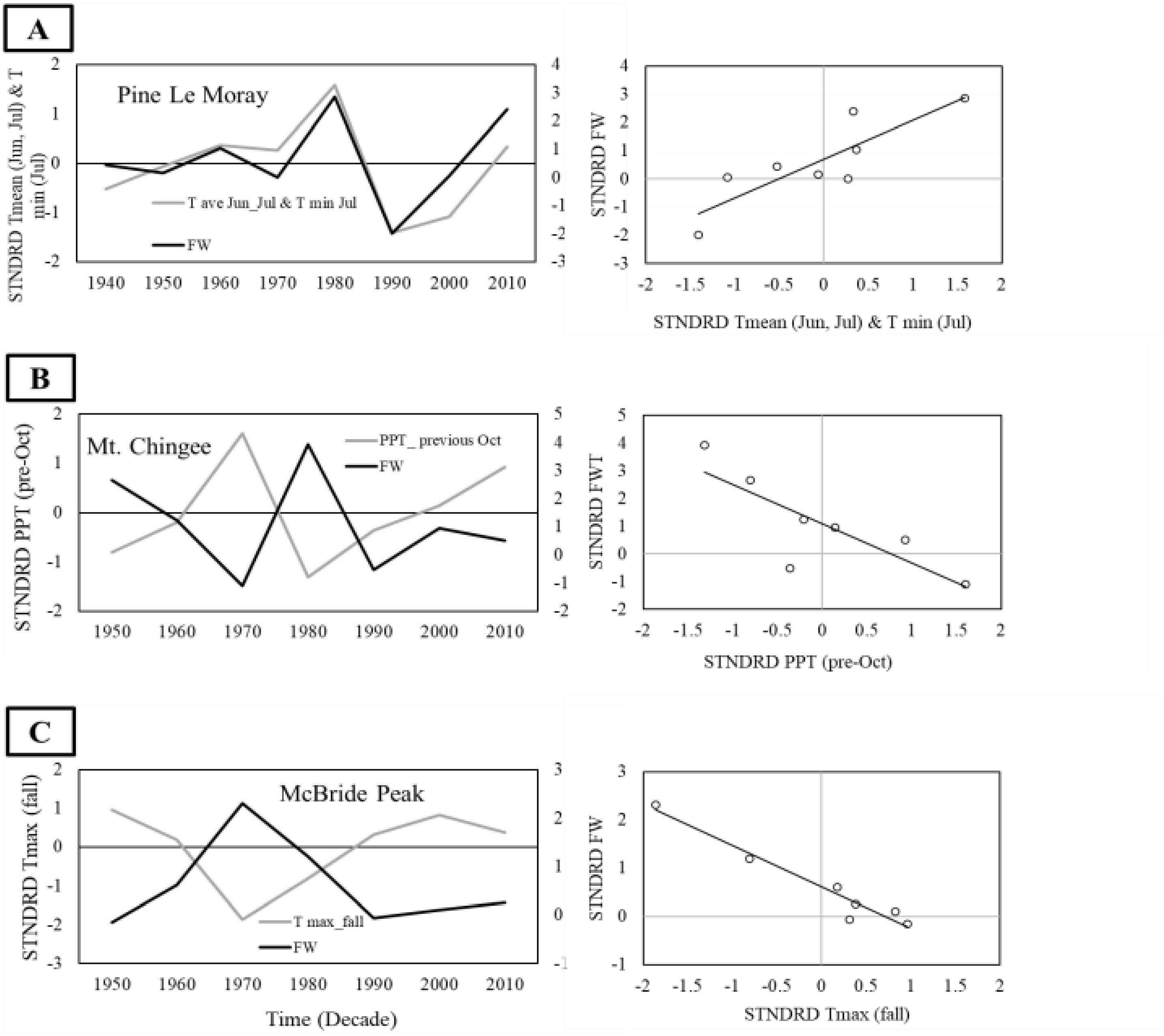

Figure 2.7 Relationships between temperature and precipitation, and fibre width (FW) at Pine Le Moray, Chingee and McBride Peak sites during 1940 to 2018. A: Relation between average temperature of June and July combined with minimum temperature of July, and FW (Left), and linear relation of average temperature of June and July combined with minimum temperature of July, and FW in Pine Le Moray during 1940-2018 (Right). B: Relationship between previous October precipitation and FW (Left), and linear relation of previous October precipitation and FW at Chingee during 1950- 2018 (Right). C: Relationship between fall maximum temperature and FW (Left), and linear relation of fall maximum temperature and FW at McBride Peak during 1950-2018 (Right). Tmean / ave= mean temperature, Tmax= maximum temperature, Tmin= minimum temperature, PPT = precipitation, pre = previous, STNDRD= standardized, sm= summer, Oct = October, Jun = June, Jul = July.

Chronologies

Chronology lengths for study sites were between 69-103 years at Pine Le Moray, 55-95 at Mount Chingee, 68-138 at Mount Averil, 55-148 at Grizzly Den and 56-86 at McBride Peak (Table 2.7). The year of residual series cut-off was variable for radial growth characteristics and was based on accepted minimum number of trees with common starting year at each site (Table 2.7). At each site, 2-4 chronology series were disregarded from further analysis due to unsuccessful cross-dated series (Table 2.7). Normality of RW, EW, LW, EWD, LWD, MD and ring density chronologies were tested using SPSS before correlation analysis. Results determined most data was normal with the exception of Averil-RW, Averil-EWW, Averil-EWD, Averil-MND, Grizzly-LWW and Grizzly-MXD (Table 2.3).

2.4.3 Climate Correlations

Several significant correlations were found from comparisons of winter (October to March) and spring (April to June) circulation indices - Pacific Decadal Oscillation (PDO) and mean winter and spring temperatures at study sites (Table 2.8; Figure 2.21- 22). Winter PDO was significantly and positively correlated with winter temperature at Pine Le Moray, Mt. Chingee, Mt. Averil, Grizzly Den and McBride Peak sites at 99% confidence (Table 2.8). Spring PDO was significantly and positively correlated with spring temperature at Averil and McBride sites (Table 2.8; Figure 2.22). In general, PDO cooling phase during 1940s to 1970s matched with local climate trends at study sites. Similarly, local climate variations at study sites during 1980s to 1990s followed PDO warming phase during 1980s to 1990s (Figure 2.21- 2.22).

Table 2.7. Master chronology statistics for study stands (Pine Le Moray, Chingee, Averil, Grizzly Den and McBride Peak) along north-facing slopes of Rockies in northern interior British Columbia. ring width (RW), earlywood width (EWW), earlywood density (EWD), latewood width (LWW), latewood density (LWD), maximum density (MXD), minimum density (MND) and ring density (RD). MSI = Mean series intercorreltion: indicates the strength of correlation between samples taken from the same location, based on 50-year overlapping segments.

Site Name	**Chronology Type**	**MSI**	**Chronology Length**	**Cut off series length (start year)**	**Mean Length of Series (year)**	**Accepted series Length**	**# of Trees Successfully Crossdated**
Pine Le Moray	RW	0.563	1915-2018	1940	85	80	19
	EWW	0.612					
	EWD	0.643					
	LWW	0.559					
	LWD	0.711					
	MXD	0.686					
	MND	0.531					
	RD	0.51					
Mt. Chingee	RW	0.664	1923-2018	1950	67	70	18
	EWW	0.596					
	EWD	0.642					
	LWW	0.701					
	LWD	0.612					
	MXD	0.559					
	MND	0.614					
	RD	0.771					
Mt. Averil	RW	0.744	1880-2018	1940	101	80	19
	EWW	0.696					
	EWD	0.723					
	LWW	0.632					
	LWD	0.753					
	MXD	0.713					
	MND	0.651					
	RD	0.618					
Grizzly Den	RW	0.693	1870-2018	1940	101	80	18
	EWW	0.722					
	EWD	0.634					
	LWW	0.748					
	LWD	0.761					
	MXD	0.663					
	MND	0.629					
	RD	0.592					
McBride Peak	RW	0.743	1932-2018	1960	64	60	18
	EWW	0.777					
	EWD	0.729					
	LWW	0.614					
	LWD	0.672					
	MXD	0.662					
	MND	0.779					
	RD	0.726					

Table 2.8. Relationships between circulation indices including winter (October – March) and spring (April-June) and temperature of winter and spring in study stands (P, C, A, G, M). PDO- Pacific Decadal Oscillation. All sites are Significant at 0.99 (P < 0.01).

Site	**Longitude**	**Latitude**	**Elevation (a.s.l)**	**Slope**	**PDO_winter (R^2)**	**PDO_spring (R^2)**	**sig (*P* value)**
Pine Le Moray	55° 24′	-122° 32′	1120	N	0.268		<0.0001
Mt. Chingee	55° 01′	-122° 53′	1200	N	0.283		<0.0001
Mt. Averil	54° 24′	-122° 25′	1270	NW	0.308	0.326	<0.0001
Grizzly Den	53° 46′	-121° 30′	1250	N	0.308		<0.0001
McBride Peak	53° 19′	-120° 07′	1330	W	0.302	0.342	<0.0001

2.4.3.1 Relation between climate parameters (temperature and precipitation) and RW, EW, LW, MXD, MND, RD

Some significant correlations ($p < 0.05$) were found between subalpine fir's tree-ring characteristics (RW, EW, LW, MXD, MND, RD) and the previous and current monthly and seasonal temperature and precipitation of Pine Le Moray, Mt. Chingee, Mt. Averil, Grizzly Den and McBride Peak sites. (Figures 2.8 - 2.13). Results show that intra-annual wood characteristics including (EW, LW, RD) have stronger and more significant correlations with climate variables than do annual-ring width. In general, because of the availability of statistically significant correlations ($P < 0.05$) between subalpine fir radial growth and climate, the null hypothesis is rejected.

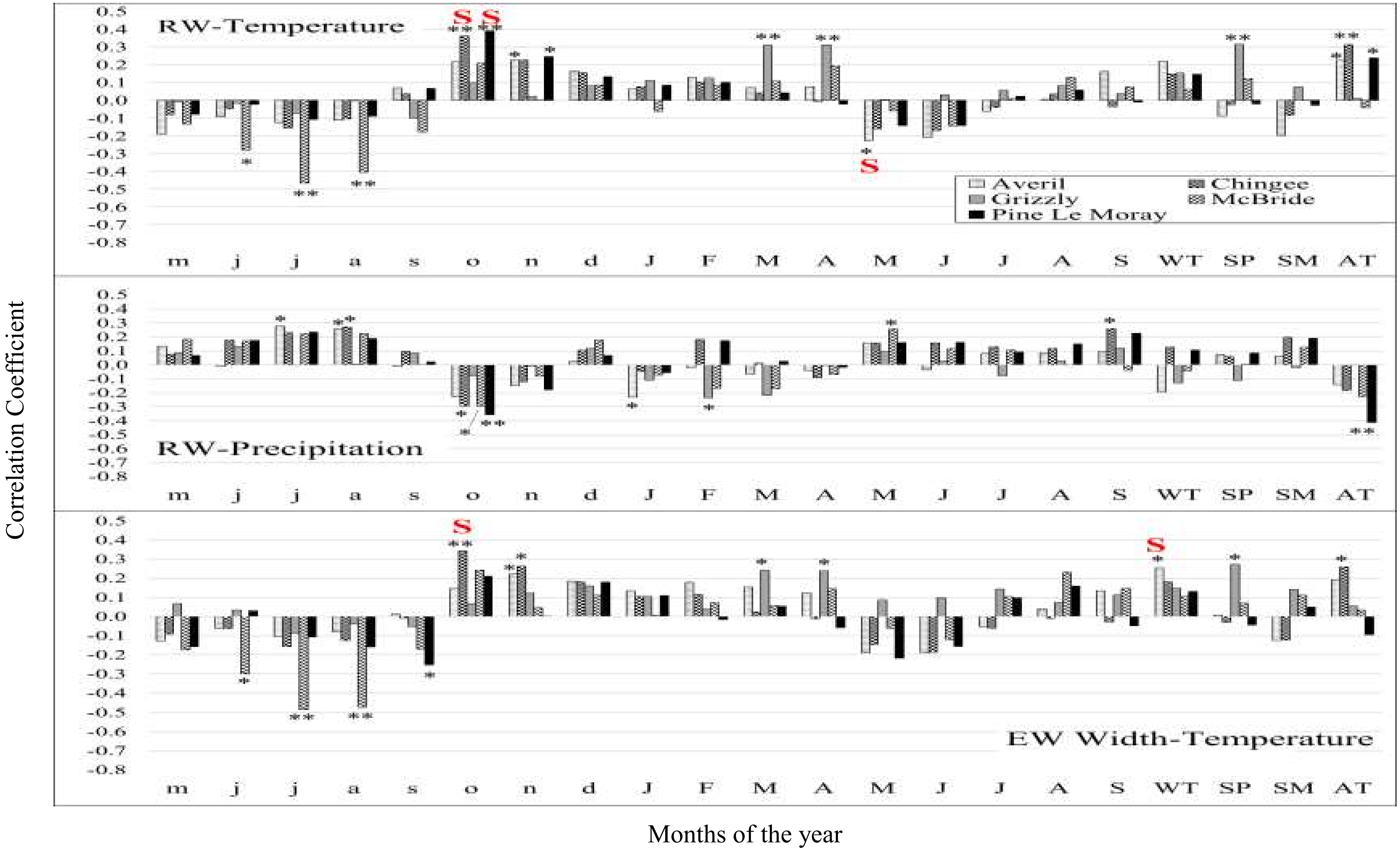

Figure 2.8. Correlations between mean monthly temperature and precipitation at Pine Le Moray, Mt. Chingee, Mt. Averil, Grizzly Den and McBride Peak stands and ring width (RW), earlywood width (EWW) along north-facing slopes of the Rockies in northern BC. Significant correlations are depicted by ** for $p < 0.01$ and * for $p < 0.05$. Months are represented by lower case (previous year) and upper case (current year) letters, respectively; WT = winter, SP= spring, SM= summer, AT = fall. S = Spearman's correlation coefficient.

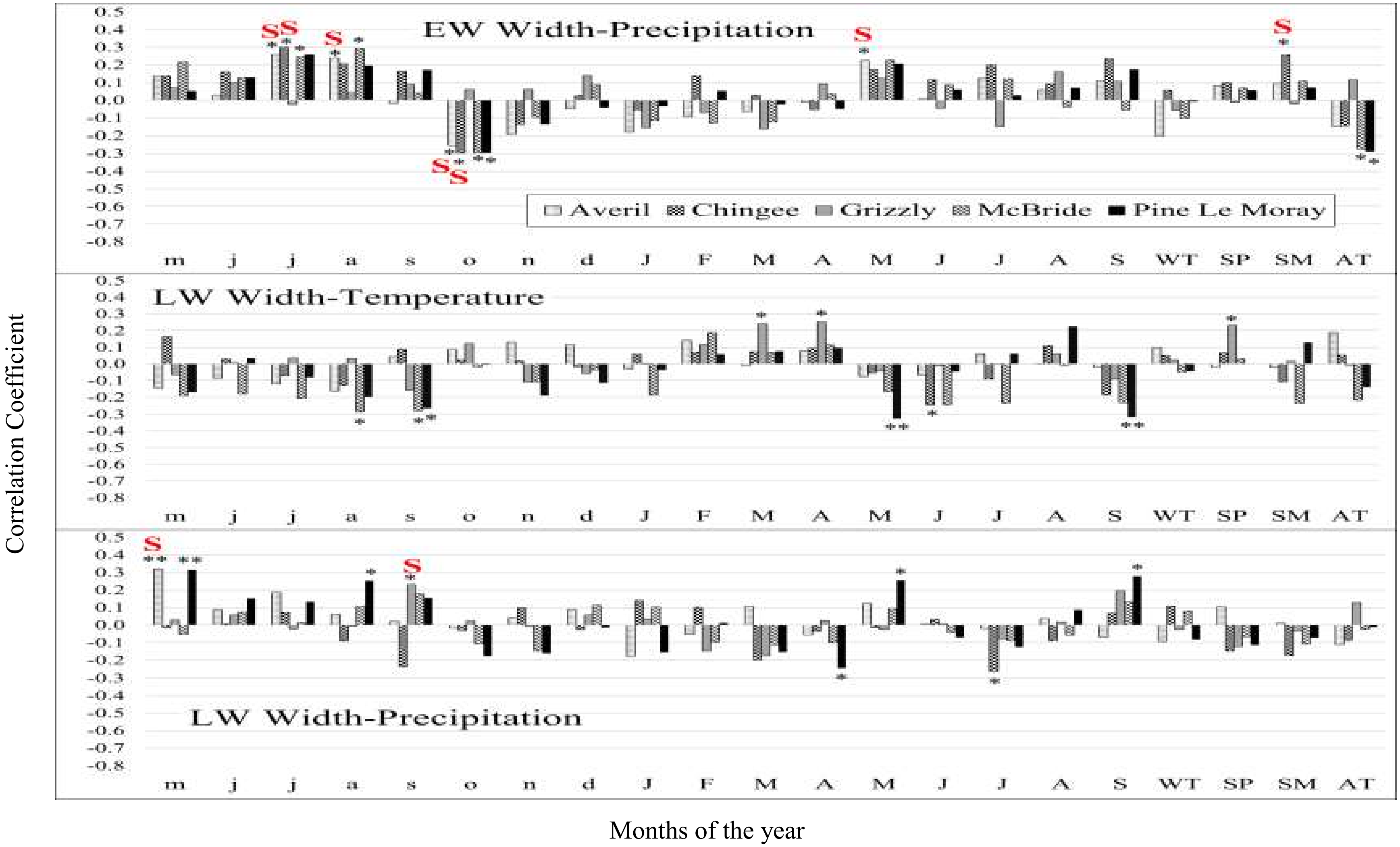

Figure 2.9. Correlations between mean monthly temperature and precipitation at Pine Le Moray, Mt. Chingee, Mt. Averil, Grizzly Den and McBride Peak stands and earlywood width (EWW), latewood width (LWW) along north-facing slopes of the Rockies in northern BC. Significant correlations are depicted by ** for *p* < 0.01 and * for $P < 0.05$. Months are represented by lower case (previous year) and upper case (current year) letters, respectively; WT = winter, SP= spring, SM= summer, AT = fall. S= Spearman correlation coefficient.

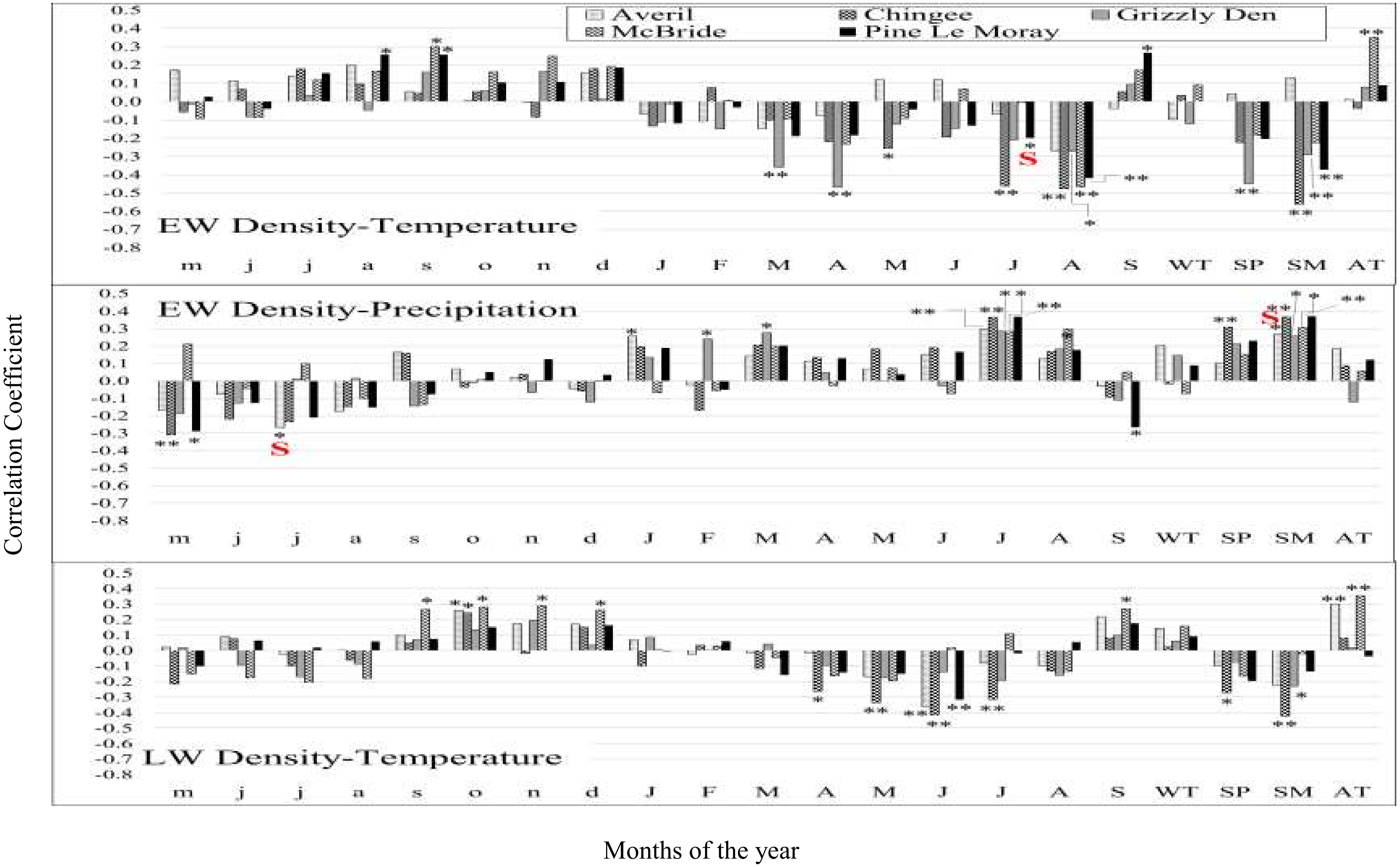

Figure 2.10. Correlations between mean monthly temperature and precipitation at Pine Le Moray, Chingee, Averil, Grizzly Den and McBride Peak stands and earlywood density (EWD) and latewood density (LWD) along north-facing slopes of the Rockies in northern BC. Significant correlations are depicted by ** for $p < 0.01$ and * for $p < 0.05$. Months are represented by lower case (previous year) and upper case (current year) letters, respectively; WT = winter, SP= spring, SM= summer, AT = fall. S = Spearman correlation coefficient.

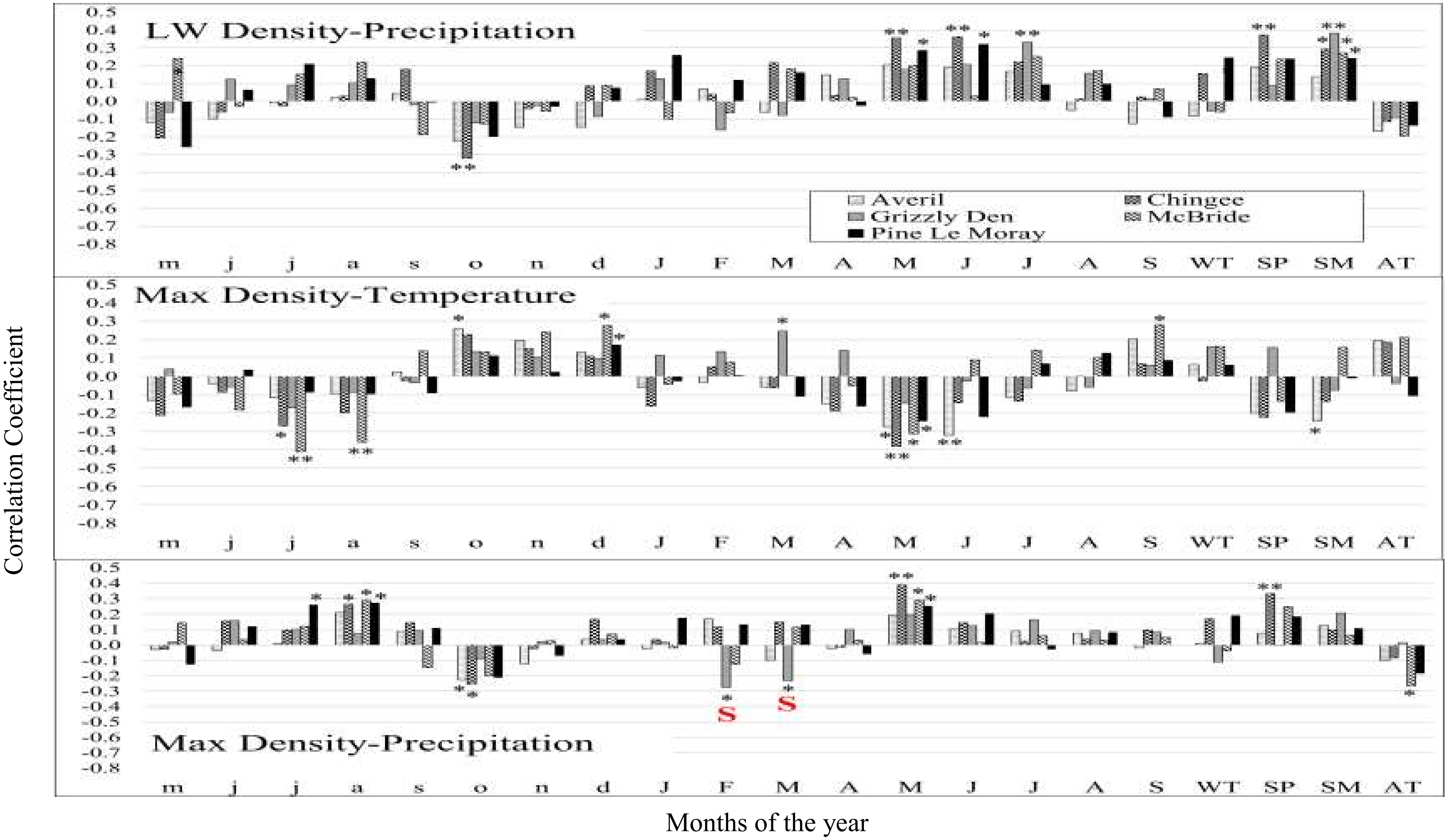

Figure 2.11. Correlations between mean monthly temperature and precipitation at Pine Le Moray, Chingee, Averil, Grizzly Den and McBride Peak stands and latewood density (LWD) and maximum density (MXD) along north-facing slopes of the Rockies in northern BC. Significant correlations are depicted by ** for $P < 0.01$ and * for $P < 0.05$. Months are represented by lower case (previous year) and upper case (current year) letters, respectively; WT = winter, SP= spring, SM= summer, AT = fall. S = Spearman correlation coefficient.

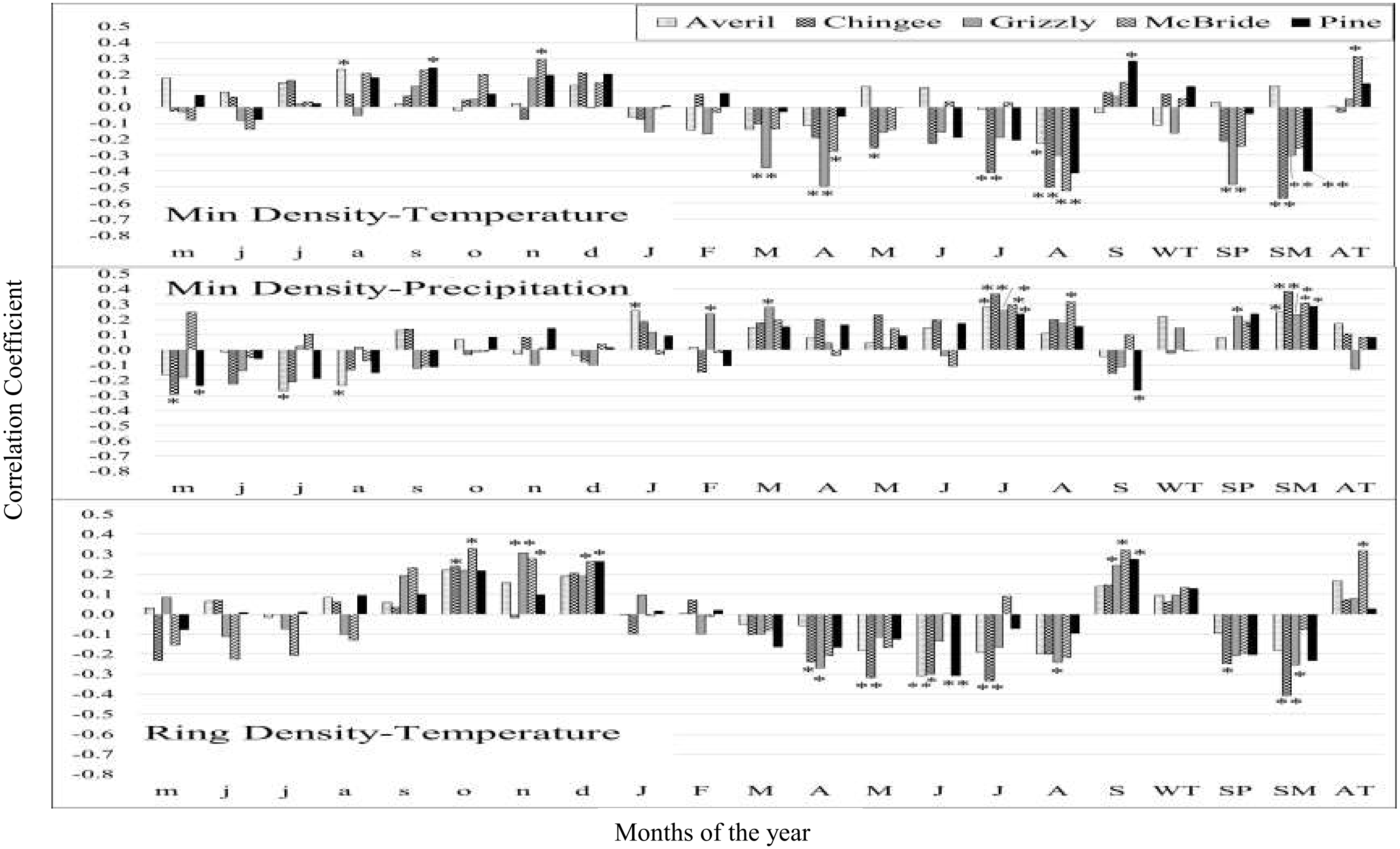

Figure 2.12. Correlations between mean monthly temperature and precipitation at Pine Le Moray, Chingee, Averil, Grizzly Den and McBride Peak stands and minimum density (MND) and ring density (RD) along north-facing slopes of the Rockies in northern BC. Significant correlations are depicted by ** for $P < 0.01$ and * = 0.05. Months are represented by lower case (previous year) and upper case (current year) letters, respectively; WT = winter, SP= spring, SM= summer, AT = fall.

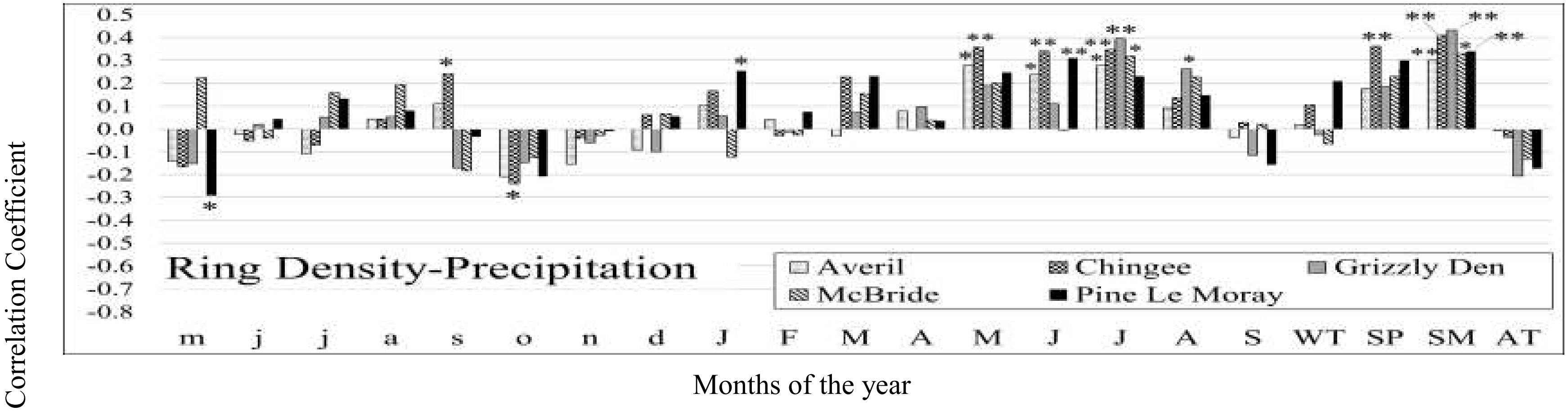

Figure 2.13. Correlations between sum of annual precipitation at Pine Le Moray, Chingee, Averil, Grizzly Den and McBride Peak stands and ring density along north-facing slopes of the Rockies in northern BC. Significant correlations are depicted by ** for $P < 0.01$ and * for $P < 0.05$. Months are represented by lower case (previous year) and upper case (current year) letters, respectively; WT = winter, SP= spring, SM= summer, AT = fall.

2.4.4 Regression Analysis and Comparison of Measured and Modelled Values

Results of Durbin Watson statistics showed that some independent variables that are used to make the models stronger, were related. Therefore, we took an average of two or more climate variables and put them in the model for stronger predictions at each site (Pine Le Moray, Averil and McBride Peak sites) (See Figure A1, A2, A3, A4 in Appendix). Although there were numerous significant relationships found between climate, and radial and fibre properties growth in the study sites (Pine Le Moray, Chingee, Averil, Grizzly Den, McBride Peak), the models presented reflect the strongest relationships found between wood properties and monthly and seasonal climate (Tables 2.9 and Figures 2.14 – 2.20).

2.4.4.1 Relationships between fibre properties (FL, FWT, MFA and FW) and climate

McBride Peak

All four measured fibre properties (FL, FWT, MFA and FW) at McBride Peak were successfully modeled from climate variations. Similarity between modeled FL obtained from combination of previous fall precipitation and previous fall minimum temperature and measured FL, was high (robust) between 1950 and 2018, with some decoupling between the observations and predicted models from 1980s to 1990s (Figure 2.14 A). The predicted model of FWT from the McBride Peak site, based on minimum temperature of previous October, corresponded well with measured data (Figure 2.14 B). Measured values of MFA from McBride Peak and modeled values of MFA from September minimum temperature decoupled in 1960s, 1970s and 2000s (Figure 2.14 C). Modelled values of the FW based on fall maximum temperature followed the measured values strongly during 1950-2018 period (Figure 2.14 D).

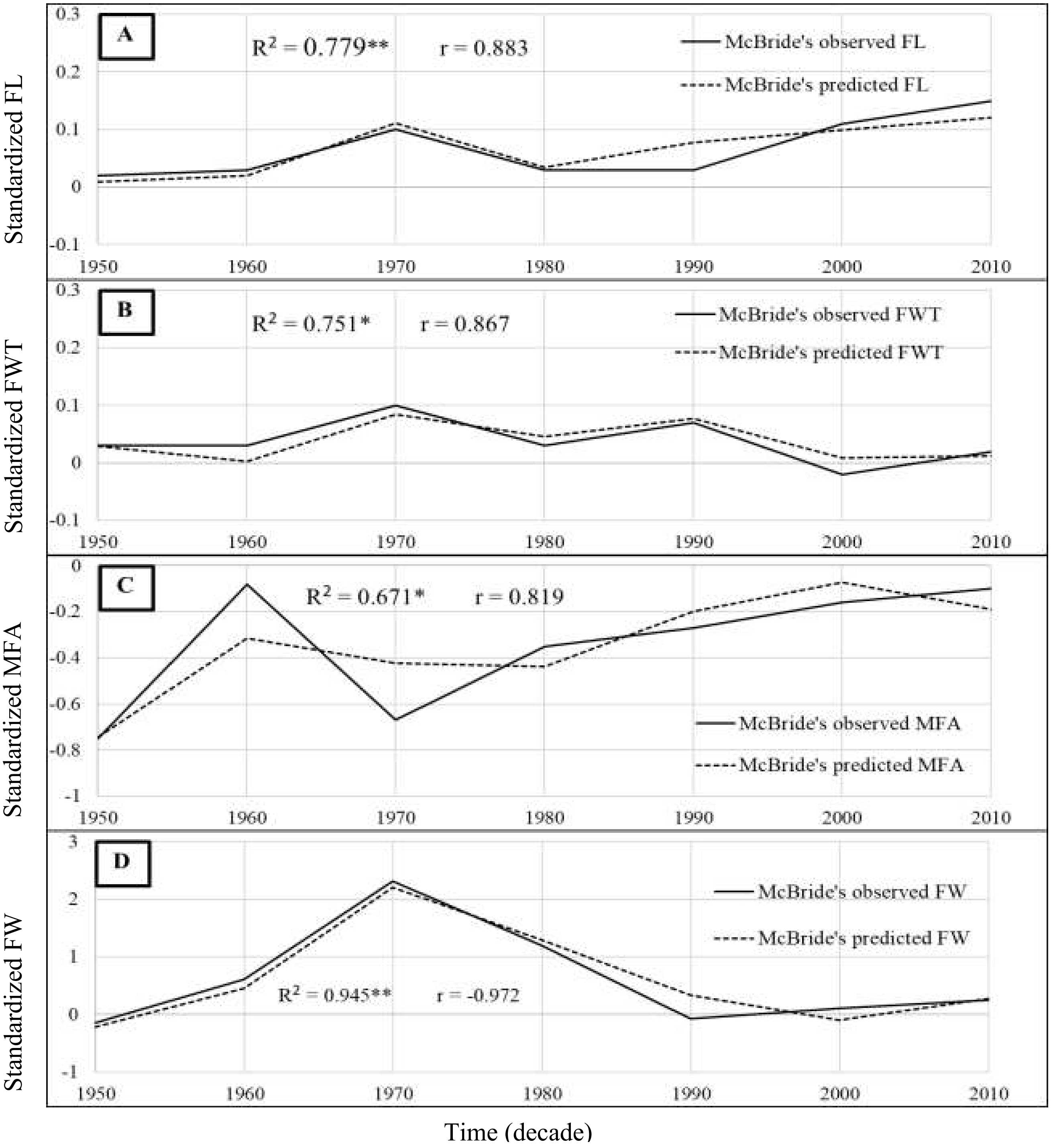

Figure 2.14 Measured fibre properties (solid line) vs modelled fibre properties (dotted line); dashed lines indicate 1 decade lagged data fibre length (FL), fibre wall thickness (FWT), micro fibril angel (MFA) and fibre width (FW) for subalpine fir at McBride Peak stand in northern British Columbia. Data modeled from combined previous fall precipitation with previous fall minimum temperature (A), minimum temperature of previous October (B), September minimum temperature (C), and previous fall maximum temperature (D). R^2 values are presented for ** $p < 0.01$ and * $p < 0.05$. Note not all axis are the same scale.

Pine Le Moray

FWT, MFA and FW were successfully modeled from climate values at the Pine Le Moray site during 1940-2018. Modeled FWT values were obtained from average and maximum temperature of May. These modelled values were decoupled from measured values in the 1970s, and 2000s. However, the highest correlation between model and measured FWT values occurred between the 1940s and 1960s (Figure 2.15 A). Correlations were high between modeled MFA values obtained from combined average temperate of August with minimum temperature of July and August and measured MFA values for the decades between 1950s, 1960s and 1980s, and low in1970s and 1990s (Figure 2.15 B). The highest correlation between modeled RW values obtained from combined average temperature of June and July with minimum temperature of July and measured RW values occurred in 1980s. The lowest correlations for the RW model and measured values occurred in the 2010s (Figure 2.15 C).

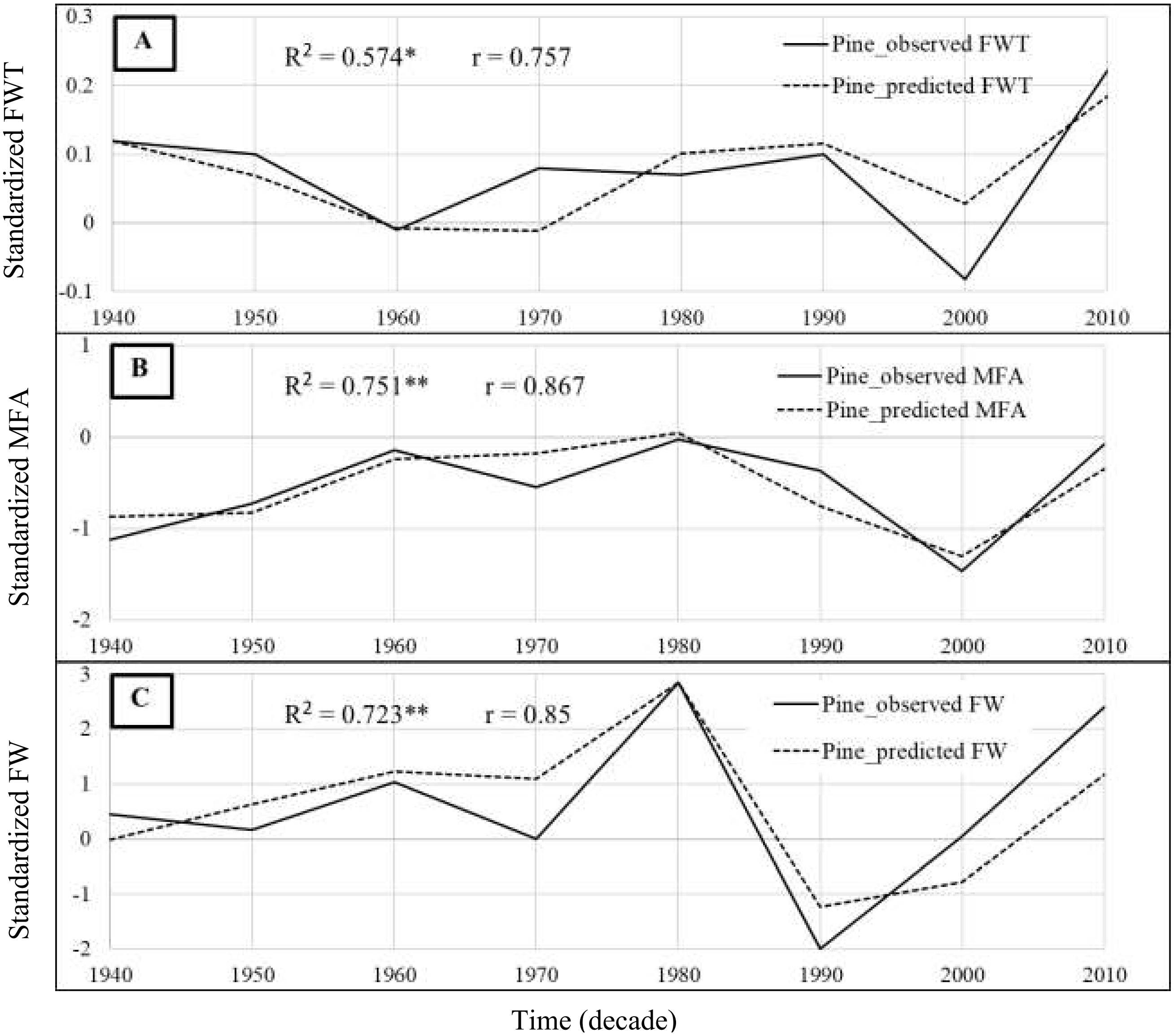

Figure 2.15 Measured fibre properties (solid line) vs modelled values (dotted line); dashed line indicates 1 decade lagged data for fibre wall thickness (FWT), micro fibril angel (MFA) and fibre width (FW) for subalpine fir at Pine Le Moray stand in northern British Columbia. Data modeled from average and maximum temperature of May (A), combined average temperate of August with minimum temperature of July and August (B), and combined average temperature of June and July with minimum temperature of July (C). R^2 values are presented with ** $p < 0.01$ and * $p < 0.05$ Note not all axis are the same scale.

Mt. Chingee

FWT, MFA and FW were successfully modeled from climate at the Chingee site. The predicted model for FWT based on July maximum temperature followed measured values well, with highest correlation between observed and predicted models in the 2000s and 2010s and lowest in the 1970s (Figure 2.16 A). The highest correlations between measured values and the predicted model for MFA calculated from July maximum temperature at Chingee site occurred in the 1970s, 1990s and 2000s while the lowest correlations occurred in the 1980s (Figure 2.16 B). During the 1960s to 1970s and 2000s, the predicted model for FW obtained from previous October precipitation strongly followed measured values. However, the weakest relationship between modeled and measured RW values occurred in the 1990s (Figure 2.16 C).

Mt. Averil

Although FL was successfully modeled from combined maximum temperature of summer and previous fall at the Averil site during 1930 to 2018, the models had some areas of poor association with measured values in 1960s, 1980s, 1990, and 2010s (Figure 2.17 A). Other fibre characteristics (FW, FWT and MFA) did not show high correlations with the most important climate variables (temperature and precipitation) models.

Grizzly Den

Like Averil site, none of FWT, MFA or FW values showed significant correlation with climate variables from the Grizzly site. Only FL values were successfully modeled from combined December mean and minimum temperatures during 1920 - 2018 (Figure 2.17 B). The strongest similarities between observed values and predicted model values occurred in the 1920s and 1930s. However, measured values and predicted model values decoupled between 1960s to 2010s (Figure 2.17 B).

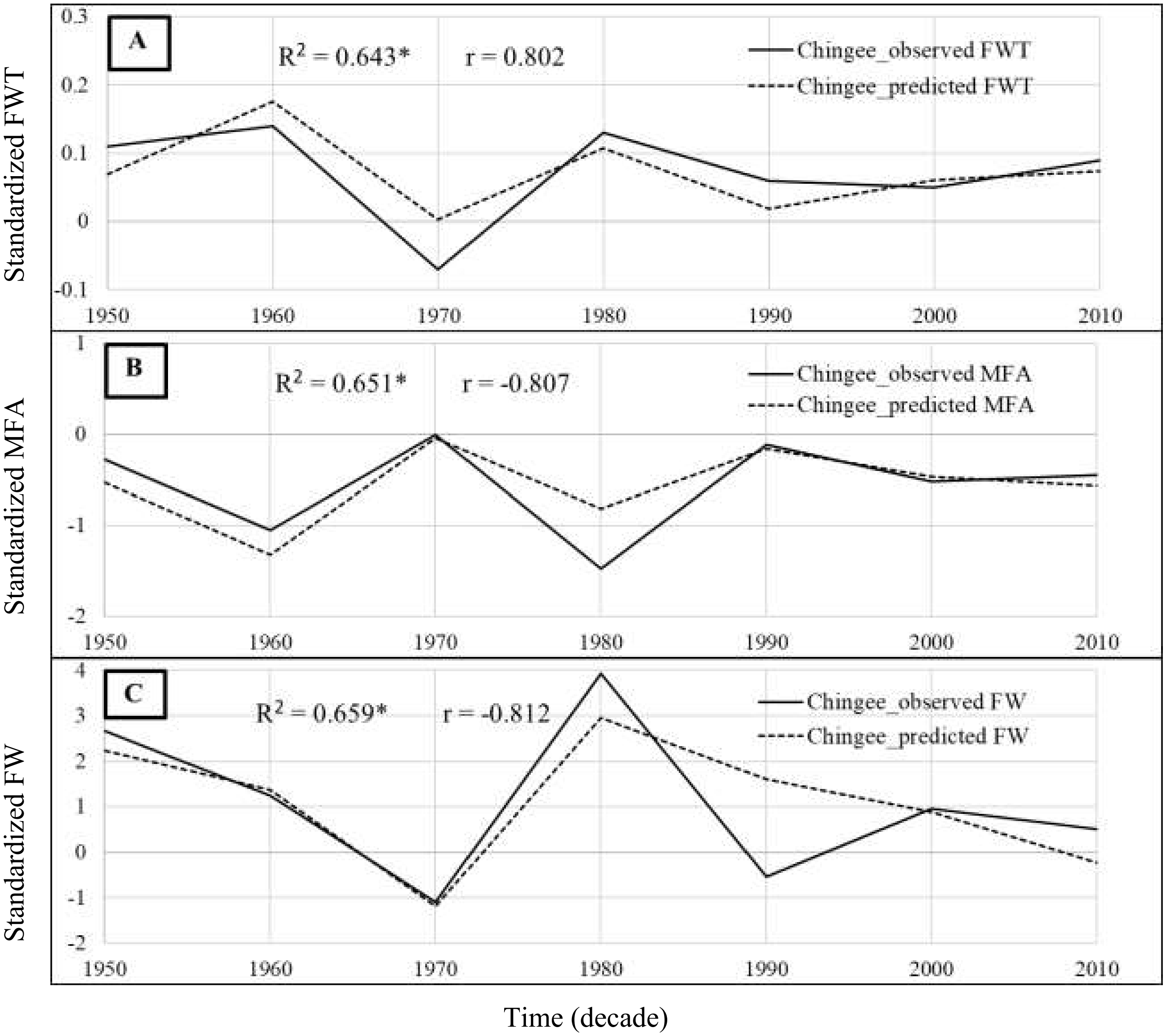

Figure 2.16 Measured fibre properties (solid line) vs modelled values (dotted line); dashed lines indicate 1 decade lagged data in fibre length (FL), fibre wall thickness (FWT), micro fibril angle (MFA) and fibre width (FW) for subalpine fir at Chingee site in northern interior British Columbia. Data modeled from July maximum temperature (A), July maximum temperature (B), and previous October precipitation (C). R^2 values are presented with ** $p < 0.01$ and * $p < 0.05$. Note not all axis are the same scale.

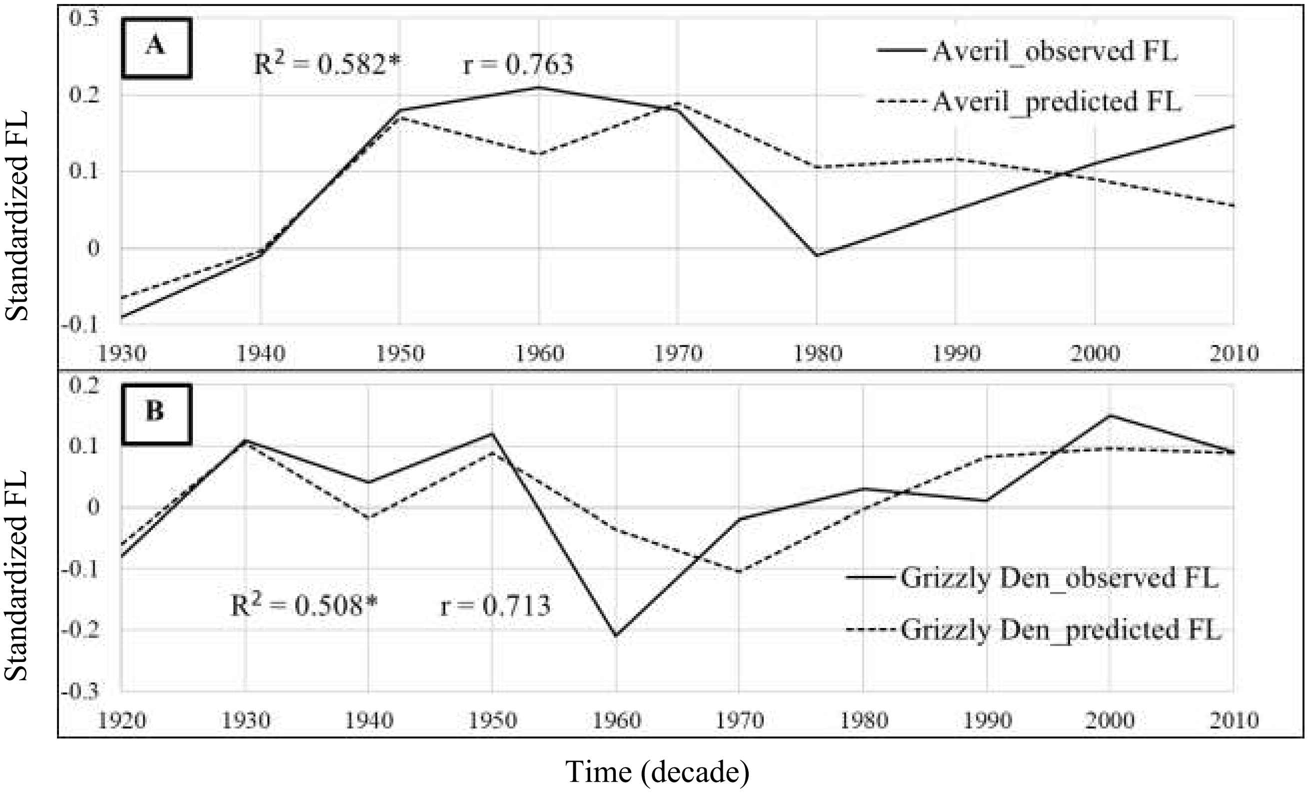

Figure 2.17 Measured fibre properties (solid line) vs modelled values (dotted line); dashed lines indicate 1 decade lagged data for fibre length (FL) at Averil and Grizzly Den stands in northern interior British Columbia. Data modeled from combined maximum temperature of summer and fall (A), and combined December mean and minimum temperatures (B). R^2 values are presented with ** $p < 0.01$ and * $p < 0.05$. Note not all axis are the same scale.

2.4.4.2 Relationship between temperature and RW, EWD, MND, EWW, MXD, RD

Like the fibre property correlations reported, only strongest correlations between RW, EWD, MND, EWW, MXD, RD and climate (R2 > 0.2; r > 0.447) were considered for modeling radial growth properties (Tables 2.9 and Figures 2.18 – 2.20).

Table 2.9. Regression analysis between climate variables (precipitation and temperature) and Earlywood width (EWW), earlywood density (EWD), minimum density (MND), ring width (RW), latewood density (LWD) and ring density (RD) chronologies for Pine, Chingee, Averil, Grizzly and McBride stands along north-facing slopes of the Rockies in northern BC. R^2 values only accepted if > 0.2. All values are significant at 0.99. Combined temperature and precipitation = precipitation of May, June, July and temperature of September, October, November, and December; Combined precipitation and temperature = precipitation of May, September, October, November and December, and temperature of May and June.

Climatic Parameter(s)	Site	EWW (R^2)	EWD (R^2)	MND (R^2)	RW (R^2)	LWD (R^2)	RD (R^2)	sig (*P* value)
August temperature & September precipitation	Pine Le Moray			0.214				<0.0001
Summer temperature	Mt. Chingee		0.331	0.321				<0.0001
Combined temperature & precipitation	Mt. Averil						0.202	<0.0001
Combined precipitation & temperature	Mt. Averil					0.203		<0.0001
April temperature	Grizzly Den			0.243				<0.0001
Ausut temperature	McBride Peak			0.272				<0.0001
Previous July & August temperature	McBride Peak	0.369						<0.0001

Mt. **Chingee**

EWD and MND chronologies for the Chingee site were successfully modelled from current summer temperature and showed significant relationships to measured values over the time series with the strongest correlations from 1957 to 1958, 1965 to 1969, 1989 to 1990 and 1995 to 1995 (Figure 2.18 A). However, EWD and MND models were poorly correlated with measured values from 1973 to 1975, 1983 to 1987 and after 2002 (Figure 2.18 A).

McBride Peak

In general, MND, EWW and RW for subalpine fir in McBride site were strongly correlated with August temperature, a combination of previous July and August temperature, and previous July temperature, respectively (Figure 2.18 B, C; Figure 2.19 A). Correlation was high between measured MND values and modeled values obtained in McBride site for the years between 1979 to 1982. However, measured MND value showed low correlation with modelled values between 2001 and 2002 (Figure 2.18 B). The second time period with the highest correlation between measured and modeled MND was between 1967 to 1968 (Figure 2.18 B).

EWW values from the McBride site were modeled from combined previous July and August temperature. This model showed low correlation with measured EWW from 1968 to 1980 (Figure 2.18 C). The modeled chronology for RW values from the McBride site, obtained from previous July temperature, was generally more strongly correlated with measured RW after 1980 compared to prior to 1980 (Figure 2.19 A). The strongest correlation between modeled and measured RW was observed from 1987 to 1989. However, the weakest relationship between modeled and measured RW was between 1975 to 1980 (Figure 2.19 A).

Grizzly Den

Subalpine fir MND chronology from the Grizzly Den site was modelled from current April temperature. This model showed weak to moderate correlation with measured values (Figure 2.19 B). Some similarities between the modeled and measured chronologies included: 1945- 1946, 1968-1969, 1975-1976 and 2012-2013 (Figure 2.19 B).

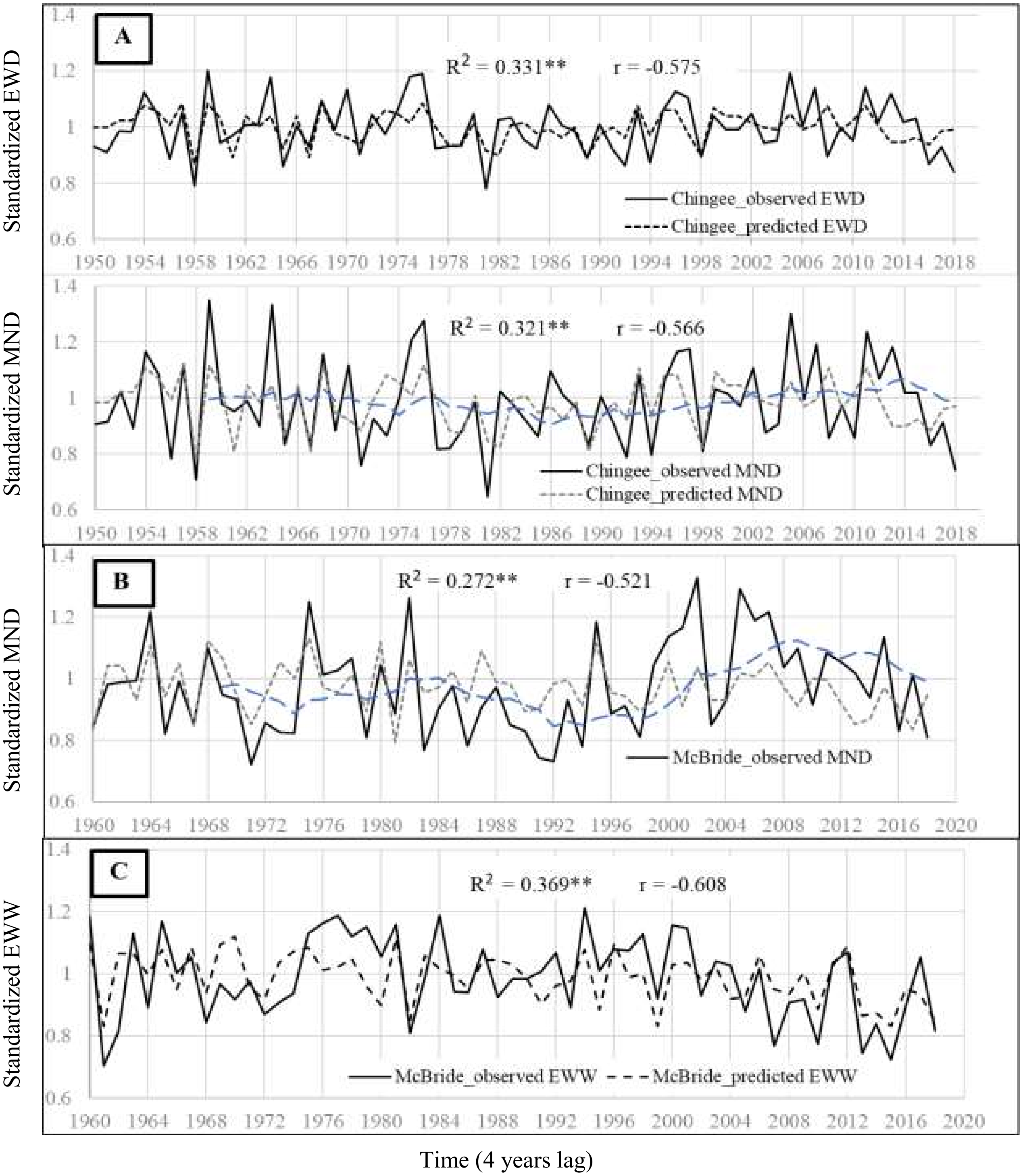

Figure 2.18. Measured (solid line) vs modelled (dotted line) earlywood density (EWD), minimum density (MND) and earlywood width (EWW) for subalpine fir trees at Mt. Chingee and McBride Peak sites along the Rocky Mountains in northern British Columbia. Data modeled from summer temperature (A), August temperature (B) and mean previous July and August temperature (C). R^2 values are presented with ** $P < 0.01$ and * $P < 0.05$. Crossed solid line indicates 4-year lagged data. The dashed blue trendline represents a 10-year moving trend line.

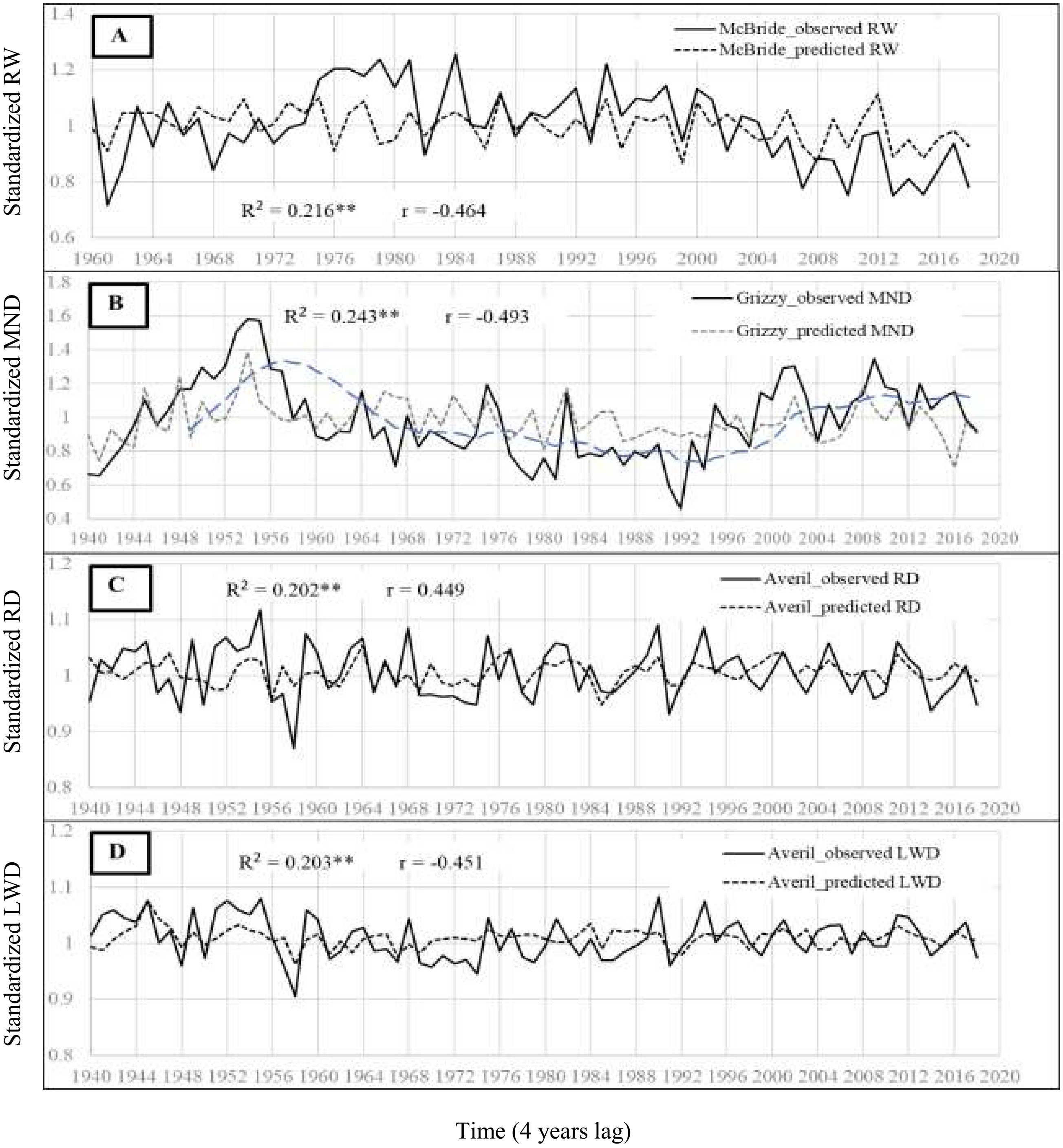

Figure 2.19. Measured (solid line) vs modelled (dotted line) ring width (RW), minimum density (MND), ring density (RD) and latewood density (LWD) of subalpine fir trees at McBride Peak, Grizzly Den and Averil stands along the Rocky Mountains in northern British Columbia. Data modeled from previous July temperature (A), April temperature (B), precipitation of May, June, July and temperature of September, October, November, and December (C), Precipitation of May, September, October, November and December, and temperature of May and June (D). R2 values are presented with ** P < 0.01 and * P < 0.05. Crossed solid line indicates 4-year lagged data. The dashed blue trendline represents a 10-year moving trend line.

Mt. Averil

RD and LWD chronologies from the Averil site were modelled from a combined precipitation of May, June, July and temperature of September, October, November, December, and from Combined precipitation of May, September, October, November and December with temperature of May and June, respectively (Figure 2.19 C). The RD model corresponded well with combined precipitation of May, June, July with temperature of September, October, November, December, and was moderately correlated with measured values (Figure 2.19 C). Modelled RD values decouple from measured values prior to 1960. However, strong correlations between model and measure values were obtained from 1965- 1967, 1977-1978 and 2010-2013 (Figure 2.19 C).

LWD chronologies from the Averil site were modelled from combined precipitation of May, September, October, November and December, with temperature of May and June, and were moderately related to measured values over most of the time series during 1940- 2018 with some areas of decoupling occurring in this model between 1969 – 1974 and 1978 - 1990. (Figure 2.19 D).

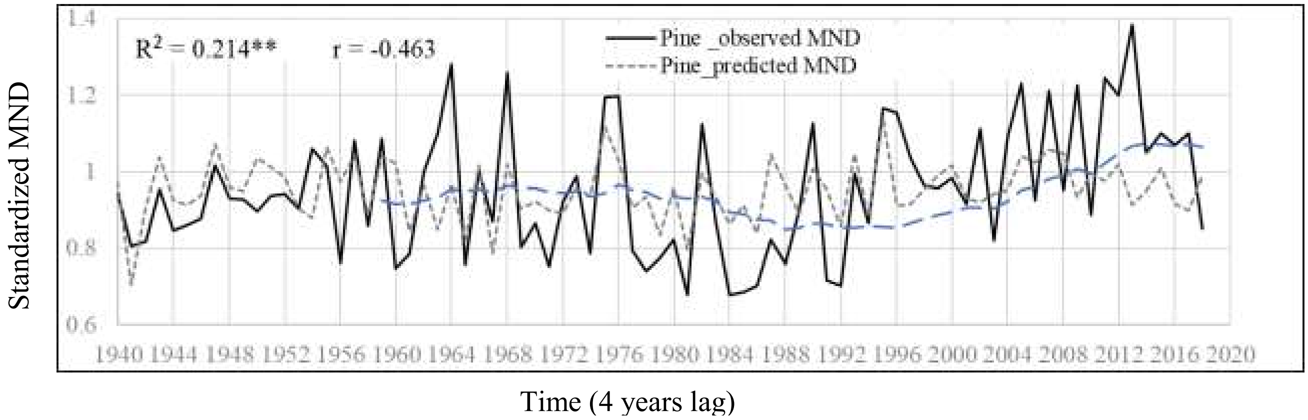

Figure 2.20. Measured (solid line) vs modelled (dotted line) minimum ring density (MND) for subalpine fir trees in Pine Le Moray site along north-facing slopes of the Rockies in northern British Columbia during 1940 -2018. Data modeled based on combination of August temperature and September precipitation. R^2 values are presented with ** *P* <0.01 and * *P* < 0.05. Crossed solid line indicates 4-year lagged data. The dashed blue trendline represents a 15-year moving trend line.

Pine Le Moray

MND chronology values from the Pine Le Moray, were moderately related to models based on mean August temperature and September precipitation (Figures 2.20). Decoupling between modeled and measured values occurred in 1950-1951, 1963-1964, 1975-1979, 1984-1989 and after 2000 (Figure 2.20). However, strong similarities between modeled and measured MND values occurred in 1958-1959, 1966-1967 and 1994 (Figure 2.20).

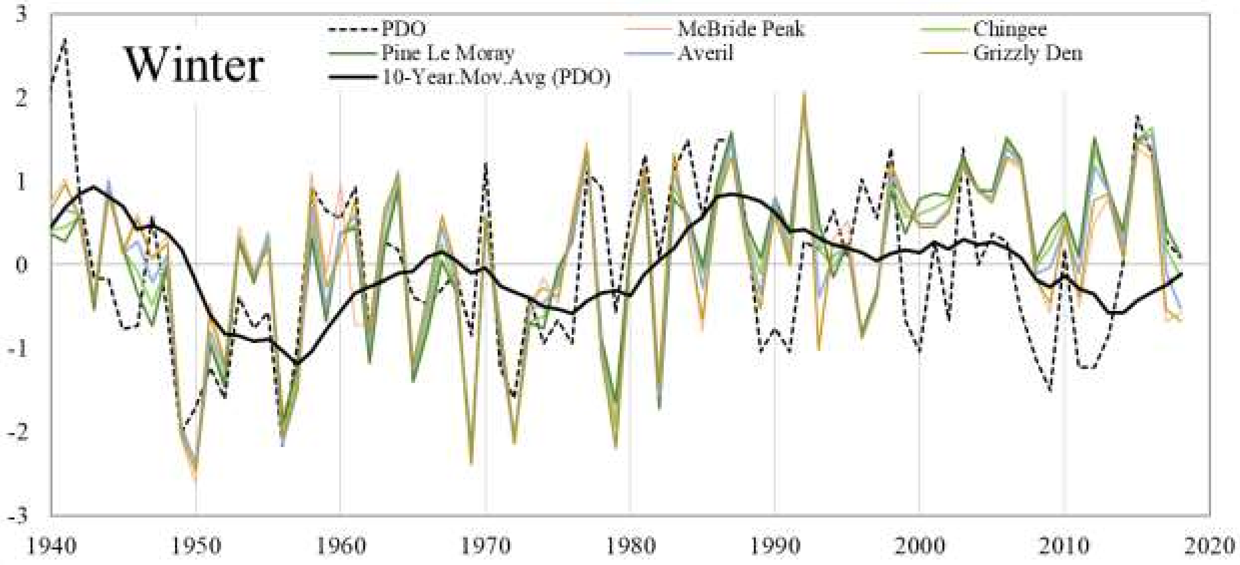

Figure 2.21. Average winter Pacific Decadal Oscillation Index (PDO), and average winter temperatures at Pine Le Moray, Chingee, Averil, Grizzly Den and McBride sites.

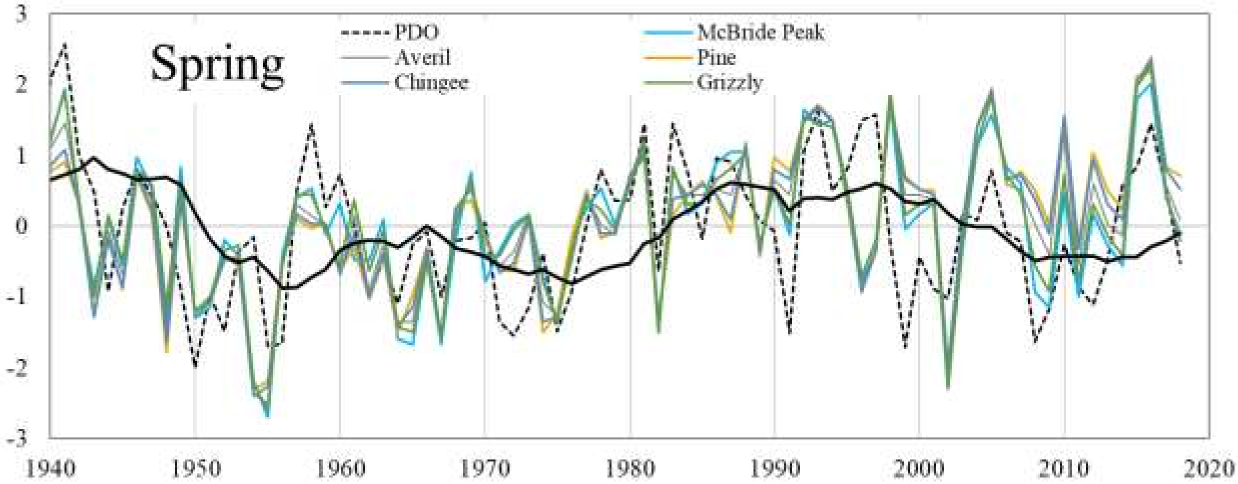

Figure 2.22 Average spring Pacific Decadal Oscillation Index (PDO), and average spring temperatures at Pine Le Moray, Chingee, Averil, Grizzly Den and McBride sites.

2.5 Discussion:

I assumed that subalpine fir growth would be responsive to climate in the locations we targeted and ring density to be more sensitive to climate than ring width orders. Therefore, according to the results and existence of significant correlations between subalpine fir radial growth and climate variables, my hypothesis is confirmed. Due to stronger ring density (MXD, MND, RD) relationships with climate than annual-ring width (RW) relationships, second part of my hypothesis is also confirmed.

Most of the study sites showed climatic conditions characteristic of their latitudinal position, and likely optimal for the support of subalpine fir growth. Pine Le Moray was the highest latitude site studied and generally had wetter winters, and colder summers compared to other sites (Delong et al 1993; Wang et al. 2016). The Mt. Chingee, Mt. Averil and Grizzly Den sites occurred at lower latitudes than Pine Le Moray, but were within 200 m elevation of each other (Table 2.1), and also experienced wet winters and cool summers. Typically, snowpack at Pine Le Moray remained longer on forest floor than other sites, and comparatively, accumulation of snowpack at Chingee and Averil sites were higher than at lower latitude sites (Grizzly Den and McBride Peak). Annual temperature changes at Pine Le Moray, Chingee, Averil and Grizzly sites all show an increasing trend between 1940 to 2018 while precipitation decreased (Figure 2.2). At the lowest latitude (McBride site), compared to other sites, climate was drier with an increased air temperature and, to a lesser extent, increased precipitation between 1940 and 2018 (Figure 2.2).

In general, I came to this results that the optimal growing conditions for subalpine fir growth were wet climate with storage of water in the soil during dry seasons and the temperature at which trees showed better signs of optimal growth at study sites (Alexander et al. 1990; Alldritt-McDowell 1998). Because study sites mostly occurred at high latitudes of the Rocky Mountains where weather was cold, it was not surprising that precipitation was not a limiting factor for growth of subalpine fir because the sites received enough amount of yearly precipitation (except for some very dry years that will be discussed later in this section). However, temperature was the more important climate factor as limiting factor than precipitation for controlling subalpine fir's growth at study stands both before and during the growing season considering that most anatomical traits showed more significant correlations with temperature that with precipitation.

2.5.1 Relationship between climate, radial growth and fibre properties at study sites

Although there were numerous significant correlations between radial growth and climate, correlations will only be discussed where anatomical wood properties and fibre property models were successfully predicted from climate variables at statistical strengths of $R^2 > 0.2$ and $R^2 > 0.7$, respectively. At sites where both FL and MFA, or FWT and MFA, showed significant correlations with climate, only the strongest correlations will be discussed because fibre length and cell wall thickness have both been found to be closely correlated with microfibril angle, with smaller angles being related to longer fibre lengths and to thicker walls (Barnett and Bonham 2004; Sheng-Zuo et al. 2004; Hiller 1964 a,b; Evans et al. 2000). It also has been confirmed that, for a large range of ring widths, latewood width remains relatively constant between rings, so that variations in ring width are more closely related to earlywood width (Brazier 1970; Zhang et al. 1996; Savva et al. 2010). Therefore, between EWW and RW properties, I will discuss only those with higher correlation (i.e. higher R^2) with climate. Furthermore, EWD and MND almost tell the same story and measure almost similar values (not the exact values as EWD is an average measurement of density across all the earlywood while MND is the measurement of lowest density). I will discuss only those characteristics that showed statistically stronger and more reliable models for each site because I found significant overlap when testing both EWD and MND in their relationships to climate variables.

In the following paragraph I try to meet objective (ii) about evaluating whether intra-annual wood characteristics show stronger correlations with climate indices or not.

The reasons why intra-annual variations as reflected by monthly climate variables (Figure 2.8-2.13) showed stronger correlations with monthly climate variables were because in many applications annual-ring width (RW) estimations give just a growing season portrayal of climatic information (D'Arrigo et al. 1993). In addition, tree rings for the most part records seasonally change in climate parameters not at specific and/or short time periods like the beginning or end of the growing seasons. However, to measure and understand the exact ecological changes even in small periods of time under changes in climate, intra-annually wood properties estimations demonstrate higher connections to climatic variables than do RW orders (Wimmer and Grabner 2000; Davi et al. 2002).

I found a lack of significant relationships between climate variables and FWT, MFA and FW at

Averil and Grizzly Den, and a lack of significant relationships between climate variables and FL at Chingee and Pine Le Moray. These findings may have been due to small sample sizes (only 7 to 9 decades were applied using 10-year sections; i.e. n = 7-9) or possibly because of the strength of influence of genetic factors (Zobel and Buijtenen 1989; Donaldson 2008). Alternatively, other environmental factors like wind speed, could have influenced MFA development directly as a result of flexural stress (Wimmer et al. 2002a).

In the following I will provide some evidence to cover objective (i) about comparing variations in subalpine fir wood properties with climate data:

Influence of temperature

As expected, due to global climate change, mean annual temperatures at all study sites, from lowest to highest latitudes, have increased by 0.6 ºC to 1.5 ºC during 1940 to 2018 (Figure 2.2). This increase coordinates with the general increase of 0.9 ºC on average observed across Canada (south of 60 ºN) over the last century (Zhang et al. 2000). Mean temperature can vary with both latitude and elevation (Peterson and Peterson 2001). Both the current growing season and pre-growing season's temperatures affected wood properties at all five of my study sites. Temperatures within summer months were by far the most influential climate variables on tree growth and wood formation in the subalpine fir sampled, according to the relationships identified.

Ring densities generally decreased as summer temperatures increased and summer precipitation decreased. However, in September, this relationship reversed, and temperature became positively associated with density at all sites as LW cell needs enough temperature for formation at near the end of growing season. Normally, cells produced in the early part of the growing season display larger radial diameter, thinner cell walls with a larger lumen and relatively lower density while near to the end of growing season, cells with thicker wall and smaller lumen area are produced with higher density (Larson 1969; Worall 1970; Nicholls and Wright 1976; Dutilleul et al. 1998). Precipitation is the stronger limiting factor for wood density throughout the majority of the summer, until September when we observe temperature form a stronger relationship to density and become more limiting (Figures 2.12 and 2.13). This finding is consistent with Wimmer and Grabner (2000) who showed that average temperature of late summer (September) positively related to average ring density in Norway spruce (*Picea abies*).

Increases in air temperature during summer could result in prolonged earlywood formation. At Pine Le Moray and Chingee, decreases in MND and EWD values during the summer months could also be associated with higher snowpack accumulation in comparison with cumulative snowpacks at lower latitude sites. Therefore, larger snowpacks later lead to delay in onset of the growing season and formation of earlywood cells at Pine Le Moray and Chingee sites. This delay in growth initiation could mean that production of earlywood cells continued until mid-summer resulting in lower MND and EWD values at high latitudes. Lesser MND values because of mid-summer temperature and during the growing season was also found by Franceschini et al. (2013) and was interpreted as a result of the prolongation of the maturation of earlywood tracheids leading to wider earlywood cells. Therefore, production of larger rings, led to lower MND values (Mäkinen et al. 2002; Franceschini et al. 2013).

At Grizzly Den, a lower latitude stand compared to the others sampled (Pine Le Moray, Averil and Chingee), the proportion of earlywood cells increased at the beginning of the growing season leading to decreased MND values at this site. The accumulation of snowpack was smaller than at sites located at higher latitudes, caused by increased April temperature which improve thermal conditions by raising soil temperature in the spring, and removing snow cover allowing trees to photosynthesize earlier (See Figure A5 and A6 in Appendix) (Tardif et al. 2001a; Rossi et al. 2011;

Dolezal et al. 2016).

The transition from higher to lower latitudes along the sampling gradient coordinates with an amplification of the negative relationship between tree growth and summer temperature. For instance, at the lowest latitude site (McBride Peak), where weather was warmer and drier and precipitation was lower than the other sites, previous warmer summers (July and August) (See Figure A7 in Appendix) could increase water moisture stresses at this site, decrease in photosynthesis and consequently reduction of growth and EWW values. This result is supported by King (2013), who suggested that spruce radial growth was increasingly negatively correlated with previous July and August temperature. Also, Chopin et al. (2002) suggested that prolonged warm temperatures reduced soil moisture, which was needed for tree growth during low precipitation periods.

It can be inferred from my results that summer and fall temperature also affected fibre properties at study sites. Pine Le Moray and McBride show a positive relationship between MFA and summer temperatures, and Chingee shows the opposite. This indicates that summer temperature, along with other climate conditions linked to temperature, such as growing season length, were more optimal for straighter microfibrils at Chingee. Microfibril angle responses to climate is similar to that of growth rate and ring width (Drew et al. 2013) with the more earlywood cell production associated with the larger fibre angles (Donaldson 2008). Warmer temperatures in presence of adequate water and release of water stresses may result in higher MFA, as is supported by Drew et al. (2013). Conversely higher temperatures and therefore decreased depth and water content of snowpack (or drought-like conditions) may lead to lower water availability later in the growing season and reduced MFA and FL. This theory is supported by a study by Jarvis and Linder (2000) who realized that increased temperatures during fall and winter reduced length of snow cover or winter precipitation depth, or insulation, leading to deeper soil freezing. These dry-like conditions caused delayed growth onset and shortened growing period which in turn reduced RW and EW cells (Robertson et al.1990), and resulted in formation of smaller fibre lengths and MFA because both form at the time of earlywood cells formation (Zhang et al. 2020).

Trees tend to form larger diameter fibres (FW) early in the growing season (Jozsa and Middleton 1994) when earlywood cells are normally produced. Thus, continuous earlywood formation in summer be a reason for formation of wider fibres at Pine Le Moray. However, at low latitude sites like McBride, higher than normal temperatures in fall prior to growing season potentially raised soil temperature leading to increased water stresses (Alfaro 2010) and therefore thinner fibres.

Previous season fall and winter temperatures significantly influenced the growth rates and formation of annual-rings. Warmer temperatures in seasons prior to growth allow for energy store to be maximized for use the following year (Fritts 1976; Rolland and Schueller 1994). It is also possible that the intimate relationship between temperature and snowpacks played a role in the optimization of growth on sites where snowpack plays an important role in the insulation of roots during long cold winters, and for the provision of water in spring (Lo et al. 2010; Fleming and Whitefield 2010). December temperatures influenced fibre length during the following growing season at Grizzly Den, while fall temperatures and precipitation influenced fibre length in the following season at McBride; both Grizzly Den and McBride were the lowest latitude sites, perhaps indicating that lower latitudes rely more heavily on previous years to meet optimal growth requirements in subsequent years.

Influence of precipitation

Similar to temperature, precipitation also affected wood formation and wood radial growth, but was the limiting factor for growth in fewer instances, as demonstrated by fewer significant correlations between wood properties and precipitation variables. Since selected study sites were located at high latitudes and on the north-facing slopes of the Rocky Mountains, the effect of precipitation on wood properties was less than that of temperature. Spring to early summer precipitation and precipitation of previous fall affected wood property growth at Averil, Chingee and McBride sites. According to the results, RD surprisingly increased with spring and early summer precipitation (May, June and July) at Averil site. Since precipitation falls as snow during May and early June at high altitude regions in BC (DeLong et al. 1994), increased snow would lead to a delay in spring snow melt. Therefore, this delay would mean that the growing season began later in the spring or early summer, and resulted in formation smaller cells and thinner rings in which proportion of latewood cells were high inducing higher RD at Averil site.

Because McBride Peak was drier than other sites, increased precipitation before the growing season at this site could have increased soil water storage, and resulted in preservation of enough water during the growing season necessary for onset and continuation of physiological activities. Fibre elongation would then be able to start at the first month of the growing season in presence of optimal moisture and temperature leading to a positive relationship between fibre length and previous year fall precipitation at the McBride Peak site. Our result is consistent with Around and Fromm (2003) who suggested that early summer drought significantly reduced fibre elongation. At higher latitude sites like Chingee, however, the story was different: increased previous fall precipitation may have increased winter snowpacks, which caused snow cover to stay on the ground for longer and the growing season to start later. Thus, a shorter growing season resulted in reduced fibre width.

2.5.2. Temporal comparison among sites based on wood fibre property changes under impacts of microclimate variations and macroclimate thermal phases (PDO)

Over the last 80 years, temperature averages have increased at all study sites while precipitation decreased at most of the sites (Figure 2.2, 2.3). Temperatures moved from "cool phase" to "warm phase" (Mantua 2000). Therefore, possibly, a PDO shift from a cool phase to a warm phase may have influenced the environment for BC's Forests. It can be understood that likely Pacific Decadal Oscillation (PDO) spring warm phases in the 1980s and the 1990s played an important role in increasing temperature at study sites in northern BC and therefore influenced wood fibre property developments in subalpine fir trees in corresponding sites. This is specifically clear during the warm period in the 1990s during which subalpine fir trees experienced spring and early summer drought, resulting in reduced fibre lengths and thicker cell walls (Arend and Fromm 2007).

According to the results, some similar fluctuating trends occurred for FL values at Averil, Grizzly Den and McBride sites from 1940 to 2018 (Figure 2.14 A; Figure 2.17 A). Precipitation has a basic and essential role in the formation of tracheid cells in conifers, and FL a basic function to transport water (Von Arx et al. 2012; Badel et al. 2015), therefore, increasing trends in fibre length were most possibly due to increases in precipitation from 1940 to 1970 at corresponded sites (Figure 2.3). Following that and during the 1980s and specifically over the 1990s, length of tracheids decreased at the study sites. Theses deceases in fibre elongation coincided with loss of soil water due to higher-than-average temperatures in summers during the 1980s and the 1990s at lower latitude sites (Averil, Grizzly Den and McBride Peak) (Figure 2.2). At a larger scale, fibre length decreases in corresponded decades could be due to the effects of thermal phases of winter and spring PDO which reached its peak in the 1990s and influenced local microclimate at study stands (Figure 2.21; 2.22). In a similar study, Arend and Fromm (2007) reported that early-summer drought significantly reduced fibre length. FW values were also decreased in the 1990s at Pine Le Moray, Chingee and McBride Peak likely due to higher than average summers in this decade and lack of soil water storage (Figure 2.14 D; 2.15 C; 2.16 C).

According to the moving averages at Chingee, McBride Peak, Grizzly Den and Pine Le Moray sites, during 1980s and 1990s minimum density decreased (Figure 2.18 A, B; 2.19 B and 2.20) which were apparently due to the increased temperature during 1980s and 1990s at corresponded sites (Figure 2.2) and in a larger scale because of the impact of thermal spring PDO over the whole region during 1980s and 1990s (Figure 2.22). Because increased temperature during spring induces earlywood cell productions, MND has been decreased as a result of earlywood cell formation (Xiang 2014).

2.6. Conclusion

This study aimed to investigate the effect of the most important climate factors including temperature and precipitation on radial growth properties (RW, EWW, LWW, EWD, LWD, MXD, MND, RD) and fibre properties (FL, FWT, MFA, FW) of subalpine fir at five study sites along the north-facing slopes of the Rocky Mountains in northern BC. Annual temperature has increased at the study sites over the study period since 1940. Annual precipitation trends showed overall decreases since 1940 at Pine Le Moray and Chingee, while slightly increased at McBride and remained nearly constant at the Averil and Grizzly sites over past 80 years.

I conclude that relationships between intra-annual-ring characteristics (EWW, EWD, LWW, LWD, MXD, MND) and climate variables were stronger than simple tree-ring width relationships. These findings are consistent with other studies that showed intra-annual wood properties estimations including cell size (cell divider thickness, cell numbers), fibre length, fibre divider thickness and wood thickness demonstrated higher connections to climatic variables than do RW parameters (Wimmer and Grabner 2000; Davi et al. 2002).

In general, stronger and more robust regression models calculated from the strongest correlations determined that wood anatomical characteristics of subalpine fir were firstly site specifically (latitude) affected by climate variables; secondly, strongly influenced by summer temperature, previous fall temperature, and to a less extent precipitation. The lower the latitude, the greater the negative effect of summer temperatures on radial growth at study stands.

Late summer precipitation was associated with increased ring density at study stands. It is worth mentioning that the highest number of anatomical parameters that showed significant relationships with the climate, associated with the McBride Peak site. This is likely because the McBride Peak site geographically located at the lowest latitude and warmer temperature and received lower annual precipitation. Therefore, this site was more sensitive to climate variations than the other study sites.

Finally, although some wood anatomical characteristics like LWW and RD showed significant relationships with both temperature and precipitation, most of other properties including RW, EWW, EWD, LWD, MXD, and MND showed higher correlations with temperature meaning that temperature was possibly the most important climatic factor controlling growth of subalpine fir at all five study stands in northern interior BC and along north facing slopes of the Rocky Mountains since 1940. An old study on subalpine fir in British Columbia also confirmed that temperature was the most important climate factor affecting growth of subalpine fir (Ettl and Peterson 1995) perhaps due the position of Canada’s western forests at higher latitudes than the U.S. Furthermore, in a wider range it has been confirmed that temperature was more important than precipitation when studying the growth of subalpine trees (Lara et al. 2001; Watson and Luckman 2007).

In this study I mostly focused on mathematical and statistical correlations and regression analysis to find out the relationships between wood characterises and climate indices. Therefore, according to the significant correlations, it is possible that trees respond to climate factors. However, the growth is generally based on complex combination of environmental and genetic factors and therefore, trees are responding to all sort of environmental factors including soil nutrient values, soil moisture regimes, number of sunny or cloudy days, snowpack accumulations, wind conditions, stand level conditions and so on. Therefore, I was aware of all sorts of growth-effective parameters in this study and limitations of this study in calculating subalpine fir responses to climate variables.

Overly, increased awareness of the wood quality (longer fibre, smaller MFA and denser wood) of subalpine fir under changing climate conditions in this Chapter will feed directly into knowledge of supply quality for end-uses such as pulp and paper. Results of this study Chapter may also help to guide timber supply analysis for northern BC. This research could potentially be useful to improve the Canadian forest industry competitiveness in the global marketplace, in terms of value-added manufacturing wood industry.

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Chapter 3. Legacy effects and growth resilience in northern subalpine fir stands during severe drought

3.1. Abstract

As global warming continues, drought severity and duration are expected to increase in most areas especially in dry regions. Therefore, it is very important to understand how trees react to severe drought periods. In this study I focused on the resilience and recovery of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.)) to severe drought and compared growth resilience and recovery periods (legacy effects) among five study sites along latitudinal gradient on the north-facing slopes of the Rocky Mountains in northern BC, Canada. The tree growth recovery period was found to be between 1 to 2 years for the stands investigated, indicating that subalpine fir trees were resilient to dry conditions. Dry conditions were defined as those periods with climate moisture deficit measurements greater than two standard deviations from the average. The lowest latitude stand had the fastest recover rate from drought. Results also revealed that drought resistance increased along the latitudinal gradient and toward higher latitudes.

3.2. Introduction

Due to global warming, numbers and intensity of drought events may increase in the future (IPCC 2013). The length of drought periods, as well as the severity of drought, are increasing around the world and consequently, forest dynamics are changing, as forest are vulnerable ecosystems. This is especially highlighted in mountain regions as it has been shown that temperature is rising faster than the global mean in mountain ecozones (Gobiet et al. 2014). While some forest ecosystems benefit from a climate change induced longer growing season (Reyer et al. 2014), other ecosystems are experiencing drought stresses (Allen et al. 2015). Therefore, depending on the type of forest and habitat conditions, the behavior of trees in the face of global warming is different around the world. Meanwhile, forest resilience has become a very important aspect of ecosystem management and sustainability in addressing climate change and severe climatic events (Seidl 2014; Reyer et al. 2015). In general, the capacity of a system to rebound or recover from disruption and continue in the face of perturbations is known as resilience (Carpenter et al. 2001). From an ecological perspective, resilience is the ability of a system to absorb impacts before a threshold is reached where the system changes into a different state (Gunderson 2000), while resistance is the capacity of the ecosystem to absorb disturbances and remain largely unchanged (Holling 1973). It has been suggested that tree-rings are very informative for studying the effect of drought on forest stands and forest growth responses to perturbations, as annual tree-rings provide short and long-term information on how trees respond to drought (Anderegg et al. 2015; Camarero et al. 2015b; Gazol and Camarero 2016; Gazol et al. 2017c). Studying tree-ring width can help us understand forest growth responses before, during, and after drought events and provide a measure of resilience of forests to drought (Lloret et al. 2011).

In recent years, dendrochronological methods have been used to study long-term severe climate impacts on forest ecosystems to assess forest resilience (Lloret et al. 2011; Boden et al. 2014). Recently, Gazol et al. (2016) studied that, individual tree resilience to perturbance may not be necessarily representative of stand or landscape level resilience. This is likely why responses of different tree species to drought and their resilience to severe climate events remains unclear. Fewer studies have been conducted on tree resilience in dealing with drought (Gazol et al. 2016). Also, the studies that have been done so far, regarding forest resilience to severe climate using dendrochronological methods, mostly cover past events and may not necessarily represent future climate impacts and growth resilience behavior (Radeloff et al. 2015).

Drought indices are one of the most important climatic indicators of resilience in forest stands. However, not all regions have the same effect (Steinkamp and Hickler 2015). For example, in boreal forests, reductions in productivity and widespread increases in tree mortality as a consequence of increasing drought stress have been reported (Peng et al. 2011). Therefore, predicting the resilience of trees in the face of severe climate events and recovery after drought is challenging (Gonzalez et al. 2010). Newly, a few studies have suggested that not all regions will experience widespread forest dieback if severity and duration of drought increase due to climate change (Steinkamp and Hickler, 2015; Allen et al. 2015). However, it is suggested that even in cold regions like boreal forests where tree growth is not mainly constraint by drought, reduction in productivity and widespread increase in tree mortality as a consequence of drought, can be seen (Peng et al. 2011).

Lately, studies have examined the “legacy effect” on the growth of forest species following drought (Pretzsch, et al. 2013; Camarero et al 2015; Anderegg et al. 2015; Gazol and Camarero 2016; Wu et at. 2018; Zweifel and Sterck 2018; Huang et al. 2018). Although legacy effect studies of drought are more applicable in arid and semi arid regions (Sánchez-Salguero et al. 2012; Vicente-Serrano et al., 2013), legacy effects are also studied in some wet and more mesic ecosystems (Anderegg et al. 2015; Pederson et al. 2014; Peltier, et al. 2016; Gazol and Camarero, 2016; Huang et al. 2018). Legacy effects define as multi-year lags in tree drought recovery and can be calculated as the difference between measured and modelled growth (unitless index) after a severe (2-SD) dry anomaly in the measured climatic moisture deficit (CMD) (Anderegg et al. 2015). Generally, drought happen when precipitation is bellow than evapotranspiration. CMD is an aridity metric that can be defined in simple terms as the cumulative difference throughout the year between ET0 (reference evapotranspiration) and precipitation when precipitation is less than ET0 (i.e., during moisture-stressed months only). Evapotranspiration is the water lost through plant transpiration and soil and plant evaporation. So, the larger the CMD, the drier condition. CMD has been used to quantify moisture stress during the dry season which has been shown to drive vegetation community dynamics in natural ecosystems (Stephenson, 1998) and has been applied in legacy effect studies (Huang et al. 2018; Kannenberg et al. 2019; Wu et al. 2018). Legacy effects after drought have also been studied in other plants through stomatal conductance reduction (Virlouvet and Fromm 2015; Ogle et al. 2015), tree mortality (Anderegg et al. 2012, 2013), xylem vulnerability (Hacke et al. 2001), and wood anatomy and density (Corcuera et al. 2004). Few studies have been done to determine how trees use different mechanisms to cope with water deficit within their wide distributions (Brodribb et al., 2014). Nevertheless, how tree species with different anatomical, hydraulic and functional traits, respond to drought in terms of growth resilience remains unclear.

subalpine fir (*Abies lasiocarpa*) is known as a climate sensitive species in BC, Canada (Zhang 1999). Also, growth of subalpine fir can be restricted by summer temperature specifically on drier sites (Peterson et al. 2002). Warmer summer temperature probably increase summer drought stress in subalpine fir stands (Peterson et al. 2002) especially on windswept slopes where accumulation of snowpacks is lighter resulting in soil water stress during summer and lower growth during drought (Ettl and Peterson 1995). Generally, in subalpine regions, growth condition of trees differ mostly with latitude and elevation, therefore, growth limiting factors may also change at different latitudes and elevations probably in response to variation in temperature and soil water availability (Kienast et al. 1987; Ettl and Peterson 1995). In ESSF zonal climate in BC, drought may occur due to the interaction of both parameters of lack of rainfall and rising temperatures.

Generally, resilience in subalpine fir stands is component of both individual tree species and ecosystem. Trees are one component of an ecosystem especially when specific trees are the dominant plant type in the ecosystem. Therefore, the trees also need to be resilient in an ecosystem. Individual tree resilience is a reflection of resilience of an ecosystem because trees are indicators of ecosystem. Resilience of trees to natural disturbances (e.g., severe drought) plays an important role in ecosystem survival. Trees as the main components of forest ecosystems can maintain the microclimate conditions inside the forest stands and within an ecosystem. Therefore, other smaller and understory components of ecosystem can take advantage of dominant tree resilience to climatic disturbances.

In this chapter, I will describe the ecological resilience of subalpine fir referring to periods when subalpine fir trees remain dominant and regular in growth pattern compared with period when subalpine fir shows growth changes due to drought (Gunderson 2000).

3.2.1. Research Question and Objectives

In this study, I address the following question: Do relationships between radial growth and climate show evidence of resilience to drought, in subalpine fir stands in interior BC? If so, do these relationships show differences in drought resilience with changes in latitude in northern interior British Columbia? The specific objectives of this research are to:

1) Evaluate patterns in deviations from the average in wood measurements as indicators of resistance, resilience or recovery after severe climate (e.g., severe drought) in subalpine fir forests. Compare measurements and trends at five study sites with different latitudes.

2) Evaluate how long (years) it takes to subalpine fir recover after severe drought (legacy effects) in the five study sites of the Rocky Mountains, British Columbia, Canada.

Hypothesis

Reviewing the literature, I assume that subalpine fir growth resilience and recovery period after severe drought would vary along latitudinal gradient in response to variation in the dominant growth limiting factors. Also, I assume that growth resistant to drought at higher latitudes that take advantage of almost similar colder weather and higher precipitation have similar patterns dealing with severe drought.

Null hypothesis would be assuming there is no difference in subalpine fir growth resilience by change in latitude in response to severe drought.

3.2.2. Research Gap

This research will also provide a basis for understanding the resilience of subalpine fir to accelerated climate change, a knowledge gap that exists due to the lack of information and studies focus on subalpine fir in the past. Although some legacy effect studies have been started recently to study growth resilience and recovery period after severe drought around the world (Kannenberg et al. 2019; Huang et al. 2018; Wu et al. 2018; Peltier et al. 2016; Gazol and Camarero 2016;

Anderegg et al. 2015; Pederson et al. 2014), still almost no study has been completed for drought legacy effects in northern subalpine fir forests in northern BC.

3.3. Methods

3.3.1. Site selection

Subalpine fir trees were selected for core sampling from five natural (not planted or harvested) stands: Pine Le Moray, Mount Chingee, Mount Averil, Grizzly Den and McBride Peak, all areas located on north-facing slopes of Rocky Mountains in northern interior BC (Figure 3.1). Distance between the two farthest sites (Pine Le Moray and McBride Peak) was almost 480 km. The biogeoclimatic variants of each site were determined with review of site characteristics and Biogeoclimatic Ecosystem Classification (BEC) land management handbooks, using the BEC system developed and used within BC to delineate regional differences, topography and dominant vegetation (Delong et al. 1993; Green et al. 1994) (Table 3.1). Subzones are divisions of zones that further define the climate of an area. The first part of the subzone name describes the relative precipitation, and the second part describes the relative temperature (Interior zones). The Pine Le Moray stand was located within the wet cold variant (wc3) of the Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone, classified with high precipitation and cooler temperatures. Mean annual temperature (MAT) was 1.5 ºC and accumulative annual precipitation (PPT) was 925 mm with the maximum air temperature occurring in July (19.3 ºC) at this site. The Mount Chingee site was within the ESSF biogeoclimatic zone, with wet cool variant (wk2). MAT for this site was 0 ºC and PPT was 1060 mm, and maximum air temperature generally occurred in July (16.7 ºC). At third site, cores were sampled at Mount Averil within the ESSF zone, wet cool variant (wk2), where MAT was 1.3 ºC and PPT was 1045 mm and maximum air temperature occurred in July (18 ºC). Grizzly Den, the fourth site, was characterized as ESSF zone, wet cool variant (wk1).

MAT for this site was 2 ºC and PPT was 1085 mm and maximum air temperature occurred in July (19.3 ºC). The last site, McBride Peak, fell within the ESSF moist mild variant (mm1). MAT was 1.6 ºC and PPT was 751 mm at McBride Peak and maximum air temperature occurred in July (19.6 ºC).

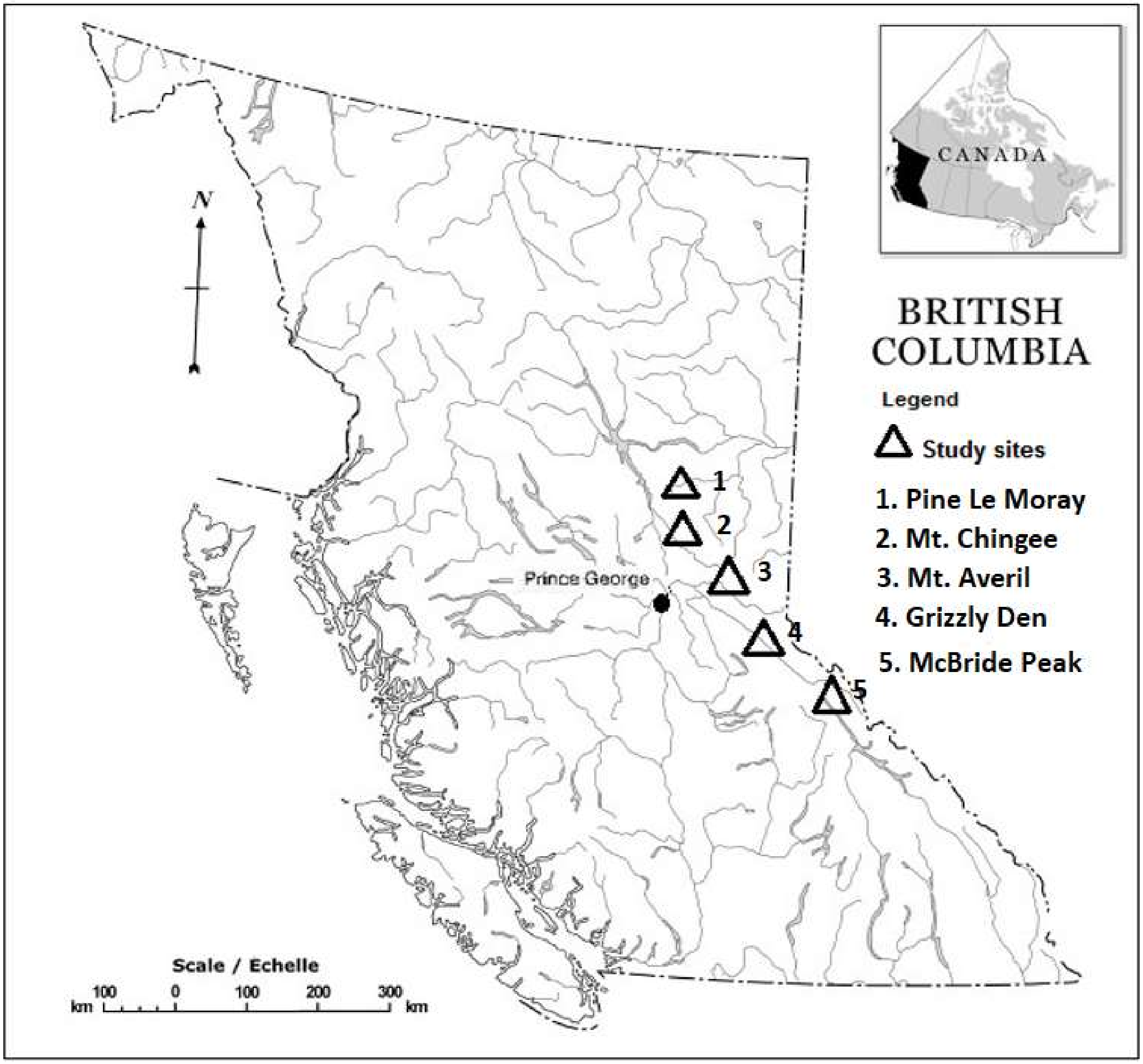


Figure 3.1. Location of sampling sites for legacy effects study in subalpine fir (*Abies lasiocarpa*) forests along north-facing slopes of the Rocky Mountains in northern British Columbia. From top (highest latitude) to the bottom (lowest latitude), subalpine fir sampled in Pine Le Moray provincial park, Mount Chingee, Mount Averil, Grizzly Den (Sugar Bowl) and McBride Peak.

3.3.2. Climate Data

The latest dataset of climate information was obtained from modeled climate data; ClimateBC (http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/) for the five study stands for the period between 1940 to 2018. ClimateBC provides climatic informative models for each region by entering latitude, longitude, and altitude of target site. The climate variable representative of drought events in ClimateBC is the climate moisture deficit (CMD) which is a common variable in legacy effect studies (Anderegg et al. 2015; Wu et al. 2018; Kannenberg et al. 2019). CMD is calculated from the equation of precipitation and evapotranspiration. Evapotranspiration increases with air temperature, solar radiation, and wind speed (Allen et al. 1998). Severe drought events are represented by a twofold standard deviation dry anomaly (i.e., 2 SD) of synthetic drought index or calculated Climatic Moisture Deficit (CMD) variables.

3.3.3. Sample Collection

Twenty-two dominant subalpine fir trees at each stand were selected for sampling. To avoid spatial autocorrelation trees were sampled at 5m minimum intervals (Dale and Fortin 2014). Healthy trees (no scratch, fire or insect damage or abnormal growth) with full crowns were targeted. Two 12 mm in diameter cores, perpendicular to the axis of each tree, were collected at breast height (1.3 m height). Increment cores were sampled parallel to the topographic contour lines of the slope to avoid the effect of reaction wood (Pourtahmasi et al. 2011). Surrounding vegetation, slope, elevation, diameter-at-breast-height (measured in the lab by adding two radial core samples together per tree) were recorded (Table 3.1).

Table 3.1. Sampling site collection information and individual chronology characteristics for five study stands along the Rock Mountains in northern BC. Biogeoclimatic variant of each site was determined with review of site characteristics and biogeoclimatic ecosystem classification land management handbooks (DeLong et al. 1994).

Geographic information							Tree characteristics		
Site	Latitude	Longitude	Aspect	Elevation (m)	BEC zone	BEC subzone	Mean age (years)	# of tree cores	Mean DBH (cm)
Pine Le Moray	55° 24′	-122° 32′	N	1120	ESSF	wc3	90	22	43
Mt. Chingee	55° 01′	-122° 53′	N	1200	ESSF	wk2	76	22	43
Mt. Averil	54° 24′	-122° 25′	NW	1270	ESSF	wk2	104	22	36
Grizzly Den	53° 46′	-121° 30′	N	1250	ESSF	wk1	107	22	42
McBride Peak	53° 19′	-120° 07′	W	1330	ESSF	mm1	71	22	41

3.3.4. Sample Preparation of 12mm Cores

Of the 110-12mm diameter cores sampled in this study from five study sites, 93 undamaged (not broken) cores were selected for the legacy effects study. Cores were extracted using 12 mm diameter increment borer and transferred to the UNBC Dendrochronology Lab. To dry the samples, cores were submerged into 95% ethanol for 48 hours. This process helps water molecules inside core samples be replaced with alcohol molecules to dry faster. Once all liquids were evaporated, cores were mounted on grooved boards and were cut into 2 mm radial pith-to-bark strips (tangentially x longitudinally) using a twin-blade saw. Resins were then removed from 2mm laths using Soxhlet acetone extraction for 5 hours. After extracting chemical compounds, samples were scanned using ITRAX densitometers, which use an X-ray laser beam to provide measurements of wood density (Evans and Ilic 2001). Radiographs obtained from software connected to the ITRAX machine were transferred into WinDendro for measuring ring width and earlywood width.

3.3.5. Master chronology

Radiographic core images were then crossdated in two steps; 1) Chronologies were visually crossdated using the skeleton plot method in WinDendro by identifying specific years (especially narrow rings) as significant marker years (Yamaguchi 1991); 2) Visually crossdated chronologies were then verified using COFECHA (Grissino-Mayer 2001). Laths were labelled with a single dot every ten years, two dots every half-century and three dots every century (Stokes and Smiley 1968). Wood laths with unique variations not representative of the stand that could not be matched with other samples within a site, were removed from further analysis. By comparing each core with the mean chronology of each site, COFECHA program generates the mean correlation between the series (MSI). COFECHA also takes note of individual series that may contain errors such as missed or false rings. The measurements are then validated until the remaining indicators disappear or until the MSI is well above 0.42, the minimum value of significance at the 99% confidence level (Grissino-Mayer, 2001). Once crossdated, step standardization was conducted using ARSTAN software and negative exponential curving method to remove non-climatic factors affecting the growth from the series resulting in dimensionless (index) values (Cook and Holmes 1999). In case first detrending curve did not fit to the series, I applied Hugershoff curve to match the chronologies and detrend the series. ARSTAN removes all non-climatic trends from series including the most important one, age related variations, knowing that young trees have faster growth in comparison to mature trees (Cook and Peters 1981).

Each series was transformed and averaged to create a master site chronology for all wood characteristics using running window of 50 years with an overlap of 25 years for sites with at least hundred years of each chronology (Pine Le Moray, Chingee and Grizzly Den), and running window of 40 or 30 years with overlap of 20 or 15 years for shorter (Averil and McBride) chronologies (Cook and Holmes 1999). EPS (expressed population signal) was used (Table 3.2) to determine when chronologies had low sample size near the beginning of a series and the accuracy (EPS >85%) of sample representation of the population (Wigley et al. 1984). Study site's mean chronology lengths were between 67-101 years (Table 3.2). The years of EPS cut-off were varied between 1940 - 1960 in study stands (Table 3.2). Stabilization of RW and EWW was achieved through application of a negative exponential curve (one-time detrending) or straight-line fit followed by a smoothing spline in ARSTAN (Cook and Peters 1981; Meko and Baisan 2001). Standard series obtained from ARSTAN at each site and were used for comparison with climate indices.

Because changes in the size of rings width (RW) or earlywood width (EWW) show the effect of drought better and more understandable than ring density, I used these traits for the legacy effects study. Chronologies from each stand were tested for normality using skewness and kurtosis values prior to correlating with CMD (Table3.3). Normality testing of RW and EWW chronologies determined most data as normal except for Averil-RW and EWW (Table 3.3). Since all data must be normal for legacy effect studies (Wu et al. 2018), non-normal data were also normalized. The formula that we used to normalize non-normal data value (e.g., x), was as follows:

Normalized value = $(x - \bar{x}) / s$

where:

x = data value

$\bar{x}$ = mean of dataset

s = standard deviation of dataset

Table 3.2. Master chronology statistics for five stands within central interior British Columbia. Statistics shown include chronology length, mean sensitivity and EPS (expressed population signal) cut off and number of trees successfully crossdated and standardized for tree-ring width (RW), and earlywood width (EWW). MSI = Mean series intercorreltion: indicates the strength of correlation between samples taken from the same location, based on 50-year overlapping segments

Site Name	Chronology Type	MSI	Chronology Length	EPS cutoff	EPS value	Mean Length of Series (year)	Accepted series Length	# of Trees Successfully Crossdated	# of Trees Successfully Standardized
Pine Le Moray	RW EWW	0.563 0.612	1915-2018	1940	>84%	85	80	19	16
Mt.Chingee	RW EWW	0.664 0.596	1923-2018	1950	>83%	67	70	18	15
Mt. Averil	RW EWW	0.744 0.696	1880-2018	1940	>84%	101	80	19	16
Grizzly Den	RW EWW	0.693 0.722	1870-2018	1940	>83%	101	80	18	15
McBride Peak	RW EWW	0.743 0.777	1932-2018	1960	>83%	64	60	18	15

Table 3.3. Normality statistics (Skewness and Kurtosis) for ring width and earlywood width chronologies measured at Pine Le Moray, Chingee, Averil, Grizzly and McBride sites along the Rocky Mountain in northern BC. Data normality tests for Skewness and Kurtosis z-values > +1.96 or < -1.96 were not accepted as normal data. Bold values indicate non-normal values. SE= standard error.

	Tree-Ring Width				Earlywood Width			
Site	**Skewness** **SE**	**Z-value (dividing skewness by its SE)**	**Kurtosis** **SE**	**Z-value (dividing kurtosis by its SE)**	**Skewness** **SE**	**Z-value (dividing skewness by its SE)**	**Kurtosis** **SE**	**Z-value (dividing kurtosis by its SE)**
Pine Le Moray	0.020 0.290	0.069	-0.440 0.570	-0.772	0.110 0.290	0.379	-0.460 0.570	-0.807
Mt. Chingee	0.007 0.310	0.023	-1.170 0.610	-1.918	-0.010 0.310	-0.032	-1.170 0.610	-1.918
Mt. Averil	0.840 0.270	**3.111**	0.640 0.530	1.208	0.760 0.270	**2.815**	0.590 0.530	1.113
Grizzly Den	-0.150 0.270	-0.556	0.440 0.530	0.830	0.080 0.270	0.296	-0.950 0.530	-1.792
McBride Peak	-0.120 0.310	-0.387	-0.590 0.610	-0.967	0.210 0.310	0.677	0.770 0.610	1.262

3.3.6. Resistance, Recovery and Resilience

To study the growth of subalpine fir trees under episodic drought stress, I applied indices for resistance (Rt), recovery (Rc) and resilience (Rs) as introduced and explained in detail by Lloret et al. (2011) and Pretzsch et al. (2013). The three indices were calculated for RW or EWW (standardized indices) using the master chronologies for each site. Basic components of all three indices are as follow: Gpre is 2-year mean ring width growth (RW) or earlywood width growth (EWW) in a period of the nPreDr years before the drought period; Gd is the mean RW or EWW in a period of nDr years during the drought period; and Gpost is the mean RW or EWW in a period of nPostDr years after the drought period. The resistance, $Rt = Gd/Gpre$, quantifies the decrease in growth from the pre-drought period to the drought period; $Rt = 1$ is a complete resistance (no change in growth); the further the value falls below $Rt = 1$, the lower the resistance (Figure 3.2). Recovery, $Rc = Gpost/Gd$, describes the growth reaction after the drought period. $Rc = 1$ indicates persistence of a low growth level even after 1-year length of the drought period ($nDr = 1$) (assuming an $Rt < 1$ or no change in growth if $Rt = 1$). $Rc >1$ represent fully recovered growth after one-year severe drought (Figure 3.2). Resilience, $Rs = Gpost / Gpre$, measures the difference in level of PreDr and PostDr. $Rs < 1$ shows low resilience of subalpine fir trees after drought condition. $Rs = 1$ and $Rs > 1$ represent good resilience and fully resilience of growth after severe drought, respectively (Figure 3.2).

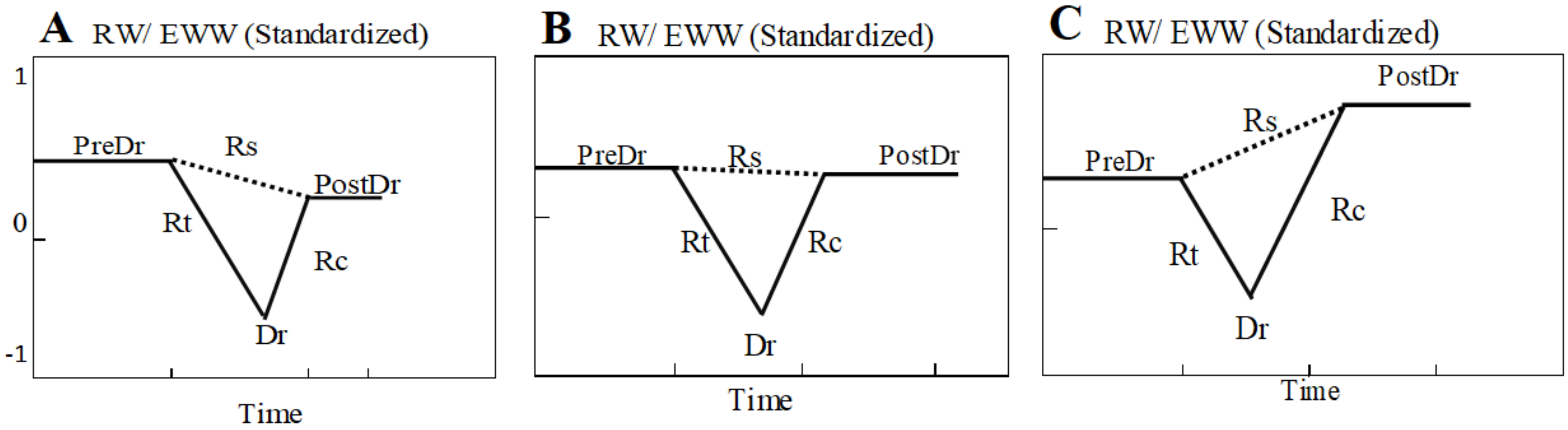


Figure 3.2. Course of growth, ring width (RW) and earlywood width (EWW), in three different stress events characterised by growth in the period before drought (PreDr), growth in the drought period (Dr) and growth after the drought period (PostDr). Indices for resistance; Rt = Dr ⁄ PreDr, recovery; Rc = PostDr ⁄ Dr, and resilience, Rs = PostDr ⁄ PreDr, are used to characterize the stress response patterns. (A) Tree with growth decrease by drought (Rs= PostDr ⁄ PreDr) if Rs< 1 indicated by low resilience (assuming drought always causes an initial decline in growth). (B) Tree with growth recovered after drought (Rs= PostDr ⁄ PreDr) if Rs= 1 indicated by complete resistance while Rt <1 indicated by weak resistance. (C) Tree with growth considerably recovered after drought (Rs = PostDr ⁄ PreDr) if Rs> 1 indicated by high resistance. In the graphs Rt, Rc and Rs are represented by the gradient of decline from PostDr to Dr, the increase from Dr to PostDr, and the difference in level of PreDr and PostDr, respectively (Presented in figure 1 by Lliot et al. 2011 and figure 1 by Pretzsch et al. 2013).

3.3.7. Legacy Effects

I defined severe drought legacy in tree growth as a departure of the observed unitless growth (RW or EWW) from predicted tree growth in a period ranging 1-4 years after a severe drought event for each of study stands following the methods Anderegg et al. (2015). Only single drought events (no consecutive drought within 4 years after a -2 SD dry anomaly) lasting no more than 1 year were considered because capacity of trees for recovery after successive droughts reduce considerably (Peltier et al. 2016). The "predicted" growth in 1-4 years after severe drought event was calculated using linear regressions over the entire period by comparison between measured RW or EWW and the drought variable (Climate Moisture Deficit). Informative prediction of legacy response of vegetation growth after severe drought events depends on the strength (i.e., the goodness of fit) of the linear regressions between tree growth and the drought variable.

3.3.8. Analysis and Comparison of Measured and Modelled Values

Regression analysis was completed where strong, significant Pearson's or Spearman's correlation coefficients were identified, above 0.3 (Anderegg et al. 2015) (Table 3.4). Regression models with significant correlation coefficients were visually assessed against measured values to determine model accuracy over time. To obtain stronger models, if needed we combined two climatic variables (CMD) in the same model to predict better and stronger models provided that the independent variables (climatic parameters) were not statistically correlated. To find if variables are related together or not, a Durbin-Watson statistic was used. If independent variables were autocorrelated we could potentially take an average of two independent variables and put it in the model for prediction. Split verification was then used to validate the models. The latter 50% of time series was applied to calibrate the models. All predicated site-specific anatomical traits passed the verification test at 90% significance of reduction of error values (RE) compared to actual measured data.

3.4. Results

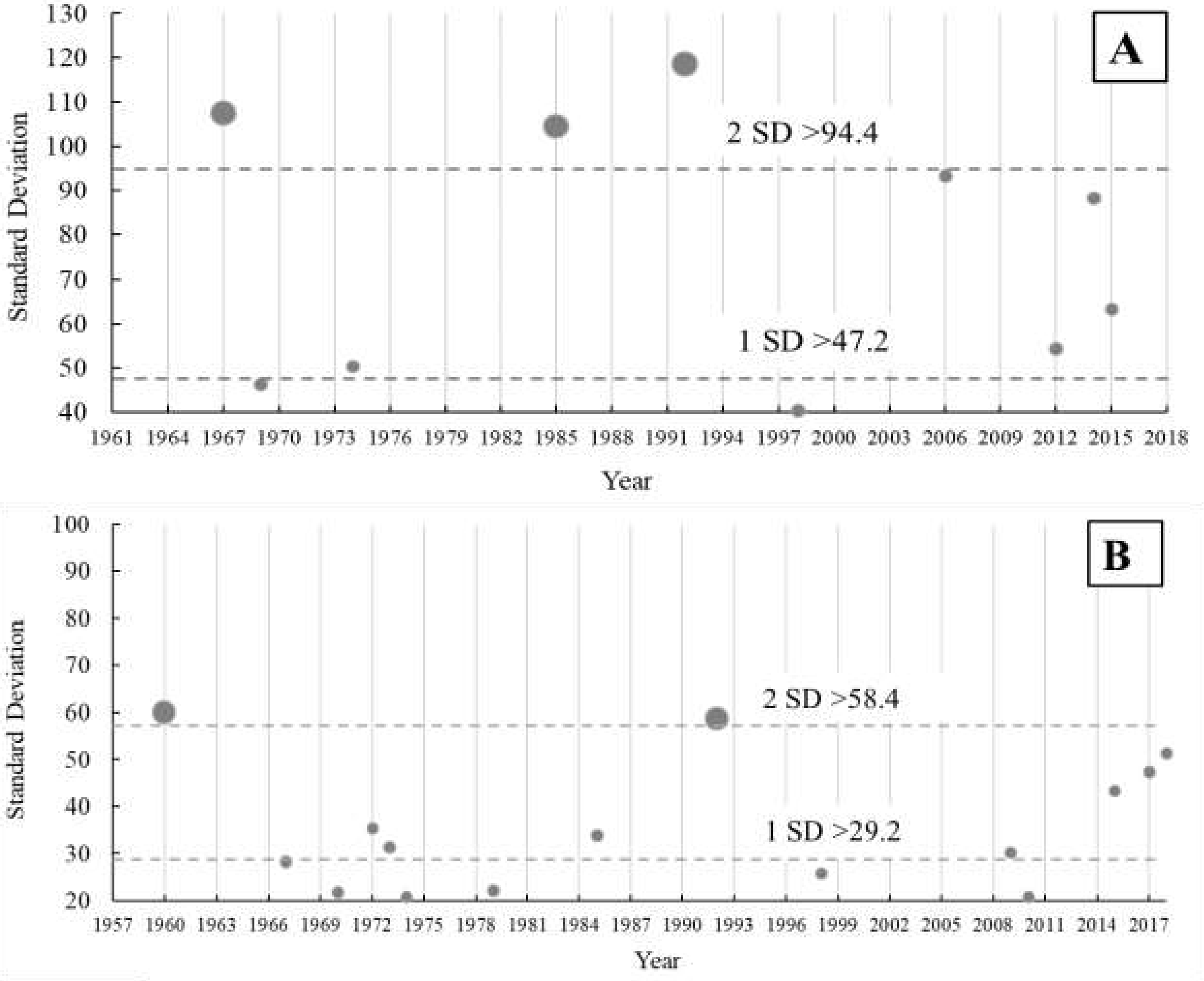
Generally, since there are significant correlations ($P < 0.05$) between tree-ring width chronologies and severe drought, null hypothesis is rejected.

3.4.1. Correlation and regression analysis for growth models

Durbin Watson test results showed that spring and summer climate moisture deficits (CMD) were related (Appendix A). Therefore, where needed, a measured average of spring and summer CMD was used to obtain stronger models for Averil and McBride sites (Table 3.4). Because the objective of this study was to calculate and to measure duration of growth suppression after drought episodes, I accepted only severe drought event to growth (RW/EWW) significant correlations where $r \geq 0.3$ (Anderegg et al. 2015). The models presented reflect the strongest relationships found between subalpine fir growth and climate moisture deficit (Figure 3.4). Since no significant correlation was found between subalpine growth (RW/ EWW) and CMD at the Grizzly Den site, regression analysis could not be completed for this site and therefore the Grizzly Den stand was removed from further legacy effect measurement in this study. However, significant correlations were found from comparison between tree-ring width or earlywood width and severe drought events (>2 SD from climatic moisture deficit) that lasted 1 to 2 years after drought event in the other four study stands including Pine Le Moray, Chingee, McBride and Averil (Table 3.4). Since correlation between RW and EWW (Table 3.4) was high, RW and EWW were replaced where one showed higher correlation with drought.

Table 3.4 Pearson correlation coefficient analysis between growth representatives (RW/EWW) and CMD, and between Ring width (RW) and earlywood width (EWW) of subalpine fir in all five study stands along the north-facing slopes of the Rocky Mountains. CMD= mean climate moisture deficit, sm= Summer, sp= Spring, *= significant correlations at 95% confidence level, **= significant correlations at 99% confidence level. Bold figures represent r ≥ $^{+}_{-}$ 0.3 which were accepted for legacy effect study.

	EWW			RW	
	Chingee	Grizzly	Averil	McBride	Pine
RW	0.959	0.8	0.961	1	1
CMD	**-0.365****	0.068	-0.187	-0.185	-0.131
CMD (sm,sp)	0.04	-0.095	**-0.3***	**-0.4****	-0.189
CMD (sm)	-0.257	0.127	-0.139	-0.136	**-0.31***


A
Standard Deviation
130
120
110
100
90
80
70
60
50
40
2 SD >94.4
1 SD >47.2
1961
1964
1967
1970
1973
1976
1979
1982
1985
1988
1991
1994
1997
2000
2003
2006
2009
2012
2015
2018
Year
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Standard Deviation
100
90
80
70
60
50
40
30
20
2 SD >58.4
1 SD >29.2
1957
1960
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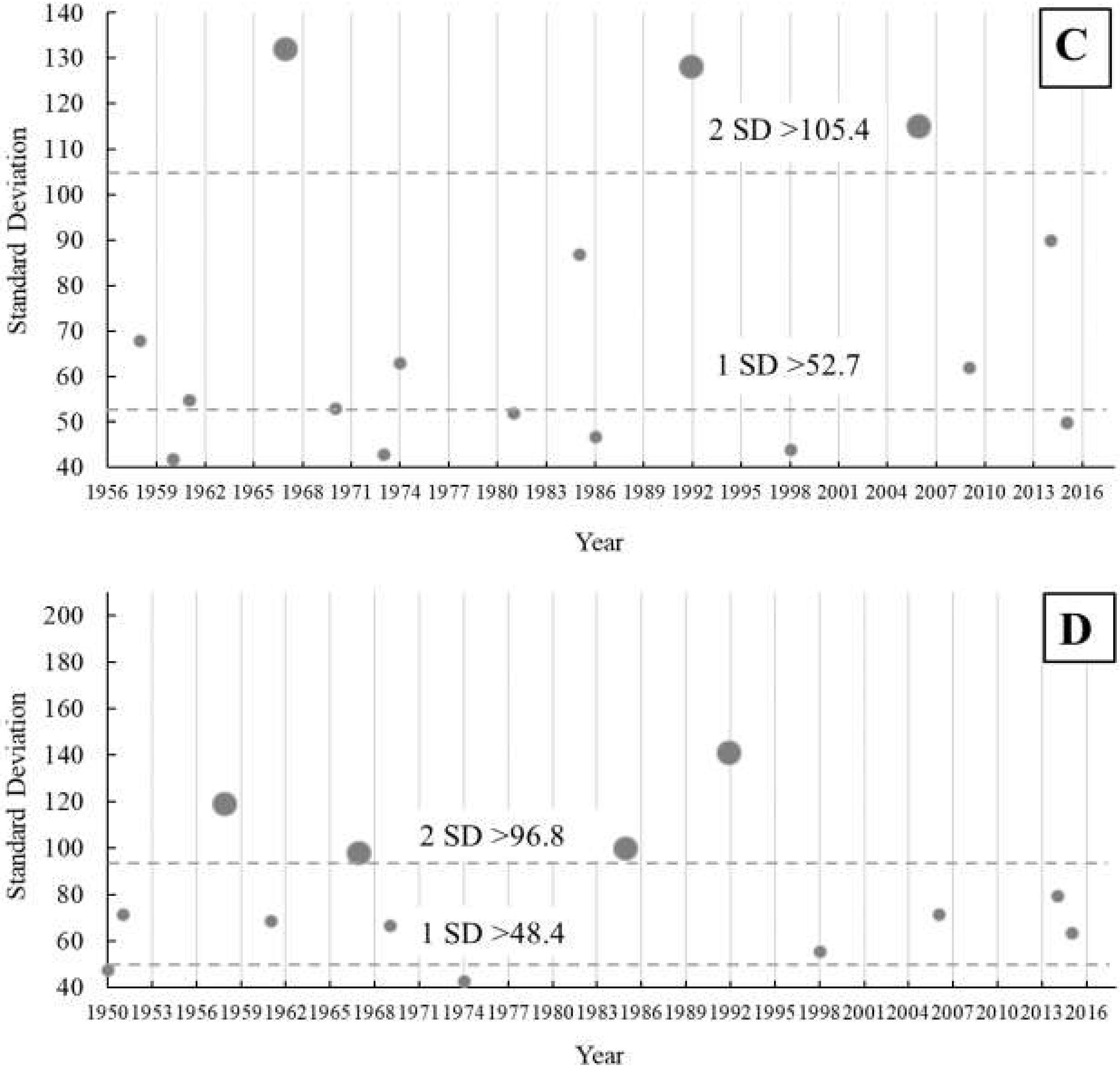

Figure 3.3 Climate Moisture Deficit (CMD) during 1950-2018 in four study regions around PG and along north facing slopes of the Rocky Mountains in northern BC. (A) CMD recognised as drought (> 1-SD) and severe drought (>2-SD) at the Mount Chingee site where three years (1967, 1985 and 1992) are marked as severely dry years measuring 2-SD mean CMD during 1961-2018. (B) Combined mean summer and spring CMD were used to calculate dry years and very dry years (1960 and 1992) at the McBride stand measuring 2-SD during 1957-2018. (C) Mean summer CMD was applied to measure dry and severely dry years (1967, 1992 and 2006) at the Pine Le Moray stand during 1956-2018. (D) Combined mean summer and spring CMD were used to extract very dry years (1958, 1967, 1985 and 1992) during 1950-2018 at the Averil site. Gray dotted lines represent the lowest levels at which 1-SD and 2-SD were met. Small circle points show CMD> SD. Larger gray circles represent severe drought years for which CMD > 2-SD. SD = standard deviation, CMD = climate moisture deficit.

Table 3.5. Resistance, recovery, and resilience indices of Subalpine fir after sever drought and growth index prior, during and after severe drought events (> 2-SD) in Chingee, McBride, Pine Le Moray and Averil stands around PG and along north-facing slopes of Rocky Mountains during 1960-2015. G_{pre} = growth prior to severe drought events, G_{post} = Growth after severe droughts, G_d = growth during severe drought, R_t = resistance, R_c = recovery and Rs = resilience.

Site	Severe Drought year	G_{pre} (2 yeras)	G_{post} (2 years)	G_d	Mean R_t	Mean R_c	Mean R_s
Pine Le Moray	1967	1.025	0.79	0.92	1.08	0.88	0.96
	1992	0.95	1.08	1.19			
	2006	0.93	0.91	1.02			
Mt. Chingee	1967	1.02	0.94	1.001	1.04	0.92	0.94
	1985	1.04	0.93	0.907			
	1992	0.86	0.87	1.089			
Mt. Averil	1958	0.3	0.09	0.24	1.10	0.52	0.60
	1967	0.3	0.09	0.2			
	1985	0.31	0.23	0.33			
	1992	0.32	0.35	0.61			
McBride Peak	1960	1	0.96	0.72	0.82	1.26	0.99
	1992	1.1	1.13	0.94			

3.4.2. Severe drought, legacy effect, and resilience studies in subalpine fir stands

My results showed that recovery of subalpine fir growth after a severe drought event (defined as a year when the CMD was greater than two standard deviations from the mean), can take from one to two years (Figure 3.4). Three years (1967, 1985 and 1992) were recognized and calculated as severely dry years at Mount Chingee, two years (1960, 1992) at McBride Peak, three years (1967, 1992, 2006) at Pine Le Moray and four years (1958, 1967, 1985, 1992) at Averil site by measuring 2-SD mean CMD (Figure 3.3). For the reference periods before and after the dry years, we finally used a 2-year length (nPreDr = 2, nPostDr = 2). Although growth periods during very dry years at study sites lied almost within middle-aged phase of chronology length and stress response patterns may change with tree age and tree size (Carrer and Urbinati 2004; Rozas 2005; Rossi et al. 2008), standardized growth (transformation by detrending and indexing of the growth rates) for both EWW and RW was applied in this study to remove all age-related trends.

The average growth before, during and after very dry years was noted at study sites. R_t, R_c and R_s were calculated for the Chingee stand as 1.04, 0.92 and 0.94 respectively (Table 3.5). Mean measured growth prior to, during and after severe drought was used to calculate R_t (0.82), R_c (1.26) and R_s (0.99) for the McBride stand (Table 3.5). The third site, Pine Le Moray, R_t (1.08), R_c (0.88) and R_s (0.96) were calculated from mean growth before, during and after severe drought (Table 3.5). The fourth site, Averil, R_t (1.1), R_c (0.51) and R_s (0.6) obtained from growth in conditions prior, during and after very dry conditions at this site (Table 3.5). According to the results (Table 3.5, Figure 3.4), resistance of subalpine fir growth to drought increased with latitude and precipitation, whereas recovery of tree growth after drought decreased with latitude. The analyses revealed that the growth resilience index (R_s) of subalpine fir varied across the studied stands (Table 3.5).

Drought legacy effects lasted between 1 and 2 years at the study sites. Results for the Mount Chingee stand showed severe dry years after which departure of observed growth level was less than average predicted growth that lasted 1 year after severe droughts (Figure 3.4 A). These effects were substantial in magnitude: there was an average of a ~13% decrease in observed versus predicted growth in year 1 after severe droughts in Chingee stand. The McBride, very dry years determining significant departure of observed growth versus predicted growth where legacy effects lasted 1 year after severe drought conditions (Figure 3.4 B). The magnitude of the legacy effect was an average of a 14% decrease in measured growth than predicted growth for the McBride stand. Substantial severe dry years were recognized as significant departures between measured and predicted subalpine fir growth at the Pine Le Moray stand during 1956- 2018 (Figure 3.4 C). Magnitude of these departures were a 20% decrease in observed vs predicted values at year 1, and 17% decrease at year 2 after drought, average, at the Pine Le Moray stand (Figure 3.4 C). For Averil, specific drought years with significant departure of measured growth from predicted growth were observed (Figure 3.3 D). Differences between observed values and predicted values showed a magnitude of a 22% decrease in average observed growth versus predicted growth in year 1 and 33% decrease at year 2 after very dry conditions at Averil site (Figure 3.4 D). Our analysis revealed that recovery ($R_c = 1.26$) and resilience ($R_s = 0.99$) of subalpine fir at the McBride site were greater than other three stands (Table 3.4). However, growth resistance to severe droughts at Averil ($R_t = 1.1$), Pine ($R_t = 1.08$) and Chingee ($R_t = 1.04$) sites were higher than the McBride ($R_t = 0.86$) site. It is interesting to note that growth recovery at McBride Peak site was higher than 1 ($R_c = 1.26$) and growth resilience was very close to 1 ($R_s = 0.99$) meaning that after severe drought years at this site, growth was fully recovered. Also, in comparison to the other sites, the McBride site was more resilient to very dry conditions (Table 3.5; Figure 3.4).

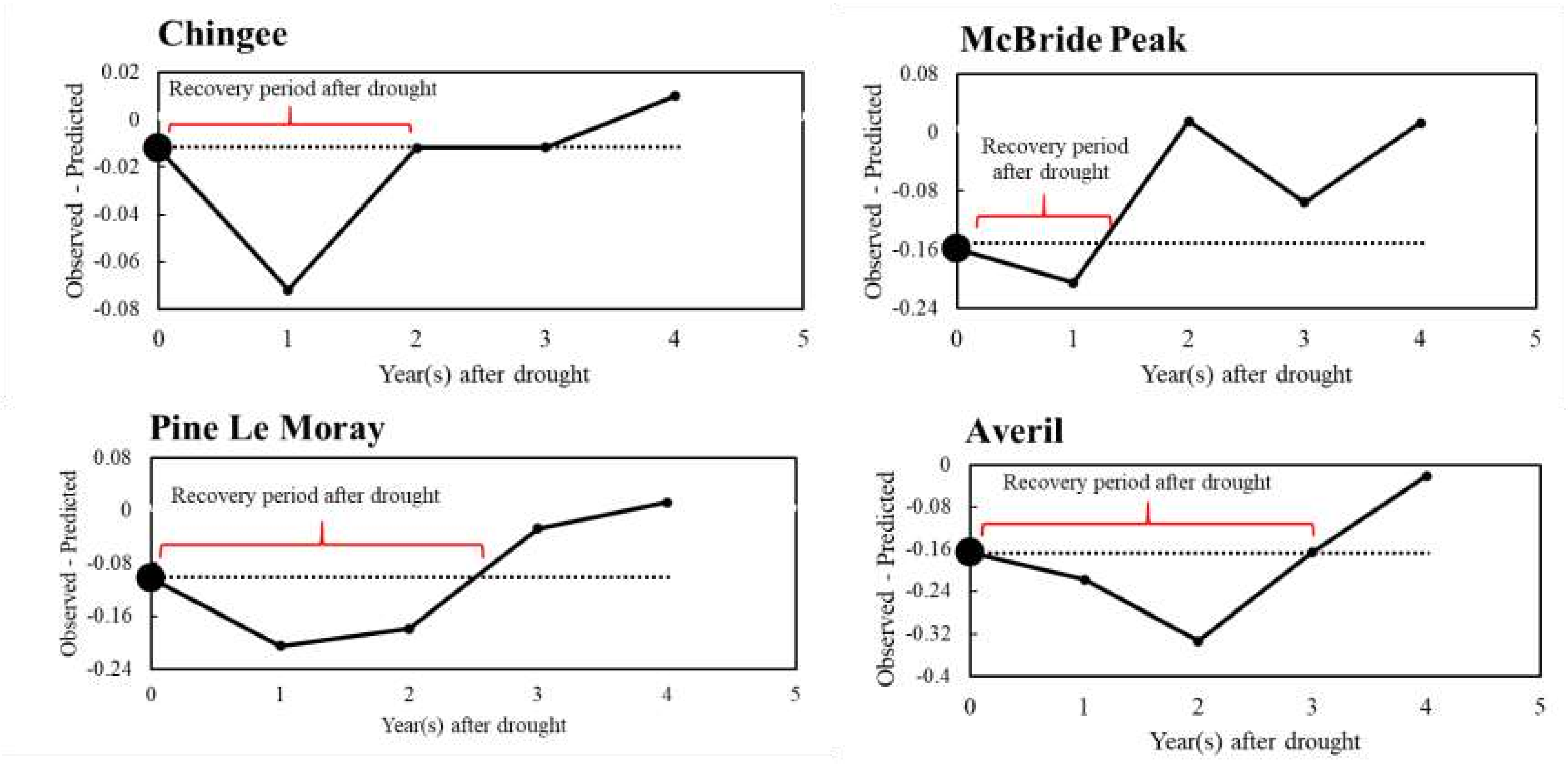

Figure 3.4. Drought legacy during 1–4 years post severe drought years obtained from differences between observed values and predicted values that extracted from correlations between Ring-Width Index (RWI) or early wood width index (EWW) and climatic moisture deficit (CMD) in four study regions around PG and along the Rocky Mountains in northern BC; (A) legacy effect in Chingee site that longed 1 year after mean sever drought between 1960-2018, (B) legacy effect in McBride site that lasted 1 year after mean sever drought from 1960 to 2018, (C) legacy effect in Pine Le Moray site that longed 2 years after mean sever drought between 1950- 2018, and (D) legacy effect in Averil stand that continued 2 years after mean sever drought from 1940 to 2018. Dashed lines mark the level where drought happens. ●= Onset of drought event

3.5. Discussion

Study of legacy effects in this research was done for the only single drought events (defined as, no consecutive drought within 4 years after a -2 SD dry anomaly) lasting no more than 1 year because the capacity of trees for recovery after successive droughts reduce considerably (Peltier et al. 2016). It also has been shown that if the time between drought events becomes shorter than the time needed for trees to recover from them, trees are likely to become increasingly prone to water stress and insect attacks (Schwalm et al. 2017).

Grizzly Den site was not used for further analysis because there was no correlation between chronologies and drought. This indicates that the trees at Grizzly Den site were responding to climate factors outside of what I investigated. Therefore, this site has other variables that I did not measure that could be influencing growth more than what I did measure in this research.

Different growth resilience and recovery period (the length of time that a tree can compensate for the decline due to drought) in subalpine fir stands by comparing growth patterns after drought at higher latitude sites and lower latitude site, consists with my hypothesis and strengthen it. Similar resistance to drought at higher latitudes which may be due to the colder temperature and accumulation of snowpack also consist with my second hypothesis. This high depth of snowpack at higher latitudes could likely persist long enough till first months of the summer to keep soil water balance.

Drought induced a decline in subalpine fir growth in our study. This pattern is not unexpected, as drought-driven declines in forest productivity and widespread increases in tree mortality have been observed at the global scale and across different biomes (Allen et al. 2010), a trend that is expected to continue into the future as climates warm (Schwalm et al. 2017). Also, this finding is consistent with a study by Peterson et al (2002) who revealed that subalpine fir growth declined with warmer summer in the western north US.

Although this study has been conducted in mountainous and cold regions of the Rockies and may not be typical place for legacy

effect studies, recent investigations of cold and more mesic forests have highlighted their susceptibility to current and future water stress at these regions (Allen et al. 2010; Pederson et al. 2014; Martin-Benito and Pederson 2015; Millar and Stephenson 2015).

I observed legacy effects on radial growth after severe drought at all sites and negative effects of drought on ring width. These results are consistent with more recent studies about legacy effects that have shown similar negative correlations that exist between drought and tree radial growth (Anderegg et al. 2015; Camarero et al. 2015; Gazol and Camarero 2016; Wu et at. 2018; Zweifel and Sterck 2018).

In the following I will provide some evidence for addressing objective (i) and (iii) about existence of resistant, recovery and resilience at subalpine fir stands, and difference in subalpine fir resilience at difference sites, respectively:

It can be inferred from results that recovery and resilience of subalpine fir trees to severe droughts at high-latitudes (Pine Le Moray, Chingee and Averil) stands were lower than the stand located at the lowest latitude (McBride Peak). Conversely, growth resistance of subalpine fir trees after severely dry years at high-latitude (Pine le Moray, Chingee and Averil) stands were greater than lower latitude stand (McBride Peak) site. These results are consistent with Gazol et al. (2016) who showed forest growth displayed different resilience at different latitudes, and while drought resistance increased along gradients of latitude and longitudinal as well as soil moisture, drought recovery decreased. Ettl and Peterson (1995) also found that growth response of subalpine fir to climate varied between wet and dry sites which was likely due to different stands soil water availability at different sites.

Higher resistance to drought at higher latitudes in comparison to lower latitude sites was due to colder weather and deeper snowpacks in winter and spring that persist long enough till first months of the summer when drought mostly happens. Therefore, soil moisture is not as limiting to growth on these sites and summer drought stress reduce by reduction evapotranspiration rates at higher latitude subalpine fir sites (Peterson et al. 2002).

Based on my results, legacy effects were detected within a maximum time lag of one year after severe drought at the McBride Peak and Chingee sites. These results show that recovery after drought was high at McBride Peak but to a lesser extent than at the Chingee site (Figure 3.4; Table 3.5). However, resistance of subalpine fir trees at McBride was lower than other study regions. Inverse relation between resistance response and resilience to drought can be supported by other studies that showed there is a negative relationship between resistance of forest growth to drought and forest recovery from drought (Lliot et at. 2011; Prestch et al. 2013). Our finding that fast recovery of growth after drought (Anderegg et al. 2015) in lower latitude forests (McBride Peak site) is supported by Beck et al. (2011) who suggested that trees at warmer sites may take advantage of favourable longer growing season conditions compared to colder regions. There are many reasons why the recovery period in a forest stand may be higher than another stand. For instance, variability in soil moisture is an important factor affecting length of recovery after drought. At lower latitude, winter snowpack does not stay for a long time on the forest floor in spring, and may melt faster than high latitude regions. Therefore, at lower latitudes optimum growth condition (optimal temperature and availability of water) is met earlier in spring and growth period extend, therefore trees have more time to compensate for lower growth of the drought. Higher temperature at lower latitudes could significantly reduce snowpack depth in winter and increase precipitation fall as rain (Mote 1999). This condition reduces snowpack accumulation in spring resulted in earlier initiation of growing period and let trees to compensate lower growth of previous year, faster.

At higher latitudes, conversely, accumulation of snowpack and colder weather conditions may result in delayed snowpack melting on forest floor, especially during the first months of the growing season, leading to dry-like condition on forest floor. As a consequence, probably shorter growing periods in current year can not compensate lower growth of previous year (drought year). This idea and my results are in consistency with other researchers who suggested that higher latitudes in the (sub) alpine zone are likely to constrain fast recovery after drought (De Boeck et al. 2016; Cremonese et al. 2017). Peterson et al. (2002) also found that depth of spring snowpack in subalpine fir stands persist long at higher latitudes and colder sites and produced a growing season length limitation specially on northern slopes.

In the following paragraphs I will provide some evidence to cover objective (i) about duration of drought legacy effect at study stands:

Anderreg et al. (2015) suggested that legacy effects in boreal forest usually takes 2-4 years. In our study, legacy effect in subalpine fir trees from four study sites along the Rocky Mountains took between one to two years after drought. I found that drought legacy effects in the study regions did not necessarily cause weaker drought resilience (i.e., much larger reduction in forest growth after drought). Instead, I observed drought resiliency (i.e., smaller growth reduction after severe drought) (Gazol et al. 2017a) in study stands. This 1-to-2-year(s) recovery after drought (resilience) may be due to the specie's hydraulic conductivity in drought condition, which is related to xylem plasticity, which may substantially help to increase resilience, and tolerate very dry conditions (Lopez-Iglesias et al. 2014; Anderegg et al. 2015; Anderegg and HilleRisLambers 2016; Lopez et al. 2016). Apparently due to having some morphological changes in response to dry condition (Kuuluvainen et al. 1996), subalpine fir is considered as a drought tolerant species (Hinckley et al. 1982). One thing that should be considered is that differences in growth responses to drought among sites may depend on difference in drought intensity among study sites (Zhang et al. 2017) or specific functional traits (Greenwood et al. 2017) or individual specific strategies to cope with drought (Gazol et al. 2017).

In this study, I found that legacy effects reduced growth of subalpine fir trees in study sites between 1 to 2 years after severe drought. The high resistance (smaller growth reduction after severe drought) of subalpine fir to drought observed, was consistent with findings by Maherali et al. (2004) that showed gymnosperms (e.g., conifers) have a great capacity to resist a drought which is due to xylem cells configuration. Furthermore, Clark et al. (2016) found that conifer species dominant in western North America, were well adapted to drought. It has been also suggested that under drier conditions, trees tend to increase belowground biomass allocation to improve their water foraging capacity to maintain an efficient water transfer from soil to leaves (Brunner et al. 2015; Sala et al. 2012). This process requires substantial metabolic energy, since tree transpiration is largely reduced during drought (Huang et al. 2018). As a result, drought forces trees to invest large amounts of carbohydrates in metabolism, rather than in to radial growth (Brunner et al. 2015; Huang et al. 2018).

Although Anderegg et al. (2015) suggested conifers need more time to recover their growth after a water shortage than deciduous forests, we found that mountainous subalpine fir forests recovered more quickly. It has been shown that trees have evolved many strategies to sustain drought stress. For example, stomatal closure may limit water stress when conditions are not favorable, and restricted shoot growth may result in trees having higher root-to-shoot ratios and greater capacity to take up water relative to the shoots that must be supported (Brunner et al. 2015). In addition, trees have extensive secondary growth, which allows them to increase the thickness of their cell walls and results in increased resistance against cavitation in the vascular tissues (Jacobsen et al., 2005). In severe drought condition when thresholds are reached, however, tree population especially at high-latitude regions may be in danger of extinction. In turn, low-latitude tree population may expand northward (Gazol et al. 2016) as a strategy to deal with drought. There are many reasons why tree's growth decreases in dry conditions. One of important reasons is lack of nutrient supply due to reduced decomposition and mineralization, which are both dependant on moisture and water supply (Prestch et al. 2013). There are variety of forest response strategies against drought, and while some trees show greater growth resistance to drought, other show better capacity to recover after drought (resilience). Forest response to drought sometimes depends on site characteristics like soil texture and water table depth (Phillips et al. 2016). Some specific ecophysiological responses may influence the way trees show resilience to severe climate condition. However, according to Haung et al. (2018) geographical changes along with soil water gradients play more important role for forest tree responses to drought. Huang et al. (2018) findings support my results that subalpine fir showed different resilience to drought with changes in latitude. Some site condition parameters which may change with latitude, and are important in forest response to drought, include forest composition, soil type or depth, site size and age structure site conditions (Gazol and Camarero 2016; Gazol et al. 2017b).

3.6. Conclusion

In this study, using tree-ring width data for the last six-seven decades, I presented evidence that severe droughts caused growth reductions and legacies in our study stands. The magnitude of legacy effects differed depending on the latitude. We observed that subalpine fir trees growing at higher latitudes experienced lower disturbance impact (higher resistance) to drought than those growing in lower latitude. Conversely, trees growing at lower latitude, returned faster to their pre-disturbance state (higher recovery rate) than those growing at the higher latitudes, but the mechanisms underlying these differences still remain unclear.

Overall, subalpine fir was resilient to drought at the sites investigated. Our analyses together with previous findings indicate that different drought legacy effects on different subalpine fir stands may be linked to the interactive roles of geographical changes, soil moisture gradients, water availability and plant ecophysiological traits results in diverse lagged effects in response to severe drought.

Finding of this study Chapter can be useful for drought risk assessment. Also, this finding could guide forest practitioners in silvicultural practice by directly helping to choose silvicultural proper methods like thinning and removing low resilient species to drought conditions in northern BC. Furthermore, knowledge of subalpine fir recovery period and resilience can help forest management through regulating sustainable long-term forest products like plantation of proper and more drought-resilient species and also felling cycle regulations.

We suggest that more research and understanding of the interaction between drought legacy effects and forest drought resilience is needed to better predict forest ecosystem responses to a probable warmer and drier climate in the future.

Further experiments and studies on other elevations such as timberline and/or low-elevation forests are also needed to test legacy effects and resilience of subalpine fir in western north Canada. Also, further work should seek physiological and ecophysiological mechanisms involved in drought-induced growth decline and how they can be influenced by specific species. This will ultimately allow us to more confidently predict which species, in terms of their water use strategies, and depending on site-specific climatic and edaphic characteristics, will be most beneficial for increasing the resistance of forest stands to drought.

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Chapter 4: Concluding Synthesis

This thesis aimed to determine how subalpine fir (*Abies lasiocarpa*) wood properties including RW, EW, LW, RD, FL, MFA, FW and FWT vary over time under the impacts of climate in the Rocky Mountains in northern British Columbia. The reason why I chose mountainous high elevation forests was because it is shown that global warming significantly affects ecosystems of high latitudes and elevations as mountainous high-elevated forests are more sensitive to climate variations (Becker and Bugmann 2001; Frank and Esper 2005; Anderson and Goulden 2011; Tognetti and Palombo 2013). This thesis also aimed to determine growth resilience (recovery period) and legacy effects in subalpine fir stands after drought conditions, and determining how wood properties and resilience of subalpine fir vary among the study sites and along various latitudes in dealing with climate change.

4.1 KEY POINTS

What can be concluded from research in Chapter 2 is that subalpine fir's radial growth at study sites is more likely to depend on variations in temperature and less so on precipitation, on northern aspects of the Rocky Mountains in northern BC. Moreover, our results illustrated that, compared to simple tree-ring width, intra-annual-ring characteristics generally showed stronger and more robust correlations with climate variations as have been studied by other researchers (Wimmer and Grabner 2000; Davi et al. 2002). This is likely because tree-ring estimations give just a growing season portrayal of climate information (D'Arrigo et al. 1993). However, to measure and understand exact climatic and ecological changes over smaller periods of time, intra-annual wood property estimations provide stronger relationships to climate than do RW values (Wimmer and Grabner 2000; Davi et al. 2002).

In this thesis and specifically in Chapter 2, I used climate and wood chronology data from over 80 years to study subalpine fir's fibre property responses to climate variations (temperature and precipitation). The period from 1940 to 2018 showed that summer temperature, and to a lesser extent previous fall precipitation, controlled fibre properties growth at higher latitudes. I also concluded that the lower the latitude, the greater the effect of fall temperature on fibre properties at corresponding sites. These finding are logical as water is typically not a limiting factor at higher latitudes due to colder weather and larger snowpack. Furthermore, inter / intra-annual-ring properties appeared to be more influenced by spring and summer temperature and to a lesser extent by spring and late summer precipitation at study sites in northern BC.

Climatic variants including mean temperature and sum of annual precipitation have been increased over four decades from 1940s to 1970s, which resulted in increased fibre length in study sites. Following that and during 1980s and 1990s, higher than average temperature and lower precipitation, which to the larger scale were influenced by macro-climatic phenomena like spring-summer PDO thermal phases, decreased subalpine fir fibre length from elongation at study sites. However, in 2000s and 2010s, increases in the amount of precipitation along with increased temperatures were probably the reasons for producing larger fibre lengths at study sites in northern BC and along northern aspects of the Rockies. I observed increases in fibre length at sites located at lower latitudes compared with ones at higher latitude during 1940 to 2018, possibly due to longer growing period compared to the higher latitude stands where growing periods were shorter.

In Chapter two and studying wood properties, we also came to the conclusion that maximum density was positively affected by late summer precipitation at all study sites other than at Averil, over recent 80 years. Because the study sites were located at high altitudes (1100 m-1300 m a.s.l), probably the rise in temperature late in summer over last 7-8 decades along with sufficient humidity in study sites proved optimal conditions for formation of latewood cells leading to denser latewood cells. A possible reason why subalpine fir MXD did not increase with summer precipitation at the Averil site could be because summer precipitation exceeded soil water availability at this site; Averil was wetter than all other study sites, receiving higher amount of precipitation during the year.

In Chapter 3, I found that drought events during 1940 to 2018, reduced subalpine fir radial growth in our study sites along northern slopes of the Rocky Mountains. Following that, I focused on the periods between 1950 and 2018, during which we observed few severe dry years, with 1 to 2 lags in growth after drought which obviously were important to restore ecosystem health after dry periods.

On one hand, in chapter 3 we found that at higher latitudes subalpine fir was more resistant to severe drought than the ones at lower latitudes. On the other hand, subalpine fir growing at lower latitudes showed higher recovery rate (more resilience) than those growing at higher latitudes. Also, we concluded that at higher latitudes, legacy effects took 2 years to compensate declined growth which likely suggest that resilience of subalpine fir trees at higher elevations was lower than at lower latitudes where legacy effects took only 1 year to return to pre-perturbation conditions after severe drought (recovery period). Increase in resistance to drought in forest stands at higher latitudes were also studied by Gazol et al. (2016) which might be due to them receiving more precipitation as well as better soil moisture regimes at higher latitudes and altitudes. Our results for fast drought recovery at lower latitudes, can be supported by Gazol et al. (2016) who confirmed that higher values of forest growth recovery existed in the western south USA and southern Europe at lower latitudes.

Although the exact physiological mechanisms associated with the response of trees to severe drought remain unclear, Gazol et al. (2016) suggested the existence of different strategies in forest trees to cope with droughts, including: change in the biome, geography, genetic adaptation, soil moisture gradient, water availability, soil texture and forest composition. Temperature changes at different latitudes may result in change in the sensitivity of trees to drought as Briffa et al. (1998) suggested a reduction in sensitivity of trees growth at high northern latitudes for several decades. Overall, all things considered in Chapter 2 and 3, and according to the correlations and regressions analysis, I came to the general conclusion that temperature was the most important climatic factor affecting growth and resilience of subalpine fir in the study sites. It worth mentioning than although drought is consequence of interaction (balance) between lower precipitation and higher temperature, still at higher elevations of the Rocky Mountains in Northern BC temperature controls the growth of subalpine fir. Also, subalpine fir was resilient to drought at the sites investigated along northern slopes of the Rocky Mountains in northern BC.

ClimateBC note

The most reliable way to study the behavior of trees in relation to climate is to use long-term fixed (historical) meteorological data. However, when long-term climate data is not available or meteorological stations are not available at or close to the sampling site, the best way to collect climate data is to use normal and standard reliable meteorological models. There are some pros and cons for using models, and this research was done knowing the limitations of one such model in BC, ClimateBC. ClimateBC uses information of historical climate station in BC to match the best model (Wang et al. 2016). ClimateBC model producers used ClimateWNA (version 4.6) (Wang et al. 2012) to generate climate data. ClimateWNA also downscales historical and future climate data, and outputs monthly, seasonal and annual temperature and precipitation variables, as well as derived annual climate variables of biological significance to plants (Wang et al. 2012). ClimateBC model is made using 20 reliable climate changes models (Wang et al. 2012). The program uses the scale-free data as baseline in combination with monthly anomaly data (Mitchell and Jones 2005) of individual years to calculate historical monthly, seasonal and annual climate variables for individual years and periods between 1901 and 2012 (Wang et al. 2012).

However, model accuracy remains major challenges for incorporating these projections into climate change adaptation strategies (Dormann et al. 2008; Wang et al. 2012). Furthermore, climate models of ecosystem change have been criticized for alterations to biogeochemical cycles, including increased atmospheric CO2 concentrations (Pearson and Dawson 2003; Araujo and Guisan 2006).

Accuracy of ClimateBC has been tested by model makers. To test whether the site-specific climate data generated by ClimateBC was likely to share the same relationship derived from another researcher report at Agassiz station, Wang et al. (2012) compared modelled monthly temperature and precipitation climate records to the Agassiz station data. Correlation analyses showed that mean summer and winter temperature values from the two data sets were significantly correlated ($r = 0.841$, $p < 0.01$; and $r = 0.905$, $p < 0.01$, respectively).

Considering all pros and cons for using this model, ClimateBC still is one the best models for predicting climate variations in BC and has been applied in many studies so far (Canno et al. 2012; Brochett et al. 2012; Spittlehouse and Wang. 2014; Pidwirny et al. 2019; Bahbahani and Pidwirny. 2017; Cortini et al. 2011; Meyn et al. 2010; Rose and Burton 2009; Delong et al. 2009).

4.2. CONSIDERATIONS FOR FUTURE RESEARCH

This research is a preliminary study of relationship between climate and wood anatomical properties and residence of subalpine fir located in the Rocky Mountains of northern interior British Columbia, Canada. Future research into relationships between climate and radial growth properties (RW, EW, LW, RD), wood fibre properties (FL, FW, FWT, MFA), and drought legacy effect studies could investigate additional climate variables, such as snow depth, relative humidity, wind speed and number of cloudy days in the year to improve models of radial growth and fibre properties based on climate. Investigation into variables in addition to climate, such as crown cover, forest composition, forest species could also improve estimations of variations in radial growth and resilience of forest trees. Also, further work is needed to clarify the physiological mechanisms involved in drought-induced growth decline and how they can be influenced by intra- / inter-species interactions and forest management.

Further efforts identifying which combinations of species mixtures, in terms of their water use strategies, and depending on site specific climatic and edaphic characteristics, will be most beneficial for increasing the resilience of forests to drought.

Finally, an indispensable requirement for assessing the long-term impact of drought events on trees is the availability of long-term records (Bräuning et al. 2017). Therefore, by having several periods of drought over a long period of time, we can measure a better average for the degree of flexibility of trees in response to perturbations. Also, ensuring adequate number of samples (sections) for wood fibre analysis vs 10-year average sections allow us for better and more precise fibre measurement which is lacking in our research. Furthermore, lack of significant relationships between climate indices (eg., drought) and RW, EWW at Grizzly Den stands was likely due to small sample size in this study. Due to time constraints and research costs, this study was conducted in five regions with different latitudes. It is suggested that more study sites be considered in different latitudes and altitudes gradient for future research as well as more study sites in each latitude which were lacking in this research. Also, in this study, no statistical comparison was made based on the significant correlation between the studied sites. We suggest to compare more statistical correlations between chronologies and climate between sites in future studies.

4.3. IMPLICATIONS FOR THE BRITISH COLUMBIA FORESTRY INDUSTRY

Examination of the general relationships between climate and radial growth and wood fibre variables may answer the questions regarding wood quality in subalpine fir stands of Prince George. It was demonstrated that over the recent 70 to 80 years, rising temperatures and variation in annual precipitation in Prince George were negatively, correlated with radial growth (RW) and slightly related to increased ring density and production of cells that were thicker and smaller in study stands. Producing denser wood with smaller annual-ring width may be ideal for industrial solid wood production. However, decreasing trends in precipitation, and rises in average temperature generally in study stands and over recent 70 to 80 years have reduced production of high-volume subalpine fir's wood for high-volume logs and end-use industrial purposes.

Subalpine fir trees in mountainous study stands in northern Rockies showed a relatively short recovery periods from drought conditions meaning that they are fairly resilient to drought (1-2 years legacy effects) and are well adapted (especially at McBride Peak site) to drought with respect to other environmental factors and regional climate which probably help to produce sustainable forest products future for BC and provide data for improving the Government of BC Stand Level Drought Risk Assessment Tool. Also, increased awareness of subalpine fir fibre property changes under global climate changes and regarding that fibre length have been increased in study sites over recent 70 to 80 years, could feed directly into knowledge of supply quality for end-uses such as pulp and paper in BC.

4.4. References

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Appendix 1

Following graphs were made based on climate information extracted from ClimateBC by putting the exact altitude and latitude information for each site (Wang et al. 2012; Spittlehouse and Wang 2014). To obtain stronger models, multi variable model can be applied using two or more climatic variables and putting in the same model to predict better and stronger models provided that the independent variables (climatic parameters) are not statistically correlated. To find if variables were related together or not, a Durbin-Watson statistic was applied. If independent variables were autocorrelated we could potentially take an average of two independent variables and put that average in the model for prediction. For those independent climate variables that were different (e.g., temperature and precipitation), and needed to be combined in a model, fluctuations over time were compared visually to make sure they have same trends.

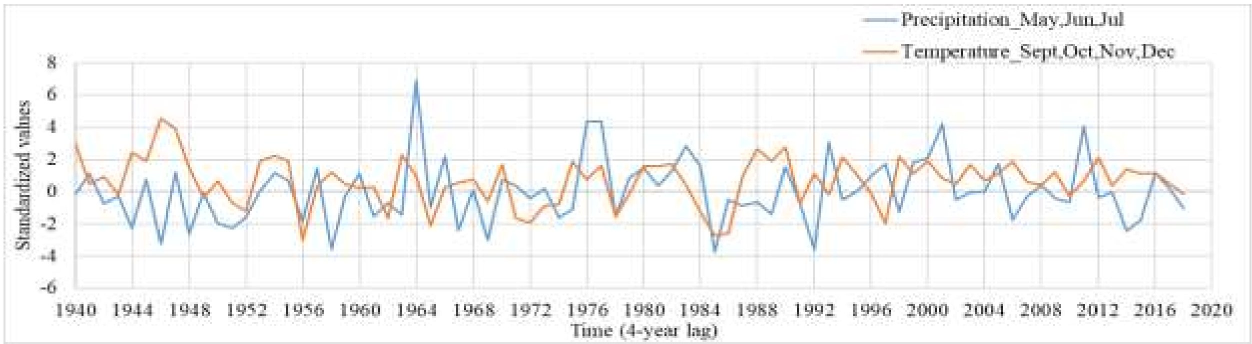

Figure A1. Comparison between standardized precipitation of May, June, July, and temperature of September, October, November and December at Averil site from 1940- 2018 along the northern slopes of the Rocky Mountains, northern BC.

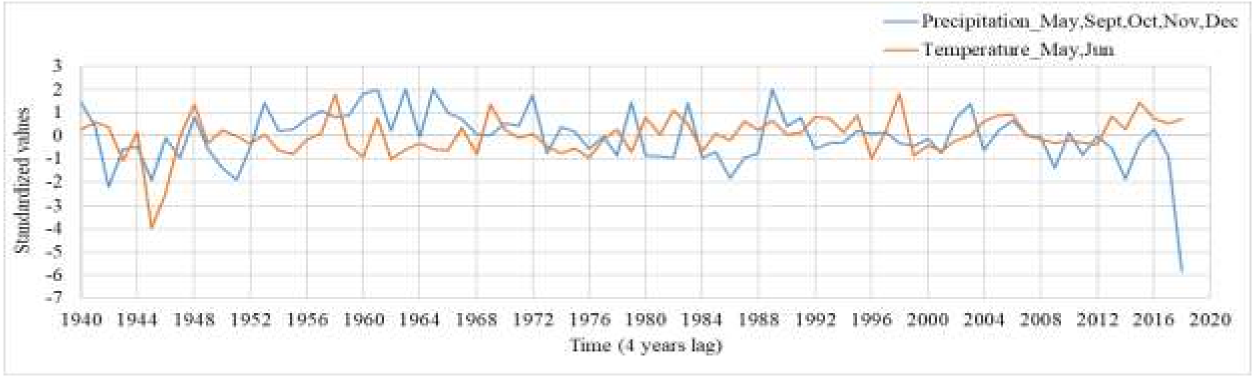

Figure A2. Comparison between standardized precipitation of May, September, October, November and December, and temperature of May and June at Averil site from 1940- 2018 along the northern slopes of the Rocky Mountains, northern BC.

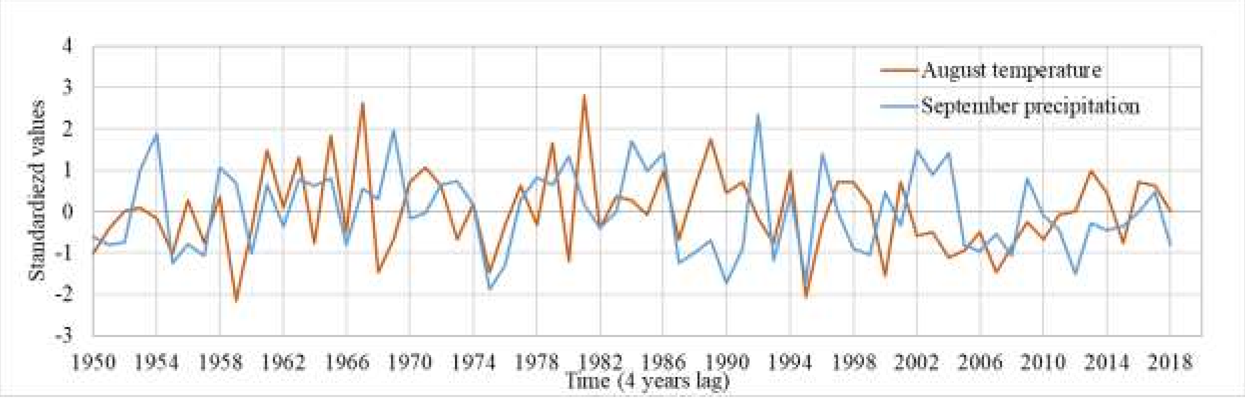

Figure A3. Comparison between standardized August temperature and September precipitation trends at Pine Le Moray site from 1950- 2018 along the northern slopes of the Rocky Mountains, northern BC.

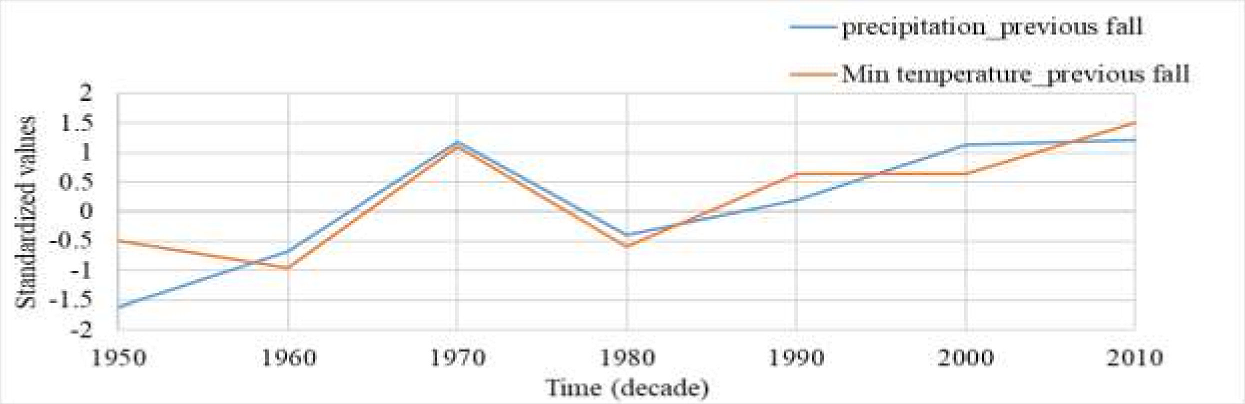

Figure A4. Comparison between standardized previous fall precipitation and previous fall minimum temperature trends at McBride Peak site from 1950- 2018 along the northern slopes of the Rocky Mountains, northern BC.

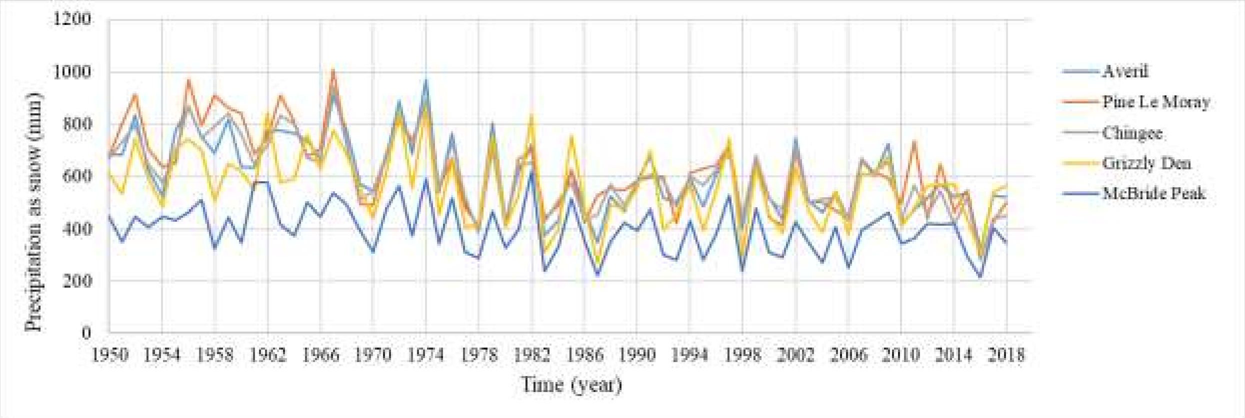

Figure A5. Precipitation as snow (PAS) at Pine Le Moray, Chingee, Averil, Grizzly Den and McBride Peak sites from 1950- 2018. Average snow depth at Pine Le Moray = 625mm, Chingee = 609 mm, Averil = 607mm, Grizzly Den = 561mm and at McBride Peak = 399mm along the northern slopes of the Rocky Mountains. Northern BC.

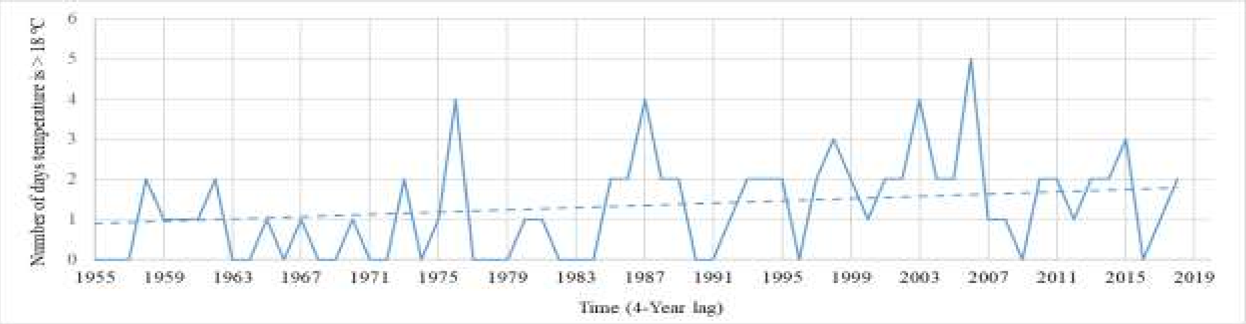

Figure A6. Number of days that temperature was higher than 18 ºC at Grizzly Den site from 1950-2018 along the northern slopes of the Rocky Mountains, northern BC. Dashed trend line represents entire trend in the study site.

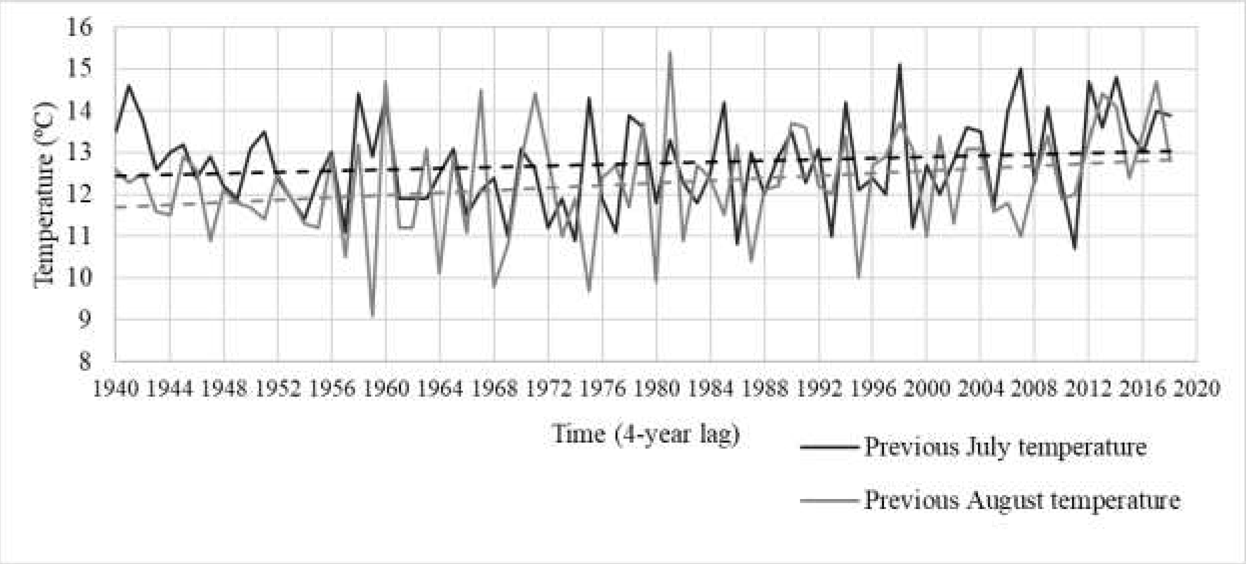

Figure A7. Previous July and August air temperature at McBride Peak from 1940 -2018. Dashed trend lines represent entire climate history trend in the study site.

Table A1. Durbin-Watson statistic for climate variations at Pine Le Moray, Averil and McBride Peak sites along the northern slopes of the Rocky Mountains, northern BC. Values ranging from 1.5 to 2.2, with of value of 2.0 representing no autocorrelation. Values above 2.2 and less than 11.5 were deemed positively autocorrelated.

Site	Climate parameters	Wood characteristic	Durbin Watson value
Pine Le Moray	Average and Maximum temperature of May	Fibre wall thickness	0.88
	Average temperature of August + Minimum temperature of Jully and August	Micro fibril angle	2.21
	Average temperature of June and Jully + Min temperature of Jully	Fibre width	1.4
	August temperature + September precipitation	Minimum density	2.3
Averil	Fall and summer maximum temperature	Fibre length	1.14
	precipitation of May, June, July and temperature of September, October, November, December	Ring density	0.9
	Precipitation of May, September, October, November, December, and temperature of May, June	Latewood density	0.9
McBride Peak	Minimum temperature and precipitation of previous fall	Fibre length	2.88
	Temperature of previous Jully and August	Earlywood width	2.43

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