CHARACTERIZING INTRA-ANNUAL XYLEM CELL FORMATION AND CIRCADIAN CYCLE DYNAMICS OF JACK PINE (*PINUS BANKSIANA*) IN THE NORTHERN BOREAL FOREST, YELLOWKNIFE, NORTHWEST TERRITORIES

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ABSTRACT

Xylem cell formation and stem radial fluctuations for jack pine in Yellowknife, NT were assessed during the 2017 season. The characterization of the timing of the onset of xylogenesis reactivation, period(s) of rapid cell development, and termination of seasonal stem growth were recorded over the estimated growing season. Two methods, microcores and automatic point dendrometers were used to better understand what the characteristics of a growth season looks like for jack pine at its northern limit within the boreal forest. It was demonstrated that onset of cell development at the study site "Treeville" occurred once temperatures had exceeded the 4-5ºC temperature threshold, the period of rapid growth was observed around June 21 for all phases of xylogenesis, aligning with the timing of annual longest photoperiod during summer solstice. It is demonstrated that jack pines in this region are much slower growing, with cell development at ~0.28 cells/day during the period of rapid growth, and site wide average of ~13 cells. Precipitation was highly correlated with the observation of the SRI phase throughout the season, most notably in the period prior to cell wall-thickening. A multi-year cell development assessment indicated a relationship with June precipitation, demonstrating lower cell counts in years with low June precipitation. Cell growth was recorded to end in late August, although some trees demonstrated cells in developing phases into early September. Overall, results suggest (1) strong relationship between the onset of jack pine wood formation when temperatures exceed established thresholds for growth, (2) demonstrated that the period of rapid growth aligns with longest daylength June, and (3) annual cell count is controlled by June precipitation.

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I never thought I would be writing my thesis acknowledgements, so here it goes. This project started back in 2015 when I first reached out to Dr. Michael Pisaric to explore the idea of pursuing graduate studies. From this initial conversation, I was fortunate enough to get to spend some time in the field in 2016 collecting cores from jack pine, marking my first time in a helicopter, and doing some stream research with my lab momma Cait Garner. I was accepted into the Master of Sustainability at Brock in 2016 and so set off my journey into graduate research. The following summer, the faithful 2017 season, I had many people join me on my weekly visits out to Treeville to collect microcores and lug a huge early 2000's laptop into the site. Most often these visits included my parents, and on one special occasion my (at the time) 94-year-old grandmother, Mabel, who is now in her 100th year of life. I learned how to process wood samples using microtomes from the best in Kranjska Gora, Slovenia and satisfied my love for travel before beginning my first year of my Master program. During that year I was fortunate to spend every Sunday with my Grandparents Doug and Judy. I watched my grandmother be victorious with a battle with breast cancer and recover from hip surgery and a heart attack. I am so thankful for the time I got to spend with them. For the many years I was in St. Catharines I had my best friend, roommate, and sidekick Alyssa along for the ride where we fought through many hungover soccer games and late-night trips to Sobeys for rice pudding. I am so thankful for her friendship. Following the field season, I spent over 500 hours cutting, dying, and counting cells on the microcore samples that were collected in 2017. I believe at one point I questioned if my eyes may just fall from my head. I thank my Water and Environment Laboratory (the WEL) mates Gait and Tyler for Caesar Fridays, and Cait's dad for all the leftovers I ate for lunch while glued to a microscope. I was lucky enough to present at several conferences like the American Association of Geographers in Boston, Mapping New Knowledges at Brock, Aurora Geoscience in Yellowknife, and le Studium's Wood Formation Conference in Orlean, France. My research video was a finalist in NSERC's Science, action! Competition, and overall winter for my photo entry into NSERC's Science Exposed competition. Our lab also hosted the student run Paleolimnology Symposium, which meant extra hours in the lab "working." I am honoured for all the opportunities that I was given to share my research and learn from experts in the field, as well as, again, travel and explore new places.

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Thank you to Dr. Michael Pisaric for the continued support and all the opportunities for learning throughout my time as a graduate student. Thank you for sticking this through with me and the time you have spent on virtual calls talking me off a ledge. Thank you to Greg King for his help with the GAM's and SCAM's and your endless knowledge on tree growth. Thank you to Dr. Marilyne Jollineau for your compassion and phone calls. Thank you to my committee for not forgetting about me after all these years. Lastly, thank you to Government of the Norwest Territories Cumulative Impact Monitoring Program (CIMP), Northern Scientific Training Program (NSTP) NSERC, Association of Canadian Universities for Northern Studies (ACUNS) for funding this research.

If I have learned anything outside of what was required and necessary for completing this program and research is that life comes at you FAST. The memories I have made and experiences I have had while procrastinating and at times straight up shirking my student duties to travel the world have all been worth it and have shaped the person I am today. At the end of the day what follows your name at the end of your email, or your CV is nothing if you are not proud of yourself and what you have accomplished. So finally, I thank myself for experiencing life while "working" on my thesis.

Sincerely,

Dana Harris

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LIST OF SYMBOLS & ACRONYMS

C – Cambial phase

DBH – Diameter at breast height

DOY – Day of year

E – Enlarging phase

GAM – Generalized additive model

GDD – Growing degree days

LG – Long cycle

LVDT – Linear variable differential transformer

M – Mature phase

REG – Regular cycle

SCAM – Shape constrained additive model

SRI – Stem radial increment

W – Wall-thickening phase

ΔR – Change in radius

CHAPTER ONE:

INTRODUCTION

1.1.Introduction

The Subarctic and Arctic regions of Canada have warmed to a greater extent during the 20th century compared to lower latitudes in response to anthropogenically induced climate change (Price et al., 2013; Osborne et al., 2018; Bush and Lemmen, 2019). Unfortunately, climate records in northern regions are temporally short and geographically sparse. Due to the limitations of the instrumental climate data, it is difficult to assess if recent climate trends (including warming and changing precipitation patterns) exceed the natural range of variability. In the absence of long-term climate data sets, it is difficult to parse variations caused by natural climate variability from those driven by anthropogenic-induced activities. A longer-term climate perspective is needed as the recent period of rapid climate change overlaps almost entirely with the period of anthropogenic activity. To assess the natural variability inherent in the climate system, we need to develop long-term proxy climate records. Proxy data records are developed using biological and non-biological records, which act as natural recorders of climate variability. Dendrochronology is a commonly used proxy data source for the reconstruction of longer-term climate records is tree-rings (and the numerous data sources contained within them) (Fritts, 1976). Dendrochronology is the science of dating and using tree-ring growth records to obtain information about a variety of events and processes that have operated during the tree's lifespan (Fritts, 1976; Speer, 2010). Proxy records help to fill in the current historical climate data sets. To better refine these dendrochronological reconstructions, intra-annual dendrochronology methodologies (e.g., microcores, pinning, dendrometers, etc.) have been developed and utilized to define growth on more refined scales. Intra-annual methodologies allow for a deeper understanding of tree growth by assessing the

critical controls for wood formation and the dynamic responses of stem fluctuations during the growing season. Intra-annual investigations provide additional details about tree-growth mechanisms for refining dendrochronological proxy climate records, to better inform the use of global vegetation models. Global vegetation models are useful in determining how terrestrial ecosystems will respond under predicted global climatic changes. Anticipated changes in plant growth and forecasted changes in forest productivity in response to climate change will have profound influences on the global carbon cycle (Price et al., 2013; De Micco et al., 2019). Under high emission model projections, mean annual temperatures in Canada are expected to increase more than 6ºC, while annual precipitation could increase as much as 24% (Zhang et al., 2019). It is important to develop an intra-annual understanding of the drivers of species-specific tree growth to better define models using tree-ring analyses and proxy datasets considering current projected climatic changes (De Micco et al., 2019; Friend et al., 2019). The characterization of the timing for onset and cessation of wood production (xylogenesis), and seasonal dynamics of wood formation provide the in-situ context for the use of proxy climate reconstructions and the development of accurate model predictions considering projected climatic changes.

In the Yellowknife region specifically, recent drought-like conditions have increased interest in long-term patterns of precipitation and hydrologic variability. Agencies such as the Government of Northwest Territories (GNWT) Public Works department and the Northwest Territories Power Corporation have become interested in climate information that can be gathered from tree-ring growth records, specifically long-term precipitation patterns. Currently, 32% of power in the Northwest Territories is generated via hydroelectric energy sources and there is an expectation that this contribution will increase in the future as the territorial government works to reduce its dependence on diesel power production (GNWT, 2011). Unfortunately, historical data

that exists for this region is short and almost entirely overlaps with the period of anthropogenic climate changes. Assessing long term climate trends is a challenge without lengthening these records. Currently there are limited numbers of studies in this region using dendrochronological methods to lengthen climate records (e.g., Pisaric et al., 2009). Pisaric et al. (2009) examined the growth of Jack pine (*Pinus banksiana*) in the Yellowknife region and demonstrated that jack pine ring formation was limited by June precipitation. However, Pisaric et al. (2009) relied solely on the use of average monthly climate data in the development of their models of climate-growth relations. Given continued and rapid changing climatic conditions throughout the Subarctic, there is a need to conduct finer and more temporally resolved investigations into the climate controls on tree growth to better refine dendrochronology climate reconstructions using jack pine specifically. Due to jack pines' unique growing habitats, this species is ideal for assessing hydrological variability. The characterization of growth on an intra-annual basis involves assessing the timing of onset and cessation of cell development and periods of seasonal rapid growth in relation to weather and environmental controls. In addition, intra-annual methods can be used to generate a deeper understanding of the characteristics of stem radial fluctuations and growth in response to varying weather conditions. Using these investigations, climate data reconstructions using dendrochronological proxy data will be more robust with better connections to the understanding of species-specific tree growth for this region.

This thesis focuses on two intra-annual methods to provide baseline investigation into the characteristics of the patterns of jack pine wood formation mechanisms and circadian cycle patterns over a single growing season. The first method, microcores, produced a chronology of cell production, including the timing of xylogenesis phase transitions, during the 2017 growing season. The analysis of weekly microcores provides information about the timing of the onset and

termination of xylem cell production, the duration that xylem cells remain in subsequent phases of xylogenesis, and highlights seasonal peaks in cell production across phases (Rossi et al., 2006; Deslauriers et al., 2007; Rossi et al., 2016; Ziaco et al., 2018). The 2017 season investigation using microcores allowed for the development of baseline information on the timings of cell development for jack pine in a northern context. Using microcore data, total mature cell counts from 2007-2017 were collected to assess the year-to-year differences between cell counts and how they may relate to weather conditions. The second method used in this thesis research involves automatic point dendrometer sensors, sensors installed on the outside of the tree which provide a continuous record of stem radial displacement and seasonal wood production (Deslauriers et al., 2003). In the future, using a multi-year investigation of these types of records from dendrometers along with instrumental climate data can estimate the influence of varying intra-annual weather on growth (Deslauriers et al., 2003; Quanyan et al., 2017). For this thesis, dendrometer sensors were used to record the daily patterns of cyclical reversible stem swelling and characterize seasonal timing of jack pine circadian cycle in the Yellowknife region. These two methods paired together offer a preliminary investigation into the timing of cell production and characterization of the stem patterns within a single season. In addition, investigation of weather influences on growth was discussed as it relates to current literature for jack pine growth within the Yellowknife region and the greater extent of the boreal forest. The use of the literature investigations helps to guide the discussion surrounding the trends observed during the 2017 season. It is suggested that these methods for intra-annual investigation of the characteristics of jack pine growth be completed over multiple years to allow for the complete assessment of the controls of growth at this particular site, and the development of a full understanding of the climate growth relationship for jack pine at its northern limit.

1.2.Research objectives

The main overarching goal of this thesis is to create a baseline understanding on the mechanisms of xylem cell formation and timing of cell development as well as identify stem cycle characteristics and circadian cycle timings during a single season for jack pine near its northern ecological growth distribution limits. To accomplish this goal, two intra-annual growth assessment methods were used; microcores and automatic point dendrometers. An intra-annual investigation has yet to be done for this species in high latitudes of the Canadian boreal forest. Insights from this research will help further our understanding of the growth responses of jack pine and assess how intra-annual methodologies will aid in future development of jack pine growth responses under changing weather and climate conditions in a rapidly changing northern climatic setting.

Additional investigations beyond the records developed in this thesis using intra-annual methodologies to assess jack pine growth dynamics in response to weather conditions will provide valuable information on the impacts of climate on an important conifer species in this region. It is expected that the baseline information produced from this research will also inform future northern intra-annual dendrochronological research. Detailed analyses using microcore and dendrometer analyses will provide key insights about the weather and climate influences on jack pine growth. These insights will help guide future dendroclimatic investigations and the development of climate reconstructions in this region using jack pine tree-ring records.

The main goal of this thesis is to develop a baseline understanding of the timing and characteristics of jack pine growth during a single season and discuss the relationships to weather considering growth mechanisms of conifers placed within the context of the literature. To do this, three objectives were set:

1. *Identify the timing of onset and cessation of wood formation (xylogenesis) seasons, the timing of xylem cell phase transitions, and highlight period(s) of rapid seasonal cell development using microcores. Identify potential controls for growth considering current literature for jack pine.*
2. *Determine the timing of jack pine circadian cycle and seasonal stem responses using dendrometers.*
3. *Evaluate the challenges and benefits of microcores and dendrometer data to assess jack pine growth in the northern environment.*

1.3.Structure of thesis

This thesis contains five chapters. Chapter one introduces the research context and provides insights into some of the methods used for this research. Chapter two presents the theoretical literature review and is divided into four subsections reviewing the following topics related to this thesis research: (1) boreal forest distribution, characteristics, and significance (2) jack pine ecology and mechanisms of tree growth (3) the significance of intra-annual wood formation research (4) intra-annual and physiological-based methodologies for analysis of tree growth dynamics and xylogenesis. Chapter three outlines the specifics of the study site and the methodologies used in this thesis research. Chapter four presents the main research results. Chapter five summarizes the main findings of the research and discusses how results from this research fit within the larger context of current jack pine and/or conifer growth investigations. Finally, chapter six provides conclusions from the research and suggests recommendations for future research using similar methods or drawing on the findings of this thesis.

CHAPTER TWO:

LITERATURE REVIEW

2.1 Introduction

Characterize seasonal growth and potential controls of growth and xylem cell production of jack pine within a Subarctic region requires knowledge surrounding (1) boreal forest distribution, characteristics, and significance; (2) jack pine ecology and tree growth; (3) the significance of intra-annual wood formation research; and (4) intra-annual and physiological-based methodologies for analysis of tree growth dynamics and xylogenesis. This chapter presents a review of the current theoretical literature and introduction to the factors influencing growth and xylogenesis that will form the basis for this thesis.

2.2. The Northern boreal forest

The Canadian boreal forest is the largest forest system in Canada, covering an estimated 552 million hectares and ~11% of the Earth's terrestrial surface (Figure 2.1; Bonan & Shugart, 1989; Weber & Flannigan, 1997; Brandt et al., 2013). Cold-tolerant genera make up the boreal forest, including *Abies*, *Larix*, *Picea*, and *Pinus*, as well as *Populus* and *Betula*. In addition to forested areas, the boreal zone is made up of lakes, rivers, and non-wooded alpine areas (Brandt et al., 2013). Boreal ecosystem dynamics are heavily influenced by climate and interactions with fire, insects, and diseases at various spatial and temporal scales (Brandt et al., 2013). Due to its vast size, the boreal forest strongly influences the global climate and atmospheric systems (Chapin et al., 2000; Hinzman et al., 2004). In response to recent climate change, boreal ecosystems are experiencing rapid changes in precipitation patterns, seasonal temperatures, permafrost distribution, snow cover, and frequency of disturbance events (e.g., fires, drought) (Weber & Flannigan, 1997; Zhang et al., 2019).

Current research estimates global mean temperatures will increase ~2°C between 2000 and 2100; within the boreal region increases will be higher and as much as 4-5°C by 2100 (Price et al., 2013). Zhang et al. (2019) indicated that under a continued high emission scenario mean annual temperatures across Canada could rise more than 6ºC by the end of the 21st century, with greater increases in northern Canada. Furthermore, Price et al. (2013) suggest that the northern boreal forest will be exposed to more intense warming in contrast to other terrestrial biomes. Due to the expanse of the Canadian boreal forest, changes in the frequency of disturbance and climate will have far-reaching impacts on the global climate system, in particular the carbon cycle. Under these warming conditions and the resulting drying of boreal regions, it is expected that increases in both severity and the frequency of fires will be recorded. The increases in fires will cause shifts from net accumulation to net loss of carbon in the atmosphere, contributing to positive feedback effects on the climate system (Walker et al., 2019).

The forecasted shift from current boreal forest net sink to a net source of carbon scenario further augments projected warming in boreal regions. It is projected that minimum temperatures in boreal regions will increase by 8°C during the winter seasons and 5°C in summer seasons (Price et al, 2013). Increases in temperature are expected to result in longer growing seasons, and frost-free periods will be extended (Price et al., 2013). In addition to seasonal temperature change, shifts in precipitation patterns are also expected, with winter precipitation increasing and summer precipitation decreasing (Soja et al., 2007; Zhang et al., 2019). Modelling experiments predict fall, spring, and winter precipitation to increase 18-20% in some boreal regions (Price et al., 2013). Future warming and changes in precipitation patterns, as well as increases in the magnitude and frequency of disturbance events in the boreal forest, will have impacts on many of the functional aspects of the boreal ecosystem (Price et al., 2013; Osborne et al., 2018; Bush and Lemmen, 2019).

The balance between changes in seasonal precipitation patterns and increases in seasonal temperatures is expected to result in an increase in evaporative demand, resulting in direct and indirect impacts on tree mortality in the boreal forest (Price et al., 2013). Furthermore, projected increases in atmospheric CO_2 concentrations may result in increases in radial growth of trees, in addition to projected increases in longer growing seasons due to earlier spring warm temperatures (Huang et al., 2007; Zhang et al., 2019). However, these impacts on increased radial growth are difficult to assess on a large scale due to compounding factors and the role of the environment on growth regulation of boreal tree species (Huang et al., 2007; Price et al., 2013). It is suggested that effects of the projected climatic changes, which lengthen the period of seasonal tree growth, may have greater controls on annual tree growth as opposed to the projected increases in CO_2 concentrations (Price et al., 2013). In general, it is projected that tree growth and forest productivity is likely to increase with warming, except where water availability is a limiting factor of plant growth. Forest productivity in response to projected changes will surely have major implications on the global climate system. Understanding the physiological responses of tree growth to environmental factors such as temperature and precipitation is thus critical for model inputs. According to Friend et al. (2019), reliance on physiological based research and expanding our current understanding of wood formation are critical for reformulating global vegetation models. To achieve this, a link between physiological wood formation and the association between photosynthesis and growth must be explicitly included (Friend et al., 2019).

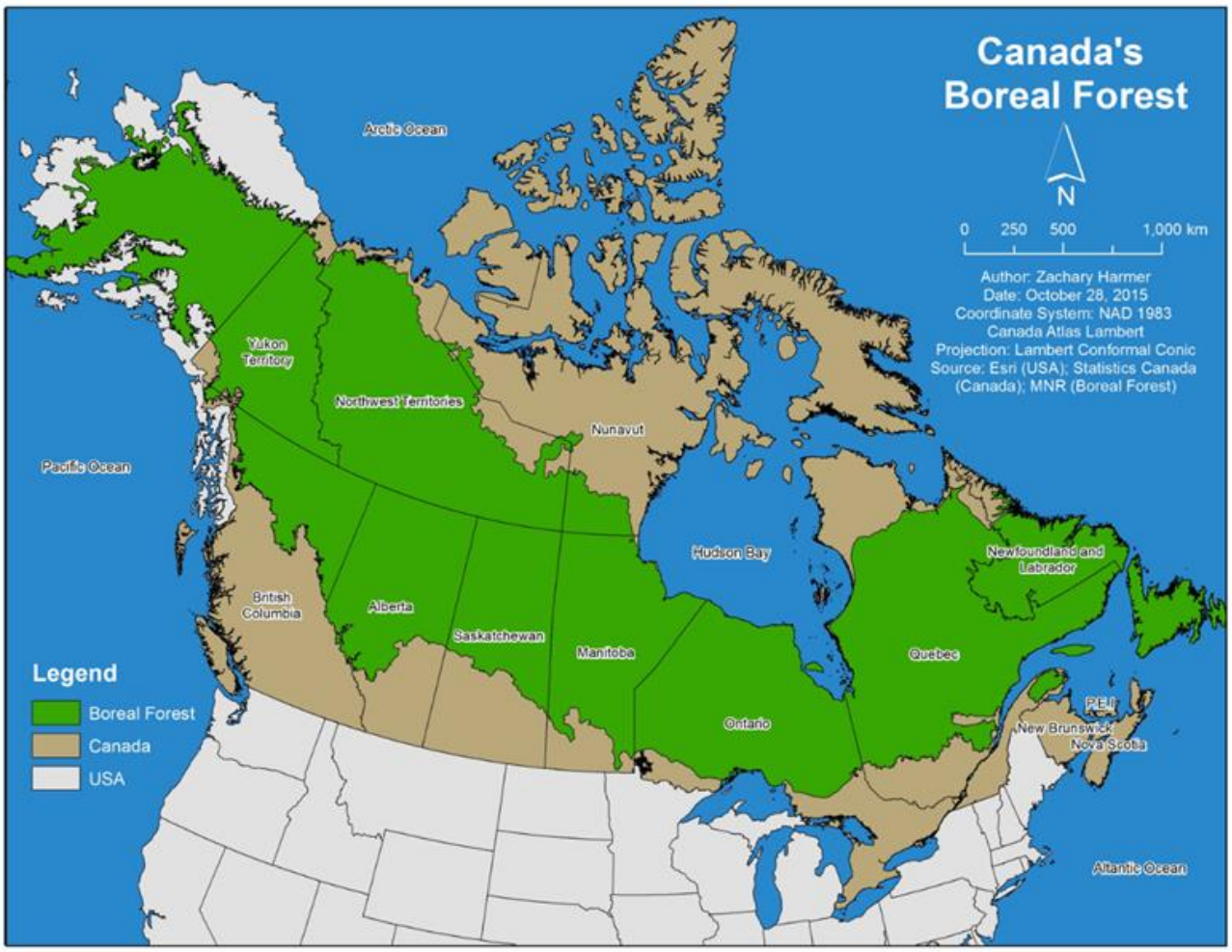

Figure 2.1. Canada's boreal forest range. The boreal forest is the largest forest system within Canada, covering ~552 million hectares. (Natural Resources Canada, 2016; Image: Zachary Harmer, 2016).

2.2.1 Climate in the northern boreal forest

The northern extent of the boreal forest gradually transitions from closed-canopy conifer dominated forest to the cold and dry tundra of the Arctic. These northern areas are more sparsely vegetated than the southern portions of the boreal forest. In most regions, snow cover may last for 6 months of the year; further north snow cover may last longer (Larsen, 1980). The climate within the northern boreal region varies significantly with respect to precipitation and temperature (Table 2.1). In general, the climate in the northern boreal zone is characterized by short, moderately warm, and moist summers, and long, cold, and dry winters, with light annual precipitation (Figure 2.2; Larsen, 1980; Bonan & Shugart, 1989; Brandt et al., 2013). The climate of the boreal forest region across broad spatial scales is controlled by continental Arctic and maritime Pacific air masses, resulting in the stark contrast in seasonal temperature differences (Bonan & Shugart, 1989).

2.2.1.1 Yellowknife regional climate

In Yellowknife, an average of 288.6 mm of precipitation falls annually, with July being the wettest month (Environment Canada, 2018). Of the 288.6 mm of annual precipitation, an average of 170.7 mm falls as rainfall (Table 2.2; Figure 2.2). Compared to Inuvik in the northern NT and Fort Simpson in the southern NT, Yellowknife (central NT) receives less rainfall (Table 1; Brandt et al., 2013; Environment Canada, 2018). In comparison, Inuvik receives 114.5 mm of annual rainfall and Fort Simpson a total of 238.6 mm. Seasonal climate in the Yellowknife area is variable due to the strong continental influences, explaining the vast differences in temperatures (Figure 2.2; Brandt et al., 2013). In Yellowknife during the winter months, daily lows can range from -20°C to -30°C. During the summer months, daily highs can range from 20°C to 25°C. Like other regions within Canada's boreal forest, the northern portion, including the Taiga shield and Taiga

plains of the NT, experience short and cool summers and long and cold winters (Figure 2.2; Ecosystem Classification Group, 2008).

Table 2.1. Climate Normals (1981-2010) for Inuvik, Yellowknife and Fort Simpson, Northwest Territories. (Environment Canada, 2018). Month in brackets for maximum and minimum annual average temperature represents the month of year with the observed value. Month in brackets for maximum and minimum annual total precipitation represents the month of the year with the highest average precipitation total.

Climate Normals (1981-2010) in the NWT Boreal Forest									
Location				**Temperature (°C)**			**Precipitation (mm)**		
Station	**Latitude**	**Longitude**	**Elevation (mASL)**	**Mean**	**Maximum (month)**	**Minimum (month)**	**Total**	**Maximum (month)**	**Minimum (month)**
Yellowknife *	62°27'46.000" N	114°26'25.000" W	205.7	-4.3	17 (July)	-25.6 (Jan)	288.6	40.8 (Jul)	11.3 (Apr)
Inuvik **	68°18'15.000" N	133°28'58.000" W	67.7	-8.2	14.1 (July)	-26.9 (Jan)	240.6	39.4 (Aug)	9.8 (Apr)
Fort Simpson *	61°45'37.000" N	121°14'12.000" W	169.2	-2.8	17.4 (July)	-24.2 (Jan)	387.6	61.4 (Aug)	15.4 (Mar)

* = WMO "3 and 5 rule" (i.e., no more than 3 consecutive and no more than 5 total missing for either temperature or precipitation)
** = At least 20 years

Table 2.2. Rainfall Days - Climate Normals (1981 – 2010) Yellowknife for May through September (Environment Canada, 2018).

Rainfall Days - Yellowknife (1981 - 2010)					
	May	**June**	**July**	**Aug**	**Sept**
[3] 0.2mm	6.6	7.6	9.6	10.5	11.2
[3]5mm	1.2	1.6	2.3	2.6	2.2
[3]10 mm	0.3	0.8	0.9	1.1	0.9
[3]25 mm	0.0	0.2	0.2	0.1	0.0

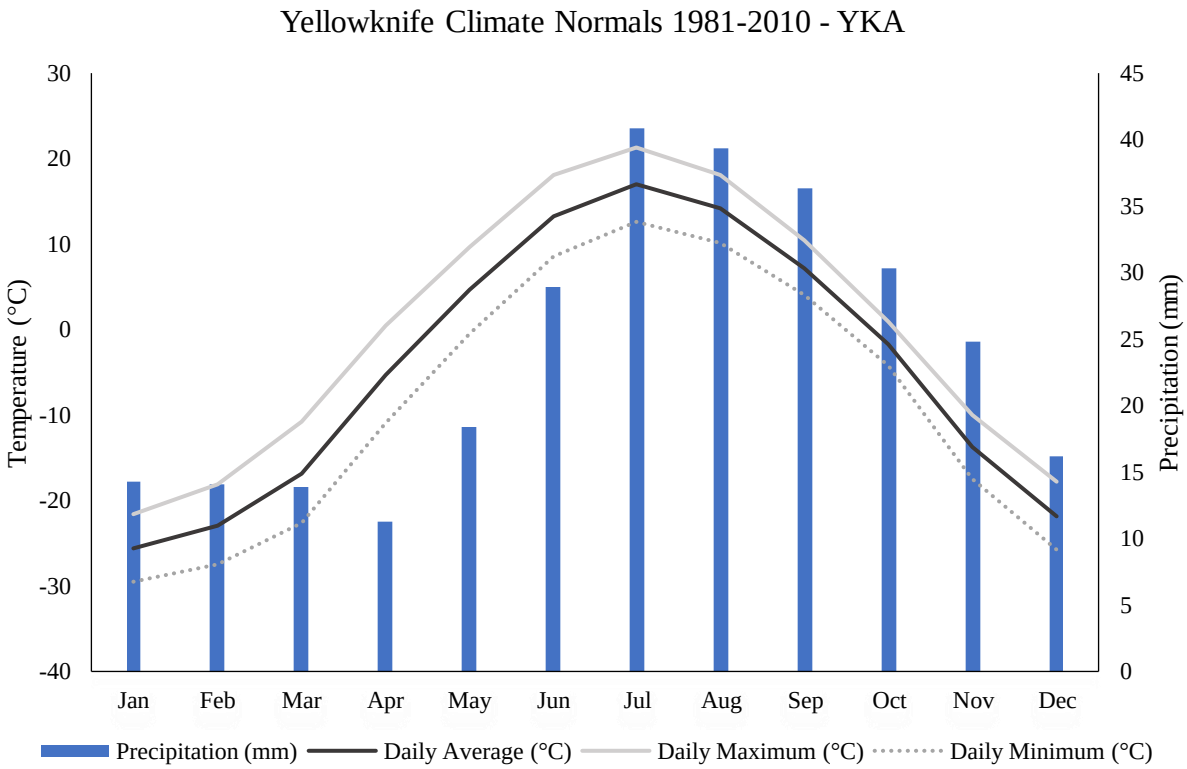

Figure 2.2. Yellowknife temperature and precipitation climate normals (1981 – 2010). Daily maximum, minimum, and mean temperatures (˚C) and monthly average precipitation (mm) for the Yellowknife Region (Yellowknife A – YKA). (Government of Canada, 2017).

2.2.2 Vegetation in the northern boreal forest

Vegetation is reflective of the varied climate and environmental conditions observed in a region, which is similarly true in the northern portions of the boreal forest (Larsen, 1980). Many boreal species are adapted for cold temperatures, as well as the light conditions in northern regions (Larsen, 1980). Woody cold-adapted plants in northern regions contain higher sugar and salt concentrations within their tissues to allow the tissues to withstand colder temperatures and reduce the damaging effects of freezing (Welling & Palva, 2006; Bigras & Colombo, 2013).

In northern regions of the boreal forest, forest communities are grouped into wet, mesic, and dry sites based on soil moisture. Dominant tree species within the boreal forests surrounding Yellowknife include black spruce (*Picea mariana*), white spruce (*P. glauca*), jack pine (*Pinus banksiana*), and paper birch (*Betula papyrifera*) (Farrar, 1995). Other important species include tamarack (*Larix laricina*), balsam fir (Abies *balsamea*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) (Larsen, 1980). The northern boreal forest system also includes small shrubs (e.g., *Betula spp.*, *Vaccinium spp.*, and *Salix spp.*) (Larsen, 1980). Lichen also represents a key component of northern boreal forest ecology. On xeric habitats (i.e., rock outcrops), lichens nearly cover all ground surfaces, whereas on mesic sites, sphagnum mosses dominate the ground cover (Bonan & Shugart, 1989).

2.3. Jack pine (*Pinus banksiana*)

The species of focus for this thesis study is jack pine (*Pinus* banksiana). Jack pine reaches its most northern extent of its distribution just south of the treeline in the Northwest Territories (NT). Jack pine was chosen for this study as it is an important species within the boreal forest system due to being the most widely distributed pine species within the Canadian boreal forest system, extending from near the treeline in NT to the Maritime Provinces (Figure 2.3; Janas &

Brand, 1988; Kenkel, 1988; Farrar, 1995; Farjon, 2013; Natural Resources Canada, 2015). The current range of jack pine in North America is within the spatial extent of the last (Wisconsinan) glaciation, suggesting its current distribution is a result of re-establishment following glacial retreat approximately 15,000 years ago (Rudolph and Laidly, 1990).

Jack pine is a shade intolerant evergreen pioneer species which grows in pure stands or mixed among other shade intolerant species (i.e., trembling aspen, balsam poplar, and tamarack) and shade tolerant species (i.e., black, and white spruce). In general, jack pine is described as a small tree, growing on average 20 m high and around 30 cm in diameter (Farrar, 1995). In 20-year-old stands in the Lake States with a density of 2,470 trees/hectare, trees were found to be 12 to 21 m high with a basal area of 6.7 and 20.0 m^2 and diameter at breast height (d.b.h) of 5.8 and 10.2 cm (Rudolph and Laidly, 1990). Jack pine is commonly found in shallow, dry soil conditions. In the Northwest Territories they commonly grow in coarse, sandy soils and on rock outcrops (Kenkel, 1988; Bonan & Shugart, 1989; Rudolph and Laidly, 1990; Farrar, 1995; Beland et al., 2003). When found on rock outcrops with thin soils, jack pine grows slowly and can attain very old ages (Pisaric et al., 2009). In these unique habitats, jack pine is particularly useful for reconstructing past hydrological variability using tree-ring analysis. Individual trees growing in particularly poor soil and on rocky sites often have stunted growth with gnarled, twisted trunks and dying branches (Farrar, 1995). Common identifiable characteristics of jack pine are their accumulation of grey pointed cones along with paired needles that are short and sharp. Jack pine growth occurs at its highest rate within the first ~50 years and tapers off after ~80 years, although jack pine stand ages can exceed 200 years (Kenkel, 1988; Farrar, 1995). Rupolph and Laidly (1990), described jack pine as one of the fastest growing trees, aside from tamarack, in the first 20 years of growth within its native range.

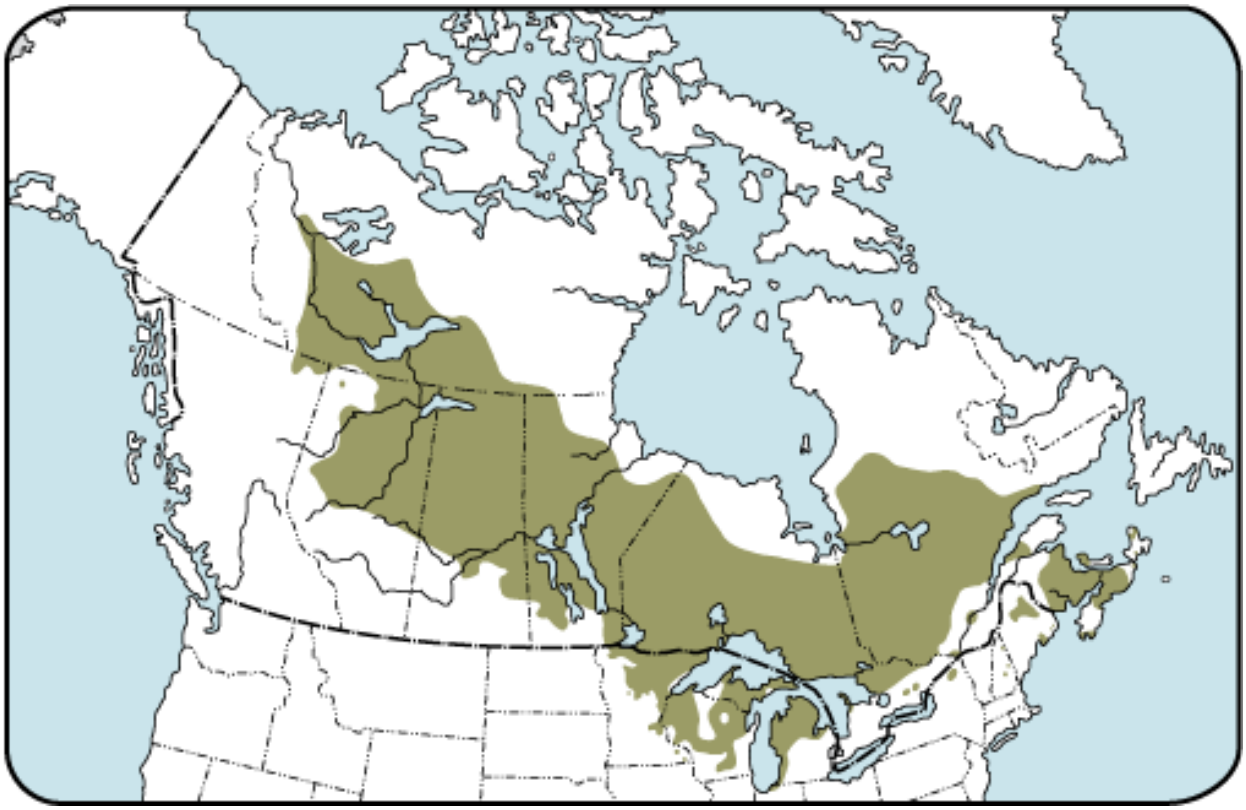

Figure 2.3. Distribution of jack pine native range in North America (Natural Resources Canada, 2015).

Fire plays a significant role in jack pine regeneration due to their resin covered, serotinous cones (Figure 2.4; Farrar, 1995; Natural Resource Canada, 2016). To release seeds and regenerate, jack pine cones must be heated, which may be either achieved naturally through high heat crown fires or occasionally from direct sunlight on hot days (Kenkel, 1988; Farrar, 1995; Beland et al., 2003). Resin from serotinous cones melts at or above 50˚C releasing viable seeds for stand regeneration (Gauthier et al., 1996). The viability of seeds may be compromised due to excessive heat from extended and intense crown fires (De Groot et al., 2004). Distribution of seeds following the opening of cones is immediate, although regeneration occurs following germination on a thin ash soil bed (De Groot et al., 2004). Thomas & Wein (1985) observed jack pine seed viability of 95%, with emergence of seedlings being greatest (35%) in the 2nd season post fire. More recent observations using seed traps estimated seed viability at ~67% following crown fire, with observed values of released seeds ranging from 64-634 seeds/m^2 of which 26–431 seeds/m^2 were viable (De Groot et al., 2004). Reid (2017) suggested jack pine is a competitive and fast-growing conifer with rapid post-fire establishment rates, outcompeting black spruce where they are codominant early in establishment. Jack pine's cones may remain closed for 10 to 15 years before opening and releasing seeds (Farrar, 1995; Martin & Lorimer, 1997).

Jack pine stands are also susceptible to insect pests including mountain pine beetle (*Dendroctonous ponderosae*) and spruce budworm (C*horistoneura fumiferana* Clemens), although pest pressure is most intense in the more southern portion of jack pine's distribution in Canada (Volney, 1988; Robson et al., 2015).

Like other northern boreal trees and conifers, jack pine growth is limited by light, temperature, and water availability (precipitation and soil moisture) (Rossi et al., 2006; Rossi et al., 2008; Genries et al., 2012). In general, the analysis of jack pine growth in boreal settings

demonstrates that the growing season begins in early May and is complete by October, depending on seasonal variations experienced each year (Rossi et al., 2006; Rossi et al., 2011; Genries et al., 2012). Previous jack pine dendrochronological research in the Yellowknife region has demonstrated the influence of early season (June) precipitation on the formation of the annual tree ring (Pisaric et al., 2009). Genries et al. (2012) indicated positive jack pine growth in responses to elevated previous year June precipitation and current year warmer April temperatures in northwestern Quebec and northeastern Ontario. Both increased temperatures in September and increased precipitation in October negatively influenced growth of jack pine growing on clay sites in northwestern Quebec and northeastern Ontario (Genries et al., 2012). In addition, jack pine growing in northern sites were found to have a negative growth response to increased precipitation in previous year October. In contrast to what was observed by Pisaric et al. (2009), increased previous year June precipitation was found to be negatively related to growth at these sites (Genries et al., 2012). However, investigation of seasonal dynamics and the influences on the onset of cambial division and subsequent xylogenesis phase transitions has not yet been explored for this species at its northern range limit. Research on intra-annual growth patterns, including the use of microcores and dendrometers has yet to be studied for this species, leaving a gap in knowledge surrounding the intra-annual growth dynamics of jack pine in northern boreal climates.

Figure 2.4. Jack pine cone and needles. Jack pine is characterized by its twisted and gnarled trunk, and accumulation of grey pointed cones. Jack pine has paired needles that are short and sharp.

2.4. Tree Growth – Wood formation

Tree growth and the process of wood formation are complex processes that involve the production of secondary xylem tracheids via the cambium (Rathgeber et al., 2016; De Micco et al., 2019) Environmental factors, namely temperature and precipitation, are the key controls of tree growth and secondary xylem (wood) production (Fritts, 1976). However, intra-annually, our understanding of the influences of weather and various environmental conditions on the physiology of conifer wood formation remains incomplete (Fritts, 1976; Rathgeber et al., 2016). Photosynthesis is the primary control for wood production and plant growth; however, the control of wood formation includes both external environmental factors as well as intrinsic phytohormonal regulation of growth (Fritts, 1976; Savidge, 1988; Rathgeber et al., 2016). Auxin is one of the main intrinsic phytohormonal growth regulators studied in the regulation of growth in plants, although additional plant growth regulators exist (Little & Savidge, 1987). This thesis research excludes the evaluation of intrinsic mechanisms of growth, as hormonal regulations are a separate, and equally complex area of plant growth research. This thesis research focuses on the external drivers of growth, these driving factors and how they impact growth is discussed in the following sections.

Developing an intra-annual understanding of plant growth is complex. Studies have indicated that physiological based research is an important aspect of determining the critical environmental factors for wood formation and thus forest productivity (Rathgeber et al., 2016; De Micco et al., 2019; Friend et al., 2019). Furthering the understanding of cellular responses and process, such as secondary xylem cell development (xylogenesis) to weather, is accomplished through the analysis of physiological wood formation on an intra-annual basis (Rossi et al., 2007). High-resolution dendrochronology focuses on understanding the drivers of wood formation, including the onset and termination of cambial activity as well as the timing and progression

through xylem formation phases over the course of a single growing season. Physiological based modelling experiments can offer insights into how trees grow, generating an understanding of the rates of cell formation and the timings of phase transition (Rossi et al., 2008; Cocozza et al., 2016; Rathgeber et al., 2016). For simplicity, this thesis research focuses on the use of external (environmental) monitoring methodologies to evaluate jack pine xylem differentiation to determine response to weather conditions versus the internal growth hormonal regulators. Outlined below are several external controls of tree growth, including the role of environmental conditions on growth, annual wood formation, and the progression of xylem cell development.

2.4.1. External controls on xylogenesis

The formation of growth rings is dependent on the production of xylem tracheids during the growing season. This process is known as xylogenesis and occurs at rates related to weather conditions and other growth-related factors (e.g., competition, disturbances). Weather is a key factor for the onset of cambial division and initial timing of xylem development (i.e., the rate at which cells undergo differentiation throughout the season), as well as the termination of xylem production (Rossi et al., 2008; Rathgeber et al., 2016). Trees undergo a period of growth during the summer months and a period of dormancy during the winter season when temperatures drop below the threshold of 4-5°C for conifers (Ziaco et al., 2016; Begum et al, 2013; Rossi et al., 2008). Cellular production is based on the interplay between multiple factors including air and soil temperatures, day length, water availability, and soil moisture. Thus, the timing of the onset of growth and the rates of production of differentiating xylem and mature tracheids are unique to seasonal differences (Rossi et al., 2008; Cocozza et al., 2016; Ziaco et al., 2017). It is widely accepted that wood formation in northern regions may last from mid-April/early-May until mid-

September, although this period may extend if temperatures remain sufficiently warm enough (Rossi et al., 2008; Rossi et al, 2014; Cuny and Rathgeber, 2016).

Xylogenesis is the process where newly produced xylem cells undergo a series of development phases in response to seasonal changes in environmental conditions (Figure 2.5; Rossi et al., 2003; Begum et al., 2013; Rathgeber et al., 2016). The first phase in this sequence is the cambial phase "C" when initial tracheid cell division occurs within the cambial zone, where hydraulic transport cells, phloem, and xylem, are produced via the cambium (Rathgeber et al., 2016). Throughout the winter months in the northern hemisphere cambium is dormant, and no wood formation takes place. The onset of the cambial phase begins as the snow melts and temperatures rise and the cambium becomes active (Rossi et al., 2008; Rathgeber et al., 2016). The cambial phase is distinguished by the multiplication of thin, radially flat daughter cells eventually differentiating into xylem mother cells towards the centre of the tree (Deslauriers et al., 2003; Ye & Zhong, 2015). The developing phase occurs when xylem cell division and differentiation is initiated from the xylem mother cell (De Micco et al., 2019). Following the development of xylem cells, the enlarging phase begins. This phase is determined by an increase in the radial enlargement of the cell and is defined by cells with thin primary walls and large lumen areas (Deslauriers et al., 2003). Due to their similarity in formation, for analysis purposes the developing and enlarging phases of xylem development are grouped into one phase, the developing & enlarging phase (E). The enlargement phase is followed by the wall-thickening phase (W), where the secondary cell wall is formed, and cell walls become more robust. At this stage, the primary wood made up of cellulose microfibrils, xylan, protein and lignin are added to the thin primary cell walls (Vaganov et al., 2006). The final phase of xylogenesis is the maturation (M) phase. This phase occurs when the xylem cell becomes fully lignified and is no longer enlarging. Cells in the mature phase

represent seasonal wood formation and the annual ring. Due to the seasonal differences between the beginning and end of the growing season the mature phase has two defined cell forms: the earlywood development (EW) and latewood development (LW). Earlywood cells develop early in the growing season, have larger lumen areas and thinner cell walls. Latewood cells develop later in the growing season and are characterized by thicker cell walls and smaller lumen areas (Figure 2.5; Vaganov et al., 2006). Weather conditions during the cambial phase and cell enlargement phase influence the rate of xylem cell differentiation (i.e., the time spent in the radial enlargement and expansion phases) and the length of the period of cell wall-thickening (Rossi et al., 2006b; D'Orangeville et al., 2013). These controlling factors are assessed to determine the role of weather and environmental conditions on the timing of phase succession and the rate of cell development throughout the growing season.

Early season cambial development in mid to high latitude regions is strongly affected by active layer thaw conditions and water availability to roots. This uptake of water initiates the enlargement phase of newly produced tracheid cells (Quanyan et al., 2017). Due to snow melt and seasonal thaw, early water availability contributes to early season growth and the onset of cellular development (Tardif et al., 2001; Gruber et al., 2009; Quanyan et al., 2017). In response to early water availability, cells produced have larger lumen area and thinner cell walls. Latewood cells which form at the end of the growing season are characterized by thicker cell walls and smaller lumen areas. It is the contrast between the newly produced earlywood cells and the previous year's latewood cells that defines the yearly ring boundary (Figure 2.6; Fritts, 1967; Rathgeber et al., 2016).

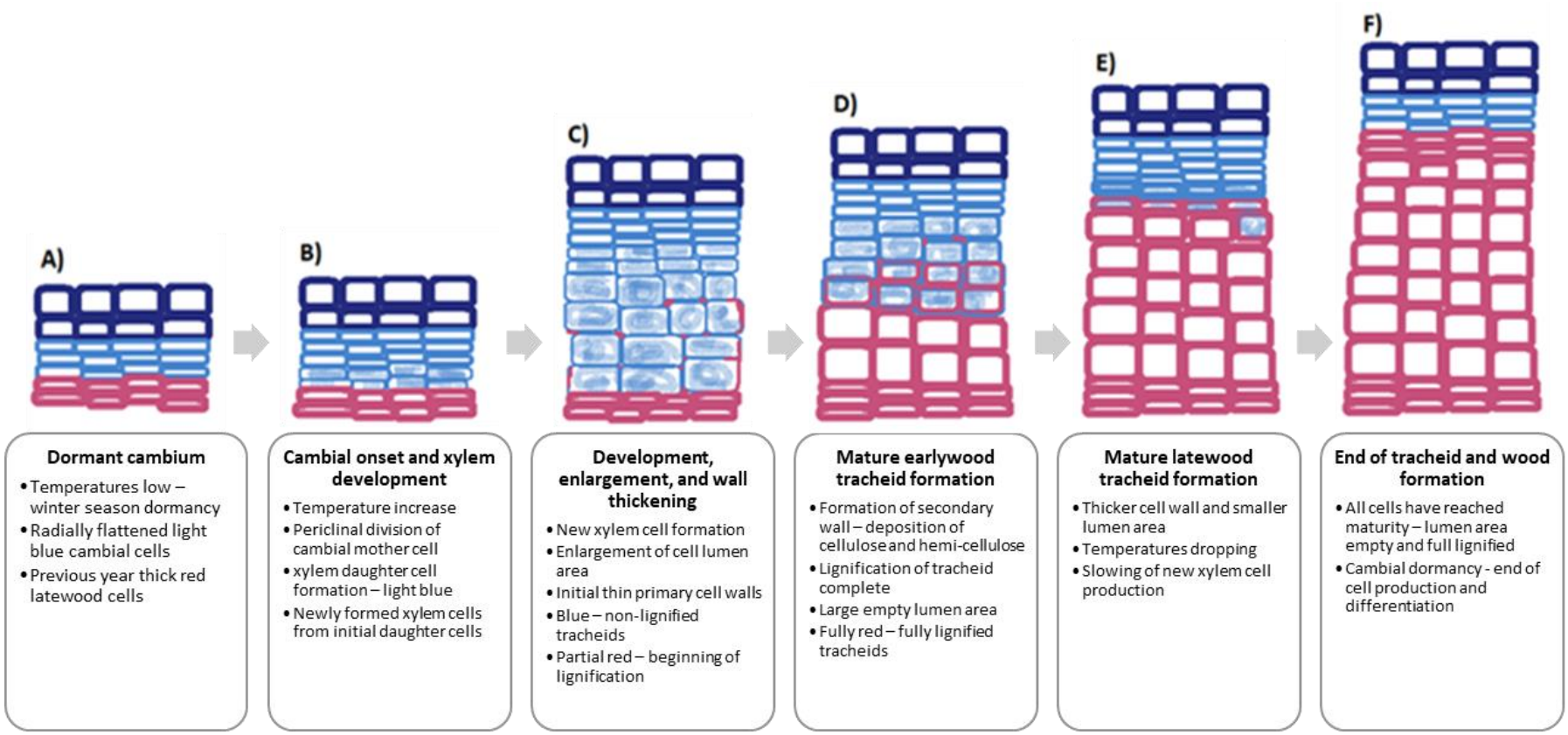

Figure 2.5. Details of seasonal development and processes of xylogenesis and ring formation. Dark blue: cambial cell; Light blue: developing xylem tracheid; Partial red: lignification of xylem tracheid; Complete red: fully lignified mature xylem tracheid. In succession of seasonal wood formation processes: A) Dormant cambium; B) cambial onset and xylem development; C) development, enlargement, and wall-thickening; D) Mature earlywood tracheid formation; E) Mature latewood tracheid formation; and F) End of tracheid and wood formation.

2.4.2 Photosynthesis and respiration

Plant growth, in general, refers to progression and development of transport cells, comprising of two growth aspects: (1) cell initiation, which is growth in terms of plant size; and (2) cell differentiation, which adds to the complexity of the plant. Plant growth relies on both respiration and photosynthesis (Salisbury & Parke, 1964; Fritts et al., 1999). Photosynthesis is the process where plants utilize light energy, carbon dioxide, and water to produce simple sugars (glucose) and oxygen (eqn. 2.1). The opposite and paired process is respiration. This process consumes the products formed during photosynthetic activity (simple sugars and oxygen) and produces energy used in plant growth and tissue differentiation (eqn. 2.2).

Photosynthesis:

$$6\ CO_2 + 12\ H_2O \rightarrow C_6H_{12}O_6 + 6\ O_2 + 6\ H_2O \quad (2.1)$$

Respiration:

$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O + (\text{energy}) \quad (2.2)$$

Analysis of the relationship between growth and respiration rates in conifers indicate that if photosynthesis is limited, available carbohydrates are utilized during respiration and lead to increased stress within the plant and limited growth (Larsen, 1980; Kozlowski et al., 1997). In woody plants, stem growth is referred to as wood formation, during which xylem cells are produced from the cambium and undergo a series of progressive phases. This is the process of xylogenesis and is defined in more detail in this section's final subsection. Correlation between respiration rates in conifers have been observed, and if photosynthesis is limited, carbon resources are exhausted during respiration which may lead to decreased growth (Kozlowski et al, 1997; Larsen, 1980).

2.4.3 Light

In general, the amount of light or day length impacts the observed photosynthetic rate. An initial linear relationship between increases in the amount of light and the rate of photosynthesis was noted by Teskey et al. (1995) and is known as the light saturation point. This response was studied for northern hemisphere conifers and demonstrated that conifer growth was highest during the periods of longest daylight (Rossi et al., 2006). For high latitude plants like conifers, this is an adaptation to the longer phototrophic periods throughout the summer months in comparison to lower latitudes. This adaptation allows for enough time for plants to grow in a region of shorter growing seasons. It is estimated that conifers growing in North American boreal forests produce a similar number of cells within a shorter growing season compared to regions with longer growing seasons due to the more rapid growth rates controlled by greater daily photosynthetic activity owing to longer day lengths (Deslauriers & Morin, 2005; Rossi et al., 2006).

2.4.4 Temperature

Numerous studies of the control of temperature on tree growth rates have demonstrated that growth responses to temperature are highly variable and species specific, although temperature has been determined to be the most influential factor on growth initiation in both boreal and temperate climates (Rossi et al., 2007; Vaganov et al., 2006). In general, the relationship between growth, temperature, and photosynthetic activity is unimodal, reaching a maximum threshold and decreasing as temperatures increase further. Rossi et al. (2016) indicated a proportional lengthening in the period of wood formation with increases in seasonal temperatures, from 83.7 days at -2ºC to 178.1 days at 12ºC (average wood formation was calculated from 39 sites across several countries and altitudes during the period between 1998-2014). Northern species, due to cold acclimatization, have a reduced temperature threshold (Bigras & Colombo, 2013; Rossi et al.,

2006). In high-latitude regions, tree-ring widths have a strong relationship with summer temperatures, during periods following onset of cell development (Vaganov et al., 2006). Larsen (1964) indicated that longer growing seasons would result in increases in the ratio of latewood development in ring formation. The development of cells, and thus the variation of ring formation, has been shown to be significantly controlled by seasonal temperatures (Anatonova and Stasova, 1997; Schweingruber, 1993; Rossi et al., 2007). Rossi et al. (2007) estimated daily minimum temperature of 4-5°C, daily mean of 8-9°C, and daily maximum of 13-14° temperature thresholds for the onset and termination of xylogenesis. Therefore, air temperatures control rates of cell production, and consequently growing season length, ranging from 3 to 5 months. These critical temperatures are also important for root growth during periods of freeze and thaw, influencing the onset and termination of growth as soil temperatures drop and gas exchange decreases (Grossnickle, 2000). Both photosynthesis and respiration thresholds are controlled by air and soil temperatures. For cold acclimatized conifer species, minimal critical air temperatures for growth range between 5°C and 25°C and are largely controlled by minimum temperatures as opposed to daily maximum temperatures (Rossi et al., 2007).

2.4.5. Water

Water availability strongly affects photosynthesis and growth by limiting stomatal conductance and root productivity (Bai et al., 2010). Experimental evidence suggests increases in precipitation lead to increased seedling root production (Bai et al., 2010). Similarly, laboratory studies conducted by Brix (1979) demonstrated reduction in photosynthesis with increased water stress on several conifer seedlings indicating an impact on growth under drought-like conditions. Reduced growth in white spruce in the Alaskan boreal forest occurred with temperature induced drought stress (Barber et al., 2000). Körner (2015) suggests that cell expansion and differentiation

is most affected by water availability, as this phase is in direct contact with the trees' water uptake function. Therefore, water limitation in the initial development of cell formation has major implications for timing of cell development. In addition, Cuny and Rathgeber (2016) suggested soil water availability may have direct links in the formation processes for cell enlargement, impacting the cell lumen area size. Although a dynamic resource, water plays a critical role in the formation of woody cells and the productivity of growth due to its critical role in photosynthetic activity and its relationship with water balance and movement within the tree stem.

2.5. Dendrochronology

Dendrochronology is the study of tree-ring growth records and their use in the reconstruction of past climate patterns (dendroclimatology) and extreme events (Douglass, 1941; Fritts, 1976; Speer, 2010). In general, annually produced tree-rings are measured and analyzed using dendrochronological techniques generating lengthy proxy climate records (Fritts, 1976; Speer, 2010). These techniques have been used extensively to develop long-term reconstructions of climate variability, including temperature and precipitation patterns, stream flow variability, and the occurrence of drought and drought-like conditions (Ziaco & Biondi, 2018; Deslauriers et al., 2014; Munoz et al., 2016). Reconstructions using tree-rings are successful at placing recent climate and environmental trends (e.g., temperature, precipitation, stream flow) in a long-term context (Chen et al., 2016).

In general, dendrochronology techniques follow three main steps: (1) the collection and preparation of samples from a selected study site; (2) cross dating and measurement of collected cores; and (3) the development of a chronology using these measurements. The applications of these techniques can be split into two groups: (1) understanding and developing knowledge surrounding the climate-growth relations; and (2) identifying evidence of past environmental

changes contained in the rings of the samples (Norton & Ogden, 1987). These two sections are broad and do not identify all aspects of how data encapsulated in tree-rings can help researchers develop an understanding of past climates, forest dynamics, tree health, and the use of this information in predicting future climate dynamics (Fritts, 1967; Bonan & Shugart, 1989).

To collect data from tree-rings, tree cores are obtained using an increment borer and analyzed through the measurement of ring-width (Figure 2.6). Due to the growth relationship with climate, trees produce annual rings in response to seasonal weather and environmental conditions. The differences in widths of the measured rings give insight into the productivity of the growing season and are used to identify more productive versus less productive years. Climatic and environmental information contained within individual rings, such as maximum density of the wood, may also give indications of climatic variations and events. Wood density patterns are physiological changes in the development of tracheids, resulting in two types of mature tracheids (earlywood and latewood) (Fritts, 1976; Vaganov et al., 2006; De Micco et al., 2019). At the beginning of the growing season, large, thin-walled cells are produced (earlywood cells) in comparison to the thick-walled cells (latewood cells) produced at the end of the growing season. The development of latewood cells produces the boundary between different growing seasons as demarcated by the distinct differences in cell size between the earlywood and latewood cells (Fritts, 1976). In addition to the analysis of ring-width, other features like scarring can also indicate other types of events (e.g., fires and flooding events) that have occurred during the lifespan of the tree.

Figure 2.6. Increment borer in jack pine on rocky outcrop in NT 2017. (Image: Dana Harris, 2017).

2.6. Intra-annual dendrochronology

Intra-annual dendrochronology techniques are utilized to assess tree-ring formation on an annual basis, producing detailed records of the cellular development and physiological progression of wood production for an entire growing season (Rossi et al., 2008; Rathgeber et al., 2016). These records are useful tools in developing a comprehensive understanding of wood formation in response to weather and seasonal environmental conditions and helping to refine the detailed climate growth relationship of species growing in various regions of the world (De Micco et al., 2019). This detailed data is useful in refining historical records using tree-rings (traditional dendroclimatology) and modelling for future forest dynamics in response to global climatic changes (Fritts, 1976; Vaganov, 2006; De Micco et al., 2019; Friend et al., 2019). It is noted that intra-annual growth responses are highly variable among species and are not fully understood for all species (Rossi et al., 2008; Rathgeber et al., 2016). Intra-annual growth analysis utilizes previous knowledge and understanding of plant growth, tree physiology, and the kinetics of plant cell development and wood production. Methodologies used for this research aim to create a chronology of cellular development, timing of xylogenesis phase progression, and mapping the patterns of growth functions throughout the growing season. These techniques generate an understanding of the dynamics of seasonal growth patterns from which the environmental controls are discussed. Due to the complexity of wood formation and the interplay of seasonal differences in environmental conditions, these relationships are complex and varied between years, and thus remain difficult to assess. Intra-annual methodologies, discussed in more detail later in this thesis, attempt to indicate the timing of cell production, and the environmental controls of wood formation within a single growing season to generate robust seasonal chronologies of cell development and ring formation. Utilizing intra-annual data of ring formation and cell production are useful in the

analysis for tree-rings (dendrochronology) as well as critical in developing an understanding of tree growth responses to changing climate (Frits, 1976; Vaganov, 2006; De Micco et al., 2019; Friend et al., 2019).

2.7. Intra-annual methodologies

The methods used to study intra-annual cellular development allow researchers to assess tree growth on an incremental basis, creating detailed chronologies of wood formation throughout the entire growing season. Types of intra-annual dendrochronological methods include the external monitoring of reversible stem swelling and non-reversible growth via dendrometer sensors and internal physiological assessments of the timing of cell production and transitions of xylogenesis phases using microcore or pinning techniques (Deslauriers et al., 2007; Rossi et al., 2008; Mäkinen et al., 2008). These methodologies are utilized to assess seasonal variations in the dynamic growth responses of trees to environmental variables and conditions. The use of several methodologies together develops robust chronologies of cell production and the seasonal dynamics of tree stem growth. This knowledge enhances our understanding of species-specific seasonal wood formation and tree growth in relation to various environmental factors. Information and knowledge of xylogenesis and the production of woody material is useful in the interpretation of the environmental signals contained in annual rings using dendrochronological techniques as well as improving our understanding of tree responses to climate (De Micco et al., 2019; Friend et al., 2019).

Microcore and pinning techniques provide insight into the timing and duration of seasonal xylem cell production by analyzing the number of cells in phases of xylogenesis on a re-occurring basis (i.e., weekly). These techniques are useful in providing an indication of the timing and duration of each phase of growth and can assist in developing an understanding of when cells are

forming and how long they remain in each phase of xylogenesis. Pinning utilizes a thin needle that disrupts cambial activity as it is inserted into the wood stem leading to a discernable wound in the cambium zone (Mäkinen et al., 2008). This method is continued throughout the growing season on timed intervals (e.g., weekly) establishing the timing of xylogenesis phase progression during the pinning process based on visual damage to the wood (Mäkinen et al., 2008). Microcoring techniques utilize a small punch that removes a sample of wood tissue. Like pinning, these microcores are collected on a weekly basis and allow for the creation of a chronology of xylem formation throughout the sampling period (Mäkinen et al., 2008; Rossi et al. 2008). For this thesis, microcores were collected to study cellular development and to determine dates of xylogenesis phase transitions. These transitions are more easily defined using microcore methods versus pinning methods and microcore studies can be repeated for several years on the same trees (Mäkinen et al., 2008). When paired with weather data, studies of xylogenesis can provide insights about the controls that weather conditions have for the onset of cell production, peaks in cell production, and the termination of the xylogenetic processes (Rossi et al., 2006; Deslauriers et al., 2007; Ziaco et al., 2017).

2.7.2 Microcores

Microcores are small cores composed of woody tissues, ~1.5-2.25 mm in diameter and 15 mm in length (Figure 2.7). Microcores are extracted from the outermost portion of the tree stem using a Trephor tool (Figure 2.8; Rossi et al., 2006a; Stangler et al., 2016) and are used to assess xylem formation through the counting of cells in each subsequent phase of xylogenesis throughout an entire growing season (Stangler et al., 2016; Rathgeber et al., 2016). To do this, thin sections of microcores are prepared using a rotary microtome. Thin sections are used to create a microscope slide to allow for evaluation of xylogenesis phase transitions. This evaluation is done by staining

the wood sample allowing for easier identification of individual phases. Weekly cores specify the number of cells in each phase, counted along 3 radial files (Stanger et al., 2016). The evaluation of xylogenesis phase characteristics is performed by a technician who has experience in identifying anatomical features, and knowledge surrounding xylogenesis phase transitions.

Microcores can be used to evaluate the timing of the onset and cessation of woody (xylem) cell production and the timing of transition between phases of xylogenesis (Rossi et al., 2008; Rossi et al., 2014). This information, coupled with external environmental factors allows for the analysis of the environmental controls on these seasonal growth timings (Deslauriers et al., 2007). Investigations of xylem formation and wood production improve our understanding of tree biology and thus the response to changing environmental conditions (Rossi et al., 2008; Ziaco et al., 2017). Research surrounding the controls of wood formation using microcores have use in forest and climate model simulations to create accurate projections of the implications of climate change on forest dynamics and subsequent environmental changes (Ziaco et al., 2017; Friend et al., 2019).

Figure 2.7. Microcore samples stored in 100% ethanol solution to prevent drying of cells (Image: Dana Harris, 2016).

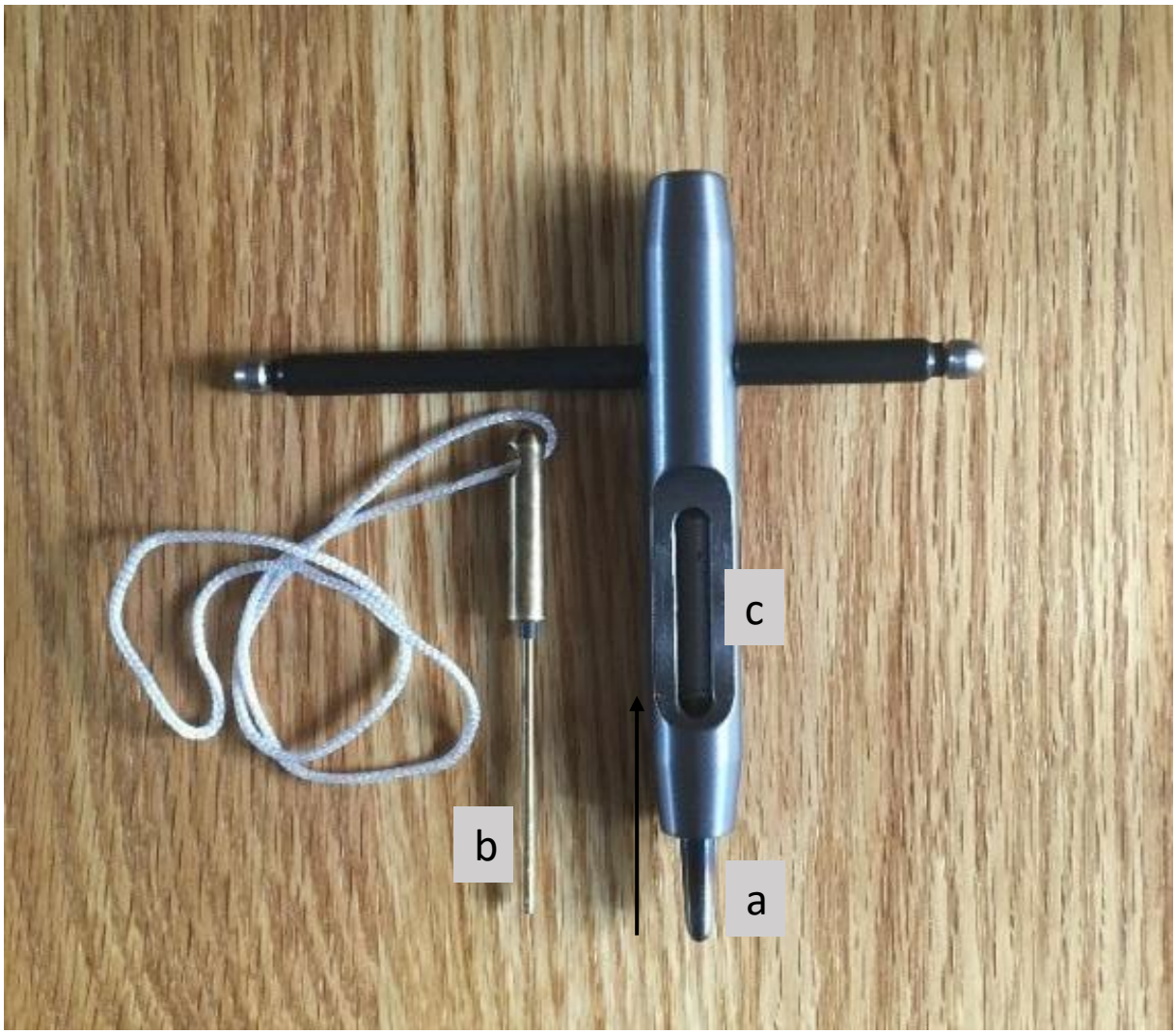

Figure 2.8. Trephor Tool used for microcore extraction. The hollow end (a) of the trephor tool is hammered into the tree stem with a rubber mallet, the wood sample is extracted by pushing the small extractor tool (b) into the hollow end (black arrow). The wood sample is collected from the small open chamber by hand (c). (Image: Dana Harris, 2016).

2.7.1 Dendrometers

Intra-annual growth may also be evaluated using high-precision sensors known as automatic point dendrometers fastened to the tree stem (Figure 2.9). These sensors provide information on intra-annual stem growth indicating when cell division and cell expansion takes place based on theoretical understanding of wood production in tree stems (Deslauriers et al., 2003; Stangler et al., 2016). Although cell division, due to the small amount of impact on radial change, it is difficult to distinguish exact timings of seasonal xylem cell differentiation from dendrometer sensors alone. It is suggested that a multi-proxy approach, where cell development can be measured, may provide a more refined understanding of growth outside of stem fluctuations alone. (Deslauriers et al., 2003; Stangler et al., 2016). Dendrometer sensors create continuous monitoring through linear displacement of the linear variable differential transformer (LVDT) of the sensing rod of the dendrometer placed against the trunk of the tree (Deslauriers et al., 2003). The LVDT moves in response to the movement of the stem and transforms the displacement into an electrical signal stored on a data logger. Signals from the dendrometer sensor are translated into stem displacement increments for the study period (Deslauriers et al., 2003: Deslauriers et al., 2007; Quanyan et al., 2017).

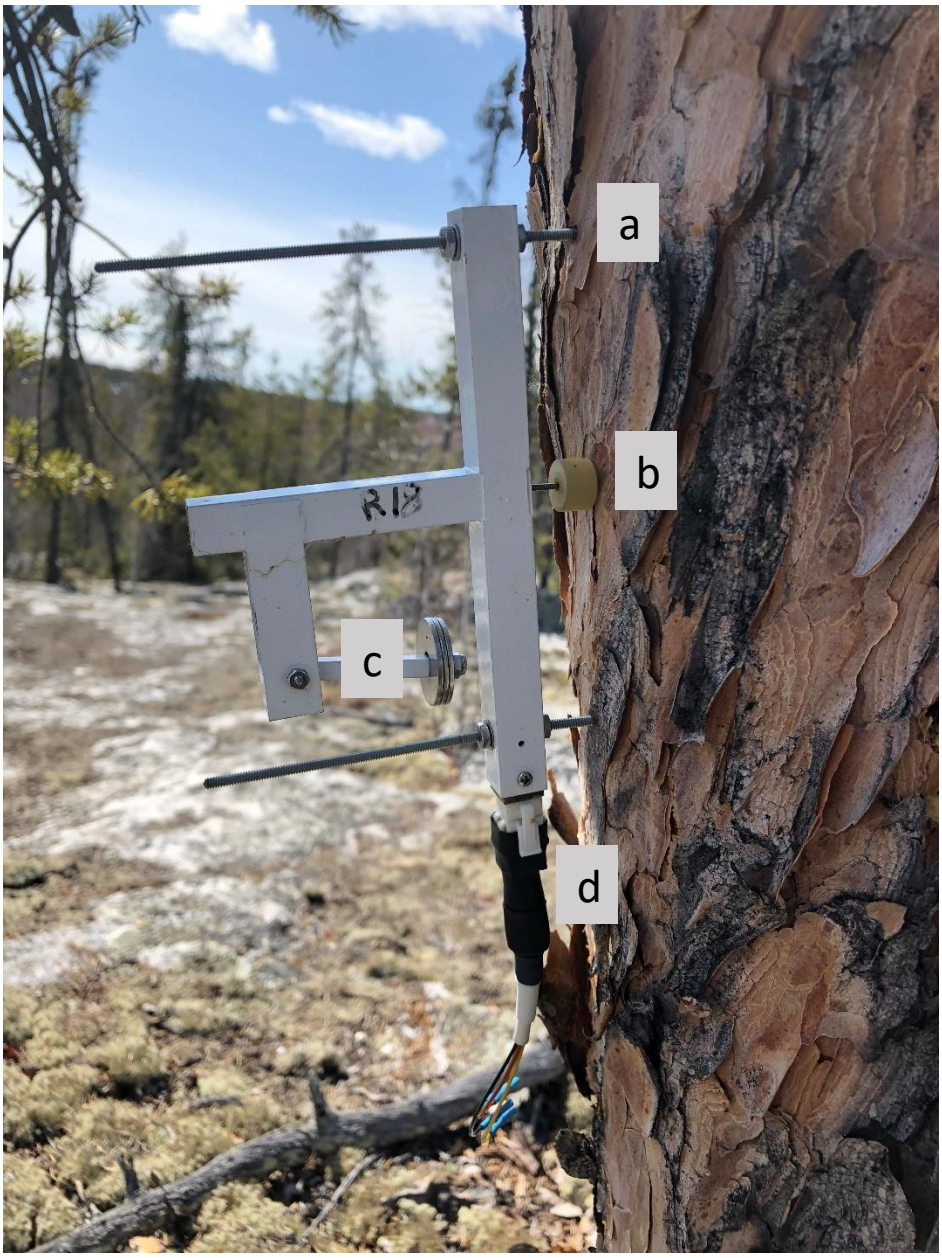

Figure 2.9. Automatic point dendrometer used for continuous monitoring of stem radial fluctuations on TV500. (a) steel mounting rod; (b) sensing rod; (c) constant force cantilever; (d) LVDT cable connection (Image: Dana Harris, 2018).

Two responses are reflected in the dendrometer data, including reversible and irreversible growth. Reversible growth is in the form of stem shrinking, typically occurring in the day, and stem swelling, typically occurring at night. Both responses occur in response to water movement and transport within the stem's cells. Reversible growth patterns make up the daily circadian cycle lasting about 24 hours, although this process may exceed 24 hours. Due to these daily fluctuations in nutrient and water availability, tree growth encompasses a circadian cycle with irreversible swelling, contraction, and recovery stages throughout the estimated 24-hour period (Figure 2.10). For analysis purposes, the circadian cycle is made up of three distinct phases and is called the fourth phase (Downes et al. 1999). The four phases are defined as the following: (1) contraction phase – occurs between the morning maximum and daily minimum values; (2) expansion phase – the full period between the daily minimum and the subsequent morning maximum (Deslauriers et al., 2003); and (3) stem radial increment (SRI) phase – a portion of the expansion phase which only occurs when the stem radius exceeds the morning maximum until the following maximum. The SRI would not be calculated if the previous cycle maximum was not reached or exceeded by the following cycle. This stem radial displacement or increment is the displacement or swelling that occurs within the tree stem during water uptake (Zweifel et al., 2006: Quanyan et al., 2017). These three phases make up the (4) phase, the circadian cycle, which characterizes the estimated complete daily cycle of stem swelling, contraction, reversible and irreversible stem fluctuations. In general, circadian cycle phase occurs at similar rates between years, and is an important characteristic of species-specific stem growth, as well as water and nutrient movement within the tree stem (Deslauriers et al., 2003). The responses observed in the dendrometer sensor measurements represent the relationship between wood production and water balance within the

tree stem. Irreversible growth, however, is representative of daily increases in xylem cell production or permanent stem growth.

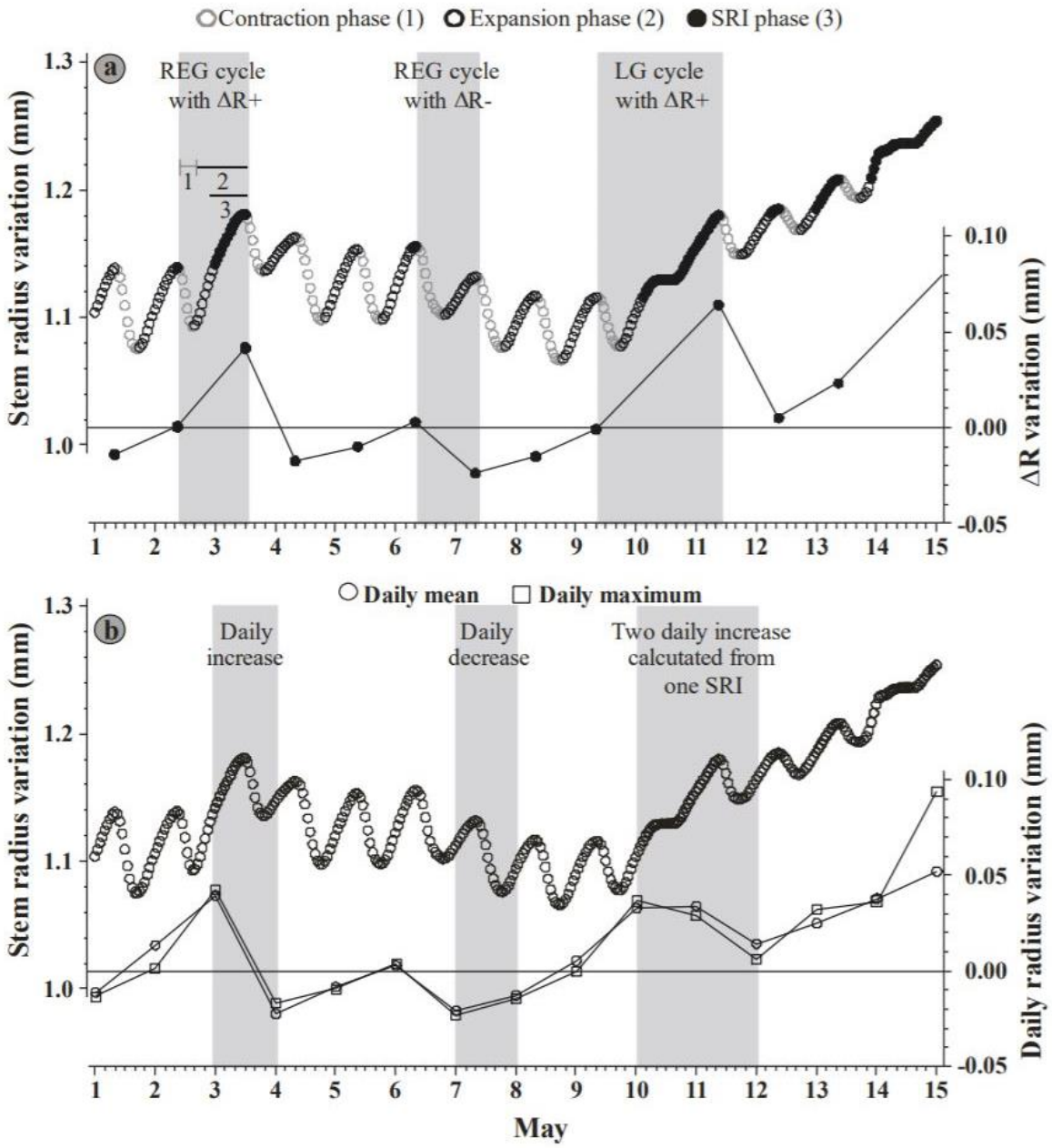

Figure 2.10. Dendrometer Cycle characterization Stem Cycle Approach with 3 distinct phases making up fourth phase: the circadian cycle**.** Phases as defined as: Phase 1: contraction phase; Phase 2: expansion phase, Phase 3: SRI phase, and Phase 4: Circadian Cycle comprising Phase 1, Phase 2, and Phase 3 (if a ΔR+). (ΔR+) occurs when stem radius exceeds morning max, (ΔR-): occurs when previous maximum not reached. REG cycle when cycles last ~24-Hours, and LG cycle when cycle lasts >24-hours. B) Daily cycle approach using time series extraction using daily mean and max values between two consecutive days. (Figure: Deslauriers et al., 2007).

Studying the dynamics of intra-annual growth (growth experienced over one growing season) enables the analysis of weather impacts on tree growth. Monitoring of seasonal stem radial variations in response to weather conditions highlights cyclical patterns, including daily and monthly patterns of reversible growth and the environmental controls of growth. Studies of intra-annual growth also present a continuous record of permanent growth for the entire growing season. Traditionally, dendrochronology and dendroclimatology suggest that temperature and precipitation are important limiting factors for tree growth (Ziaco et al., 2017; De Micco et al., 2019). However, traditional analyses relied strictly on monthly averages to assess climatic signals contained in the tree rings. Advancement in intra-annual methodologies, tools, and analysis have allowed for assessment of tree growth at fine temporal scale, allowing for a deeper understanding of tree growth and characteristics (e.g., automatic point dendrometers) and wood production using physiological based methods (e.g., microcores, pinning techniques).

CHAPTER THREE:

STUDY SITE AND METHODOLOGIES

3.1 Introduction

This research seeks to create a baseline understanding of the characteristics of jack pine (*Pinus banksiana*) growth within the northern portion of the boreal forest in Yellowknife, NT. To do this, cellular development, stem radial expansion, and daily weather conditions were studied for a single growing season covering the period of May 5th to September 29th, 2017, at the informally named study site "Treeville", located ~25 km northeast of Yellowknife, NT. The following chapter describes the characteristics of the study site and selected trees, as well as the methods used to collect, analyze, and interpret the data sets collected in 2017.

3.2 Location

3.2.1 Study site – Treeville

The study was conducted within a jack pine dominated stand, herein referred to as Treeville, which is located ~25 km northeast of Yellowknife, NT (62˚33.425 N, 114˚00.660W) and within the northern portion of the Canadian boreal forest. The Treeville site is located in the Great Slave Lowland Taiga Shield High Boreal Ecological Region based on ecoregions defined by the ecoregion classifications of the Northwest Territories (Figure 3.1; ENR, 2008). In general, the Taiga Shield is described as mixed broadleaved and needleleaved open and closed canopy forest systems (Farrar, 1995; Wulder et al., 2007). Specifically, the High Boreal ecoregion is described as "mixed white spruce and trembling aspen forests" where sites are abundant with rich moist soils, and "extensive young jack pine stands" occurring as a result of huge burns that are predominate in this region. Jack pine sites are on open rock outcrops and are mixed with spruce and lichen-shrub communities (ENR, 2008). The site has an elevation of 221 m above sea level

(a.s.l.). In addition to jack pine, tree and shrub species present at the site include small paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), and willow species (*Salix sp.*). Understory vegetation includes low lying shrubs, such as *Ledum* and *Vaccinium spp.* The study area is dominated by abundant granitic outcrops with little soil cover, typical of jack pine habitats. The rock outcrops cause rapid runoff and little infiltration; therefore, the site is characterized by xeric growing conditions. As a result, lichens are abundant at the site, including *Umbilicaria hyperborean, Cladina mitis, Cladonia stellaris,* and *Flavocetraria nivalis (*Bonan & Shugart, 1989; Ecosystem Classification Group, 2008). The trees studied at the site have an average age of 195 years (Max: 270 years, Min: 122 years), with a mean diameter at breast height (DBH) of 16.3 cm and mean height of 5.12 m (Table 3.1).

Site selection took place during summer 2016 (July) when the study location was chosen along the Ingraham Trail (NWT Highway 4) northeast of Yellowknife. Jack pine was chosen as the tree species to study because it is one of the most widely distributed pine species in Canada and the unique habitat they grow in in the Yellowknife area (i.e., thin soils on rock outcrops) are integral for assessing hydrological variability using traditional dendrochronology to generate climate reconstructions. In addition, studying jack pine using microcores and dendrometers builds on previous dendrochronological investigations in this region (e.g., Pisaric et al., 2009) and provides more detailed assessments about the climatic controls on jack pine in these northern settings. During the site selection we looked for older trees (150-200-year range) growing in rock outcrop settings. An older tree stand site was selected for this thesis research to allow for comparisons with previous dendrochronological research (Pisaric et al., 2009) and potential future use of the intra-annual jack pine data relative to historical climate data reconstructions using traditional dendrochronology for assessing long term hydrological variability. The study site was

assessed for accessibility for weekly sampling requirements, site maintenance, and potential use in a multi-year study. Signs were used to inform users in the project area and to reduce human related impacts on the study site. Increment cores taken during the 2016 field season were used to determine the ages of the selected trees within the study site (average 194 years; Table 3.1). Trees selected in 2016 were studied during the 2017 season using microcores and dendrometer sensors. Microcores were taken weekly from May 5th, 2017 (DOY 125) and ending September 12th, 2017 (DOY 256). Dendrometer sensors installed on the same group of selected tree stems, took readings of stem radial displacement (LVDT) at 30-minute intervals from May 5th, 2017 (DOY 125) until September 29th, 2017 (DOY 272) when the sensors were removed for winter storage.

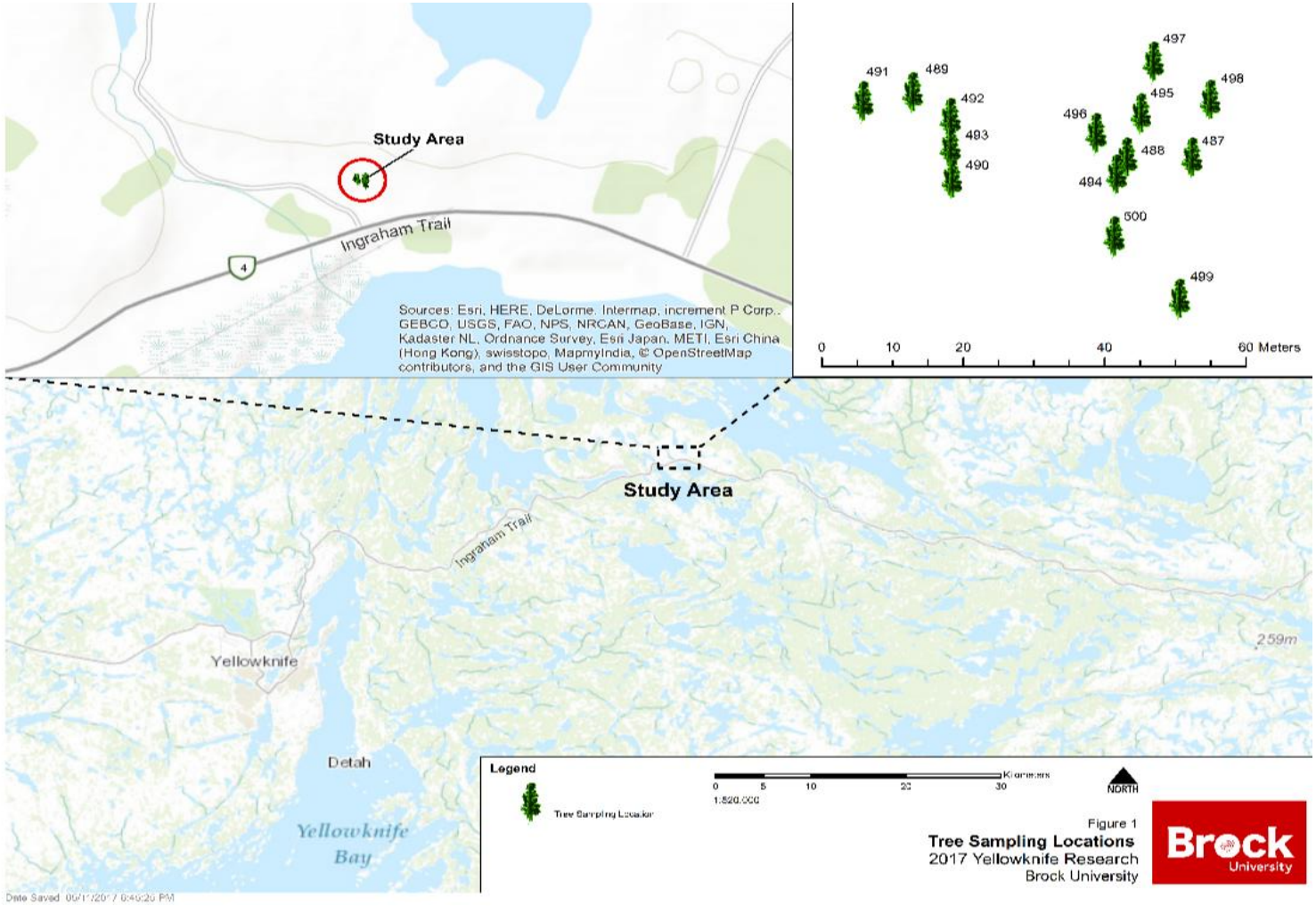

Figure 3.1. Map of the surrounding Yellowknife area and the study site location for "Treeville," northeast of Yellowknife (62˚33.425 N, 114˚00.660W). Treeville is within the northern portion of the Canadian boreal forest and within the Great Slave Lowland Taiga Shield High Boreal Ecological Region.

Table 3.2. Diameter at breast height (DBH), height, coordinates, and elevation of selected trees at the Treeville study site.

Tree #	DBH (cm)	Height (m)	Latitude (˚N)	Longitude (˚W)	Elevation (m)	Age (2016)
488	17.5	8.0	62.557082	-114.010988	226.66	153
489	15.3	6.0	62.557125	-114.01126	222.97	257
490	15.6	3.4	62.557068	-114.01121	223.06	270
491	16.2	4.0	62.557119	-114.011323	222.97	247
492	19.4	6.3	62.557108	-114.011212	221.77	136
493	15.6	4.3	62.557089	-114.011212	222.91	204
494	16.1	6.0	62.557071	-114.011001	222.68	122
495	15.3	4.7	62.557111	-114.01097	225.69	146
496	15.3	5.5	62.557098	-114.011027	221.96	253
497	13.4	5.0	62.557145	-114.010954	219.60	164
498	20.7	5.7	62.55712	-114.010882	223.07	151
499	18.2	4.7	62.556989	-114.010921	222.62	182
500	17.2	5.0	62.55703	-114.011004	223.24	238

3.2.2 Climate

In general, the Yellowknife region experiences short, cool, and dry summers and long, cold winters (Figure 3.2; Larsen, 1980). Highest annual precipitation levels are expected between the months of July and September, with 36% of annual precipitation occurring during the summer months. The month of July is normally the wettest, receiving an average of 40.8 mm of precipitation (Figure 3; Environment Canada, 2018). Highest temperatures typically occur in July, with a daily average of 17ºC, and coldest temperatures occur in January, with a daily average of -25.6ºC. (Government of Canada, 2018). On average, the growing season is expected to begin in May and as temperatures cool in September. Climate normals in the Yellowknife region suggest monthly averages of 30-49 cm and 157.6 cm of annual snow coverage, with snowfall beginning in early October and ending in mid-April (Government of Canada, 2018).

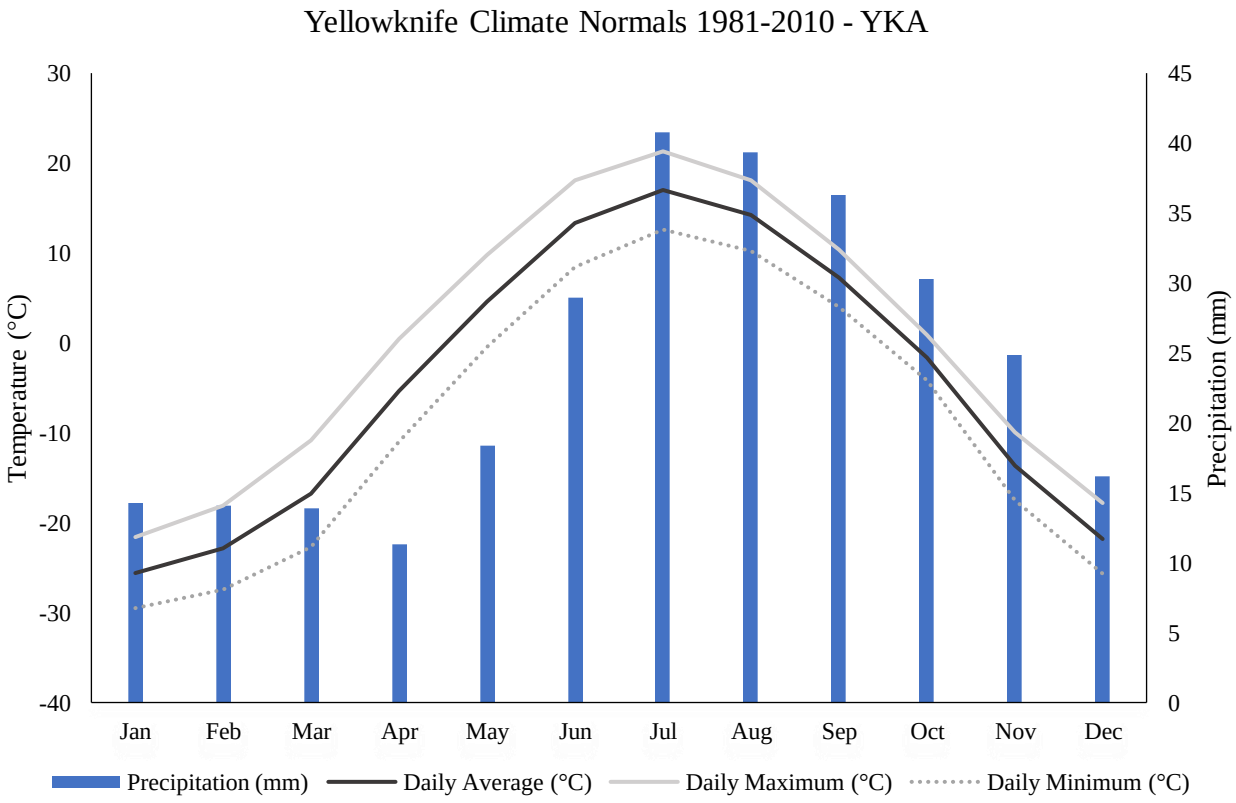

Figure 3.2. Yellowknife monthly climate averages (1981 – 2010). Lines represent daily maximum, minimum, and average temperature (˚C) and vertical bars illustrate monthly average precipitation (mm) as recorded at the Yellowknife A (YKA). (Government of Canada, 2018).

Regional weather data was obtained from the Yellowknife A (YKA) weather station located in Yellowknife (Figure 3.3; Environment Canada, 2018). At each station, daily maximum, minimum, and average temperatures (˚C) and total precipitation (mm) was used to evaluate 2017 seasonal weather.

Highest temperatures were observed in July from July 8 (DOY 189) to August 12 (DOY 224). The conditions in 2017 were comparable to 30-year climate normals for the region (Figure 3.3). YKA recorded an average seasonal temperature of 13.6˚C, with a maximum of 23.3˚C and minimum of 1.7˚C. Precipitation was highest (~14 to 30 mm) during the month of August, during the period from August 17 (DOY 229) to August 22 (DOY 234). There was also a significant peak (~12 mm) in late June, DOY period 184 to 186 (Figure 3.3).

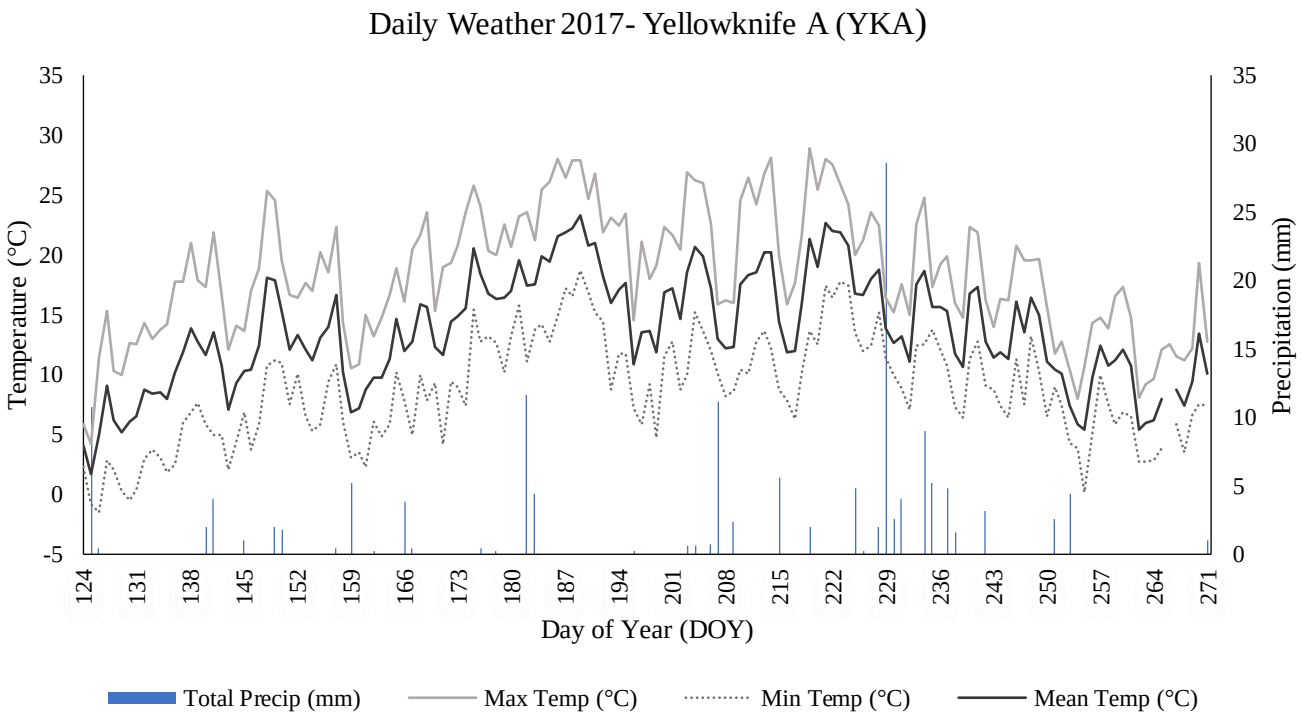

Figure 3.3. Yellowknife A (YKA) mean daily values for average, maximum, and minimum air temperature (°C), and daily total precipitation (mm) for DOY 124 to 271 (May-September 2017) (Environment Canada, 2018).

Site conditions at Treeville were evaluated to assess potential impacts between specific trees growth responses to weather. Soils at the base of the studied trees have an average thickness of 8.8 cm, which is typical of jack pine habitat (Rudolph and Laidly, 1990; Farrar, 1995; De Groot et al., 2004). Nearest neighbor measurements, which indicate the spatial distribution of the mature jack pine trees across the site, indicate the average distance between the studied trees at the study site was 2.6 m; the largest distance between a tree and its nearest neighbor was 4m and the smallest was 0.8m. The average DBH of trees across the Treeville study site was 13.1cm, slightly lower than the selected trees examined in this study (16.34 cm).

3.3 Methodologies

3.3.1 Microcores – Wood anatomy

In 2017, xylogenesis was monitored using microcores, generating a weekly chronology of seasonal dynamics of the progression of xylem cell differentiation and wood formation of jack pine (Figure 3.4 and Figure 3.5). Microcores are small wood cores about 1.5–2.25 mm in diameter and 15 mm long. Microcores are extracted from the outermost portion of the tree stem using a trephor tool (Figure 2.8; Rossi et al., 2006a). The hollow end of the trephor tool is placed flat on the tree stem and hammered in using a rubber mallet (Figure 3.4). Cores collected include the bark, cambium, and the last few rings formed. Weekly microcores were extracted to assess the onset and termination of xylem activity and characterize the timing of the subsequent xylogenetic phases over the growing season (Rossi et al., 2006b). Cores were collected on May 5 continuing collection weekly till September 12, 2017. Microcore samples were collected 30 cm upwards from where the dendrometer placement on the tree stem, usually placed at breast height, and follow an angular upward sampling design from left to right across the tree stem (Figure 3.5; Stangler et al., 2015). Cores are taken 2.5 cm apart and rows are separated by 10 cm distance to reduce cambial disruption

from the extraction process (Stangler et al., 2015). Following extraction, microcores are placed into a 3:1 ratio of acetic acid and ethanol to eliminate drying and destruction of cell walls (Wegner et al., 2013). Cores remained in this mixture for 24 to 48 hours and are then transferred into an ethanol only solution. Cores can be stored in the ethanol solution for an extended period if cores remain covered (Wegner et al., 2013). At the Treeville site, 13 jack pine trees were selected to be sampled and monitored throughout the 2017 growing season using dendrometer and microcore sampling techniques.

Figure 3.4. Microcore sampling using trephor tool and rubber mallet at Treeville Site (Image: Dana Harris, 2016).

Figure 3.5. Microcore sampling design (a) following weekly sampling direction (black arrows) and automatic point dendrometer placement (b) on TV499 at Treeville site (Image: Dana Harris, 2018).

Microcores were processed for cell counts using the STRESS methodology developed by Wegner et al. (2013). Cores were mounted to a wooden microcore holder using a clear epoxy glue (LePage clear 100% glue) and transverse thin sections were cut from the cores using a microtome (Gartner & Nievergelt, 2010; Wegner et al., 2013). Non-Newtonian fluid (a mixture of water, starch, and glycerol) was applied to the exposed microcore surface prior to cutting to reduce the tearing and compressing of cell walls (Schnieder et al., 2013). The thin sections of the microcores are prepared for mounting on standard microscope slides by rinsing the non-Newtonian fluid from the cells using distilled water. After rinsing the non-Newtonian fluid from the cells, the thin sections are rinsed with progressively increasing concentrations of ethanol (75%, 95%, 100%), and finally Histo-clear, a clearing agent used to improve clarity of stained samples (Figure 3.8; Gartner & Schweingruber, 2013; Wegner et al., 2013; Tardif & Conciatori, 2015). After ensuring the thin sections were well rinsed and dehydrated, the thin sections are stained using a 1:1 ratio of safranin and astrablue. The staining process is used to distinguish wood anatomical features and phases of tracheid development that can be seen in the samples (Figure 3.8; Rossi et al., 2006b). Non-lignified structures (phloem, cambium, and developing and enlarging xylem) are stained blue with astrablue and lignified material (mature xylem) is stained pink with safranin (Figure 3.8; Tardif & Conciatori, 2015). Following the final rinsing of the stained microcore thin sections, thin sections are permanently fixed under a slide cover to the microscope slide using Canada Balsam. Cell counts for xylem cells in the distinct phases of xylogenesis were performed under the microscope for each sample week throughout the growing season. Figure 3.7 depicts the progression through the growing season for a single tree (TV493).

3.3.1.1 Xylogenesis - cell counts

To capture growth, cells in each phase of xylogenesis (Figure 3.9) cambial (C), developing and enlarging (E), wall-thickening (W), and mature (M) were counted from weekly microcore thin sections along three radial files (Figure 3.6; Figure 3.10). Images were taken to perform counts and assess weekly changes in cellular development (Figure 3.7). Cambial phase included cambium and phloem cells, defined by their radially flattened cell morphology (Deslauriers et al., 2003; Rathgeber et al., 2016). The developing and enlarging (E) phase includes newly produced xylem cells differentiated from initial cambial and mother xylem cells. This phase is characterized by cells with large lumen areas and thin primary walls (Deslauriers et al., 2003; Rathgeber et al., 2016; De Micco et al., 2019). Cells in the C and E phases are stained fully blue by safranin. The wall-thickening (W) phase is characterized by cell walls beginning to thicken as secondary walls are forming, as seen under polarized light, and lignin is added to the cell wall as indicated by the slight pink staining and slight blue lumen area (Figure 3.9; Deslauriers et al., 2003; Rossi et al., 2003; Ziaco et al., 2018). Mature cells are fully lignified, staining completely pink with safranin and an empty lumen. Differentiation between mature earlywood and mature latewood cells is determined by evaluating changes in cell wall thickness with latewood cells having thicker more robust walls and smaller lumen area (Rossi et al., 2003; Rathgeber et al., 2016).

To evaluate cell development for this study site, total mature cell counts were performed for 2017 back to 2007 on the microcore samples. This was performed along a single radial file for 7 trees at the study site. This group included trees 489, 490, 491, 492, 493, 494, 495. This group was chosen as they were the clearest samples from the 2017 season of microcore samples. Corresponding weather data for each year was collected from the Government of Canada historical weather database (Canada, 2023). Monthly averages for maximum, minimum and mean

temperatures (ºC) and monthly totals for rain (mm), snow (cm) and total precipitation (mm) were calculated.

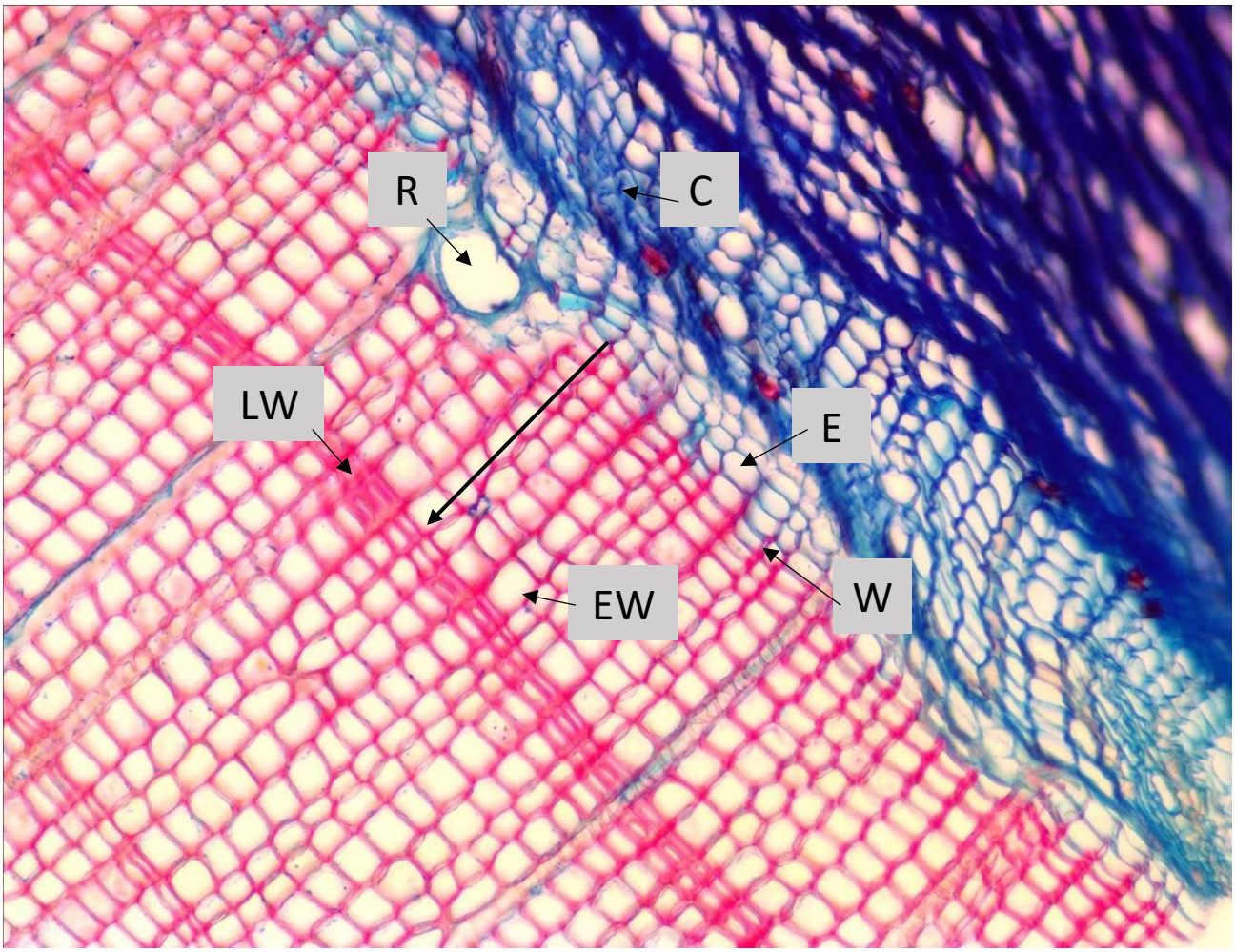

Figure 3.6. Microscope image of developing cells in *Pinus banksiana* from Treeville 2017 – TV493. Non-lignified structures (phloem, cambium, developing and enlarging xylem) are stained blue with astrablue. Lignified material (mature xylem) are stained pink with safranin. EW: earlywood; LW: latewood; E: developing and enlarging cells; W: wall-thickening cell; R: resin duct; C: cambium. Bolded black line: single radial file in direction of cell development (Image: Dana Harris, 2018).

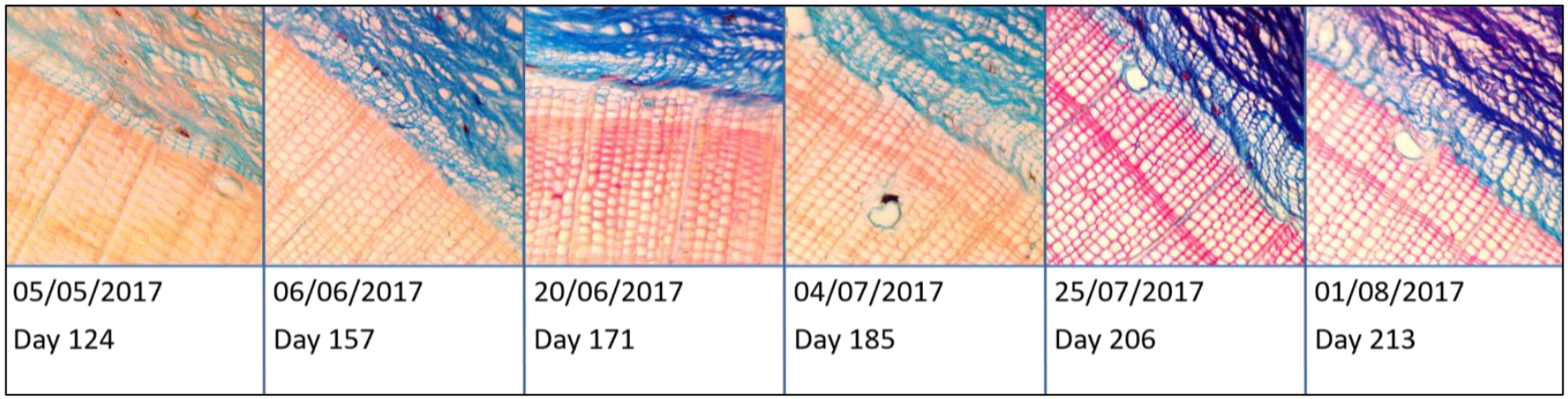

Figure 3.7. Images from seasonal chronology of cell development using microcoring technique for a single tree (TV493) throughout the studied growing season.

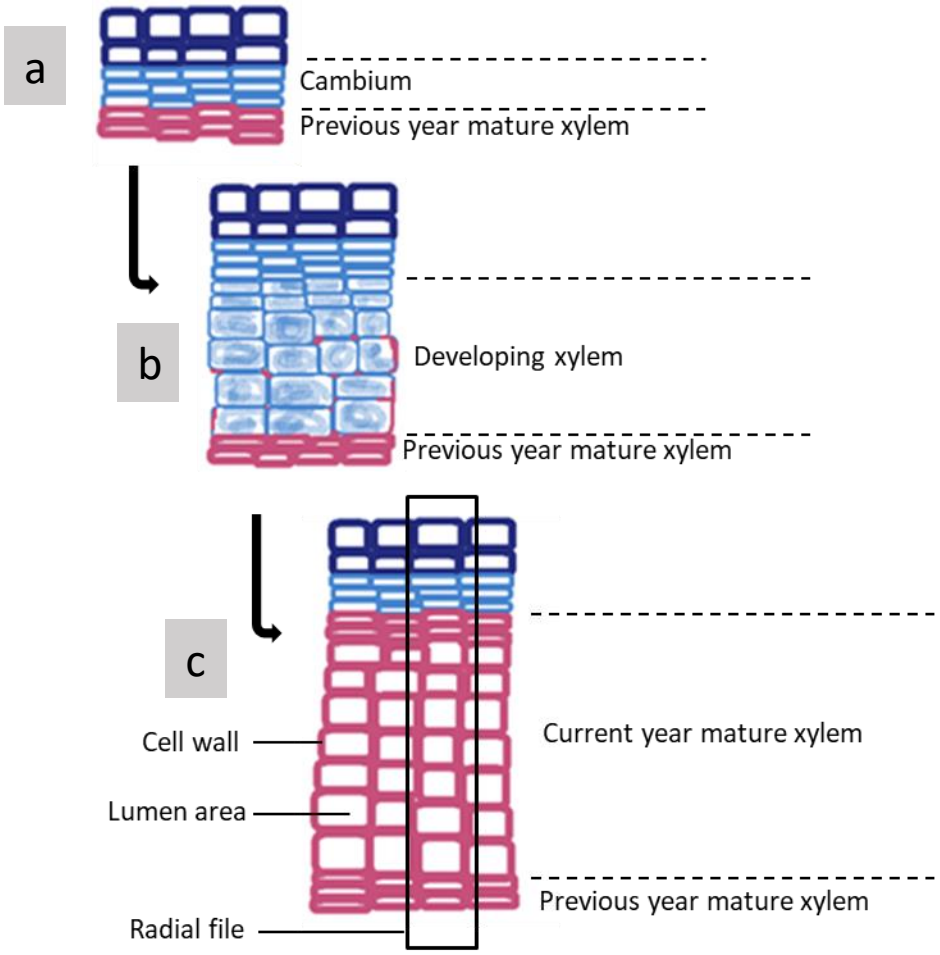

Figure 3.8. Anatomical structures of wood development. Dark blue: cambium; Light blue: developing xylem tracheid; Partial red: lignification of xylem tracheid; Complete red: fully lignified mature xylem tracheid. (a) cambial dormancy; (b) beginning of xylem cell development and partial lignification (cell wall-thickening); and (c) end of seasonal growth and annual ring formation.

3.3.1.2 GAM and SCAM functions

A Generalized Additive Model (GAM) and a Shape Constrained Additive Model (SCAM) were selected to analyze timing, duration, and peak of cell development during each phase of xylogenesis: Cambial (C); Enlarging (E); Wall-thickening (W); Mature (M). These models were selected as they are data driven and allow for more flexibility in the presented data in contrast to more rigid model types (e.g., Gompertz function). From the modelled data, daily predicted cell numbers can be estimated for each phase of xylogenesis based on the raw weekly cell counts obtained from the microcores. For this study, a GAM was applied to the C, E, and W phases and a SCAM was applied to the M phase (Wood, 2006; Pya & Wood, 2015).

GAM functions are a semi-parametric extension of Generalized Linear Model (GLM) in which the linear predictor uses a sum of smooth functions of the predictor variables. The use of GAM functions allows non-linearities in the data to be captured as the model is driven by the data and allowing the relationship of the response variables and explanatory variables to be determined by the data itself (Cuny et al., 2013). The SCAM dictates that the response variables do not predict below previous predictions. This was chosen to better visualize and predict mature cell development based on the assumption that no mature cell which has previously developed will be lost, thus continual production is captured more accurately using a SCAM. For this research, weekly cell counts in each phase of xylogenesis are expressed as a function of the DOY. Both the GAM and SCAM were applied to the cell count data using the *R* statistical platform and the mgcv package (version 1.8; Wood, 2006; Cuny et al., 2013; Pya & Wood, 2015).

Outputs from the model indicate peak timing of cell development in each phase of xylogenesis and indicate the length of time spent in each phase, calculated as cell residence time.

To calculate cell residence duration, four functions were defined for the cumulative number of cells in each respective development phase.

$$S_{ETM}(t) = n_E(t) + n_T(t) + n_M(t) \quad (3.1)$$

$$S_{TM}(t) = n_T(t) + n_M(t) \quad (3.2)$$

$$S_M(t) = n_M(t) \quad (3.3)$$

Where,

n_E = GAM prediction of the number of cells in the enlarging phase;
n_T = GAM prediction of the number of cells in the wall-thickening phase;
n_M = SCAM prediction of the number of cells in the mature phase.

3.3.2 Dendrometers – stem radius variation

Automatic point dendrometers (Agricultural Electronics) were installed on 13 trees at the Treeville study site for the 2017 season (Figure 3.9). Sensors were installed using two steel rod fasteners drilled into the tree stem at breast height (Figure 3.9; Stangler et al., 2016). Sensors are connected to a data logger via a linear variable differential transformer (LVDT) cable connector and wire system logging linear displacement values of the sensing rod against the stem in micrometers (μm) (Deslauriers et al., 2003). Each logger has a separate connection to the data logger denoted by the logger number and cable code, connection numbers were recorded along with tree identification numbers in field notebook. Each sensor is calibrated after installation to a base line pressure of ~2400 millivolts (mv) exerted on the sensing rod by the tree stem. The pressure is controlled by a constant force cantilever that keeps the automatic sensing rod firmly pressed against the surface of the tree (Figure 3.9). Displacement is fixed to 4 μm over the unadjusted range of 15,000 μm. Movement of the LVDT, due to pressure exerted on the sensing

rod as the tree grows and expands, is translated into electrical signals recording continuous data which is transformed into stem radial displacement. The precision of the dendrometers allows for the monitoring of both non-permanent reversible swelling and shrinking owing to diurnal patterns of water uptake and use as well as permanent irreversible growth experienced throughout the growing season (Deslauriers et al., 2003; Zweifel et al., 2006; Stangler et al., 2016; Ziaco & Biondi, 2018). For this study, measurements of LVDT were taken at 30-minute intervals from May 5 to September 29, 2017 (DOY 125 to 272).

Figure 3.9. Automatic point dendrometer sensor fastened to tree at Treeville study site. (a) steel mounting rod; (b) sensing rod; (c) constant force cantilever; (d) LVDT cable connection. (Image: Dana Harris, 2018).

Data from the dendrometers was downloaded following the site take down in late September 2017. Data from each of the sensors downloaded to the data logger are extracted in an Excel file format and organized to show displacement values by converting LVDT electrical outputs to millivolts and subtracting initial calibration pressure (~2400 mv). Displacement outputs were estimated and plotted in *R* using the *DendrometeR* package (version 1.0; Van Der Maaten et al., 2016) to show daily statistics and seasonal dynamics of stem swelling as well as evaluate the timing and duration of the circadian cycle of jack pine.

3.3.2.1 Analysis approaches

Dendrometers sensor outputs generated continuous data, measured every 30-minutes, that are used to illustrate seasonal growth dynamics of jack pine in response to weather (Deslauriers et al., 2003; Deslauriers et al., 2011; van der Maaten et al., 2016). Time series analysis visualizes seasonal patterns and daily statistics for stem variation phases. Trends including the reversible stem variations in response to water movements are removed from dendrometer data using *DendrometeR* package which adapted the original Deslauriers et al. (2011) SAS procedure (van der Maaten et al., 2016). The *DendrometeR* package was used to run a *stem cycle approach*, which considers the daily patterns of stem fluctuations, shrinking and expanding in response to growth mechanisms and weather (Figure 3.10). Dendrometer data defined the following phases for each sensor:

Phase 1 – The contraction phase, which is the period between morning maximum and daily minimum values;

Phase 2 – The expansion phase which is the full period from the daily minimum value to the following morning maximum value;

Phase 3 – Stem Radius Increment (SRI) phase is the part of the expansion phase from when the radius of the stem exceeds the recorded morning maximum until the following maximum (the difference between maximum of expansion and the end of third phase). When the SRI phase occurs, cycles are represented as ΔR+ (μm), R being the radius. When the previous day maximum is not reached the SRI phase is not recorded, and cycles are represented as ΔR- (μm) (Figure 3.12). The stem radius increment is an important measure typically used to estimate tree growth; and

Phase 4 – The full circadian cycle, which includes the three previous phases and lasts an estimated 24 hours (Deslauriers et al., 2007).

The *daily cycle approach* assumes cycles at 24 h, whereas the *stem cycle approach* allows for the measured circadian cycle to exceed the 24 h cycle period. Longer circadian cycles may occur in response to heavy rain events generating a longer expansion phase (Deslauriers et al., 2003). It is also noted that higher magnitudes may be observed during precipitation events and amplified in response to higher daily temperatures and sunshine (King et al., 2013). Cycles longer than 28 hours are categorized as long (LG) cycles, and cycles below the 28-hour range are categorized as regular (REG) cycles. The frequencies of LG and REG cycles observed throughout the season also provide further insights on the characteristics of growth and stem radius fluctuations during the growing season. The *DendrometeR* package produces daily statistics for maximum, minimum, magnitude, duration, and timing for each phase within each circadian cycle defined by either *daily* or *stem cycle approaches* (Van Der Maaten et al., 2016). Missing values in dendrometer data sets are filled with the use the functions fill_gaps in DendrometeR package, which uses an ARIMA model for short duration missing data not beyond a couple of hours. During the 2017 study season data was checked weekly for errors in sensor data. Data with significant gaps were excluded in the analysis of seasonal trends. Using the *DendrometeR* package, phases were

defined and the seasonal patterns for each tree were calculated for the 2017 season. The seasonal data indicates phase timings throughout the studied period of growth, observed amplitude, and the frequencies of ΔR+ and ΔR- cycles throughout the predicted growing season from May to September 2017. Information surrounding the cycle timing, and frequencies of ΔR+ and ΔR- and LG and REG cycles allow further characterization of the growing season on an intra-annual basis.

To compare the results from both datasets and observe similarities in the timings observed for critical growth changes (e.g., wall-thickening phase) a homogeneity test was run using Microsoft excel (Microsoft Corporation, 2018). The homogeneity test was used to test the homogeneity of a time series and identify when a shift occurs. The timing of this change in the dendrometer signals was used to compare with the timing of the onset of the wall-thickening phase collected from the microcores.

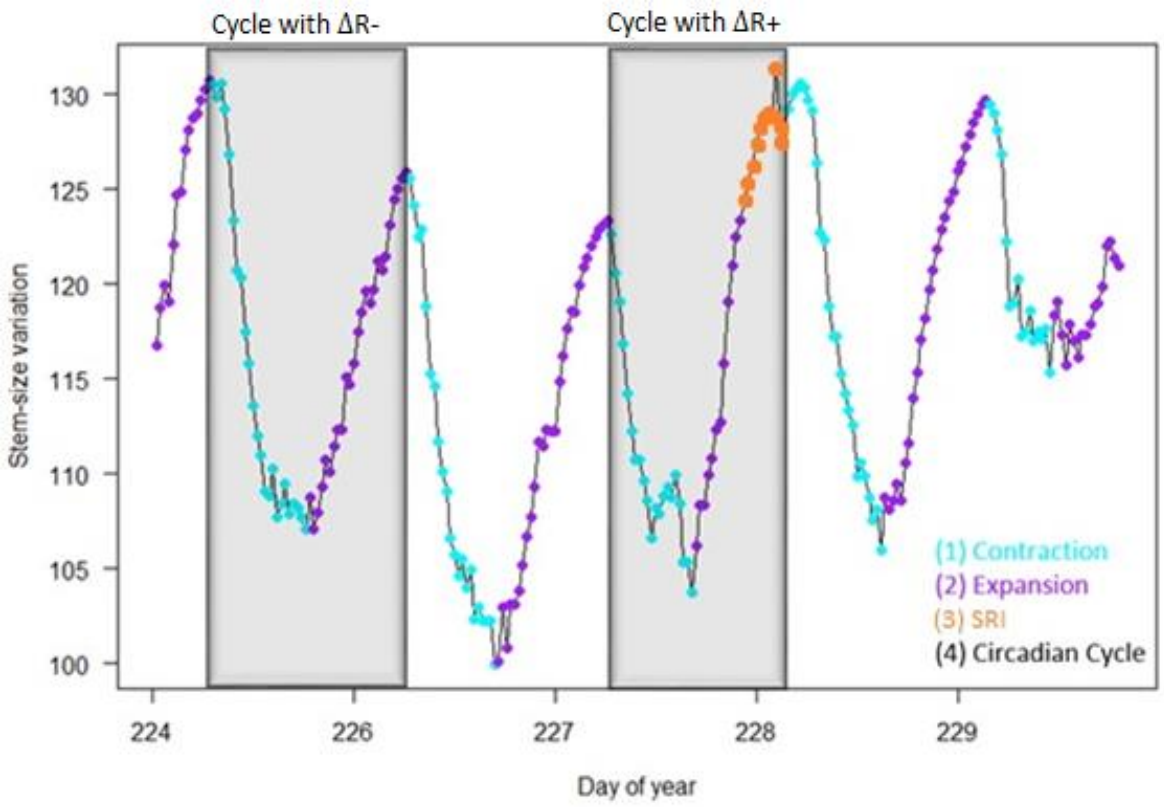

Figure 3.10. Dendrometer cycle variation using the stem cycle approach. ΔR+ and ΔR- at Treeville for DOY 224 to 230, August 12 to 18, 2017. Phases as defined as: Phase 1: contraction phase (blue); Phase 2: expansion phase (purple), Phase 3: Stem radial expansion phase (orange). Phase 4: Circadian Cycle (grey boxes) comprising Phase 1, Phase 2, and Phase 3 (in ΔR+ cycles).

CHAPTER FOUR:

RESULTS

4.1 Weather and regional climate – Yellowknife 2017

To define the 2017 growing season, weather data was collected from the Yellowknife A (YKA) Government of Canada weather station and are displayed in Figure 4.1. In general, the warmest temperatures in 2017 were observed July 1st – August 28th (DOY 182 to 240) and ranged between 25-28°C. In 2017, the coldest temperatures occurred in March, with a minimum temperature of -39.7°C on March 9th (DOY 68). The most precipitation was recorded in July, with the highest recorded value occurring on August 19th (DOY 231) at 28.6 mm.

For the estimated growing season (May to September 2017) the maximum temperature (28.9°C) was recorded on August 9th (DOY 221) and the minimum temperature (-7.4°C) on May 2nd (DOY 122) (Figure 4.1). Maximum daily total precipitation occurred on August 19th (DOY 231) with 28.6 mm (Figure 4.1).

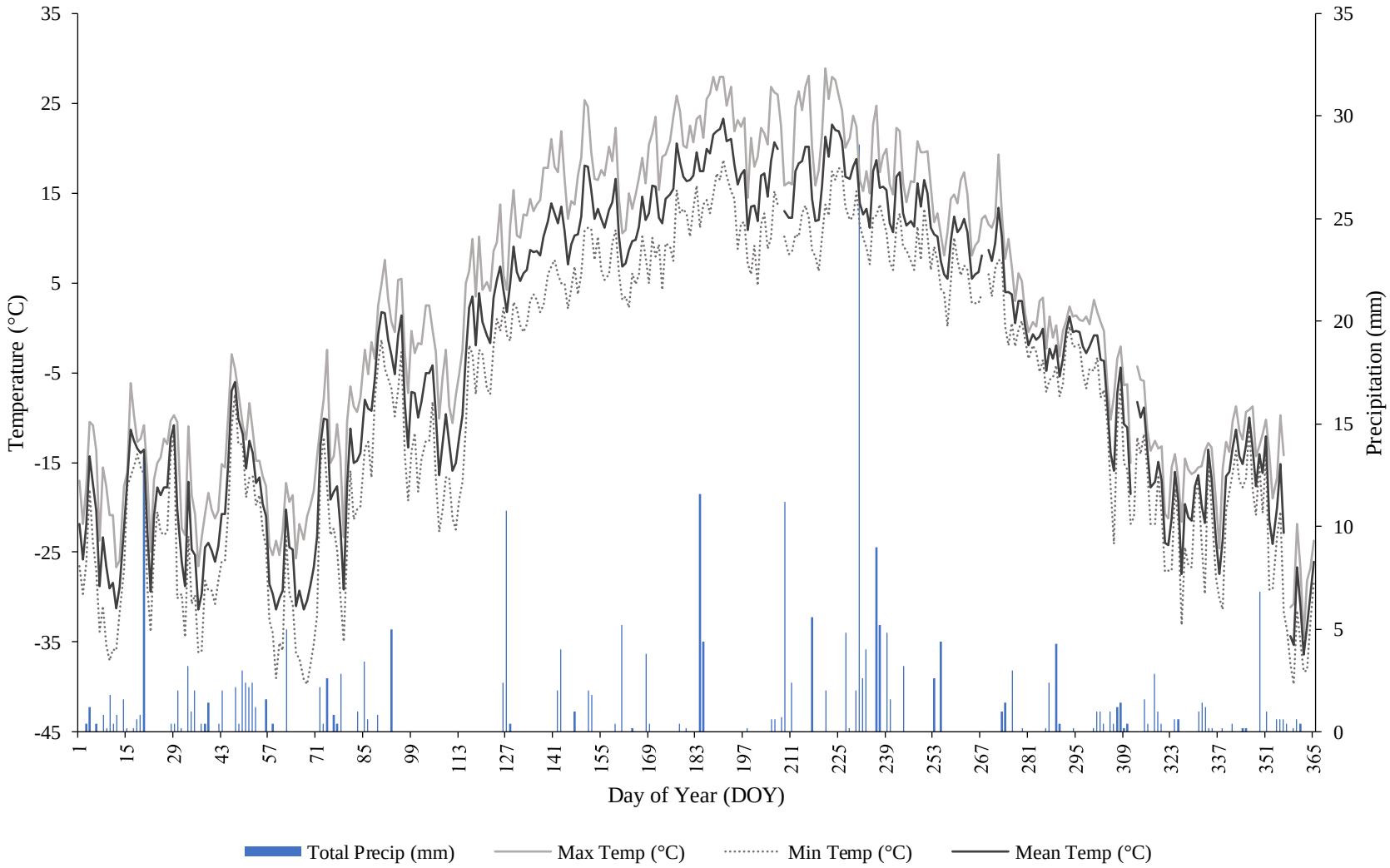

Figure 4.1. 2017 Daily weather data from the Yellowknife A climate station (YKA). Vertical blue bars represent total daily precipitation and grey lines plot maximum, minimum, and mean daily temperatures.

In general, the 2017 weather patterns were not outside of normal conditions for the Yellowknife area (Figure 4.2). During 2007-2017 the highest seasonal temperatures occurred from May 24th to September 11th (DOY 144-254) (Figure 4.2), and the highest total daily precipitation occurred June 20th to September 28th (DOY 171-271) (Figure 4.3).

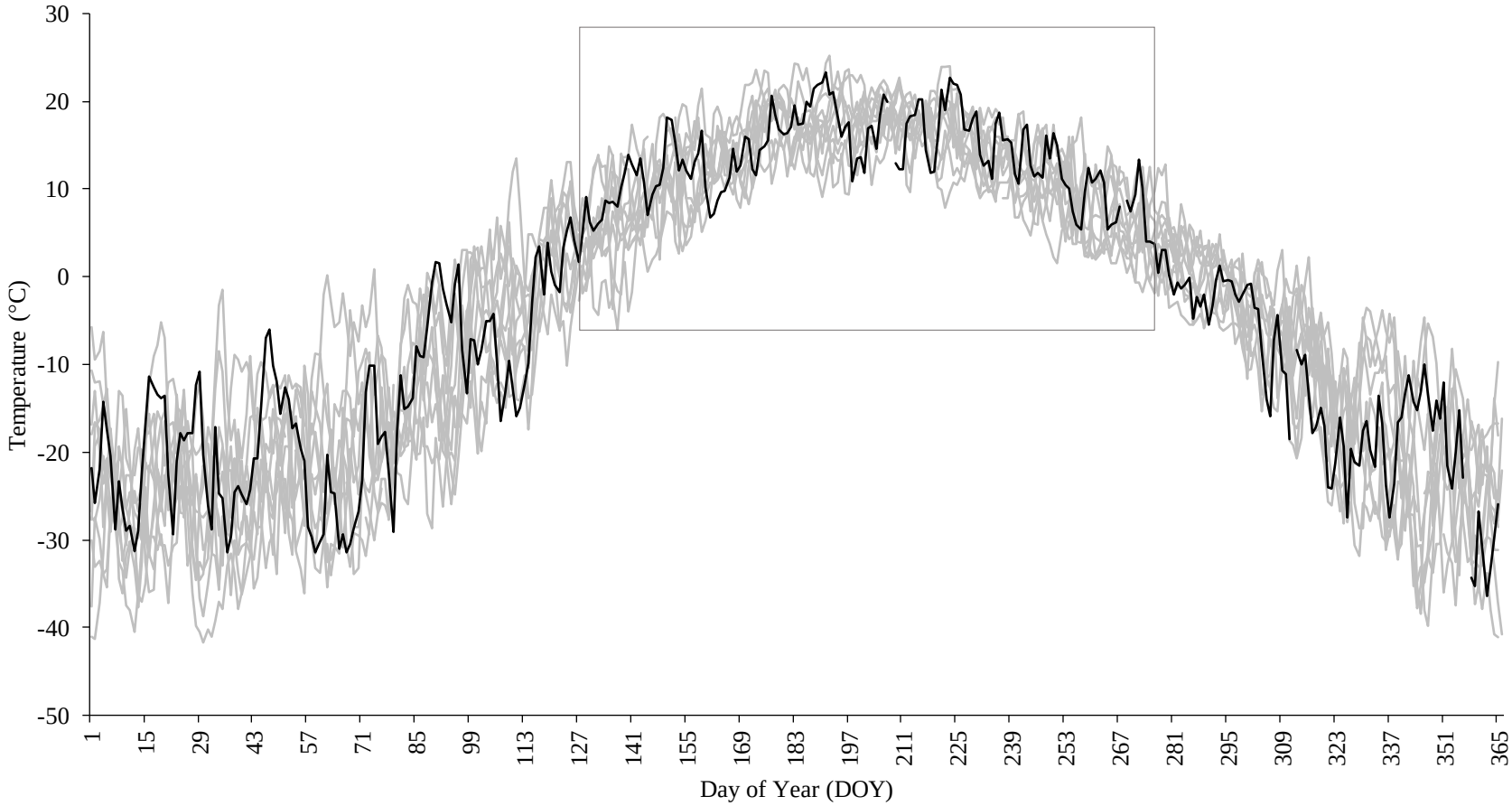

Figure 4.2. Annual Daily Mean Temperatures 2007-2017 Yellowknife A (YKA). Grey lines 2007-2016, bolded black line is 2017 weather. Grey box represents estimated annual growing season.

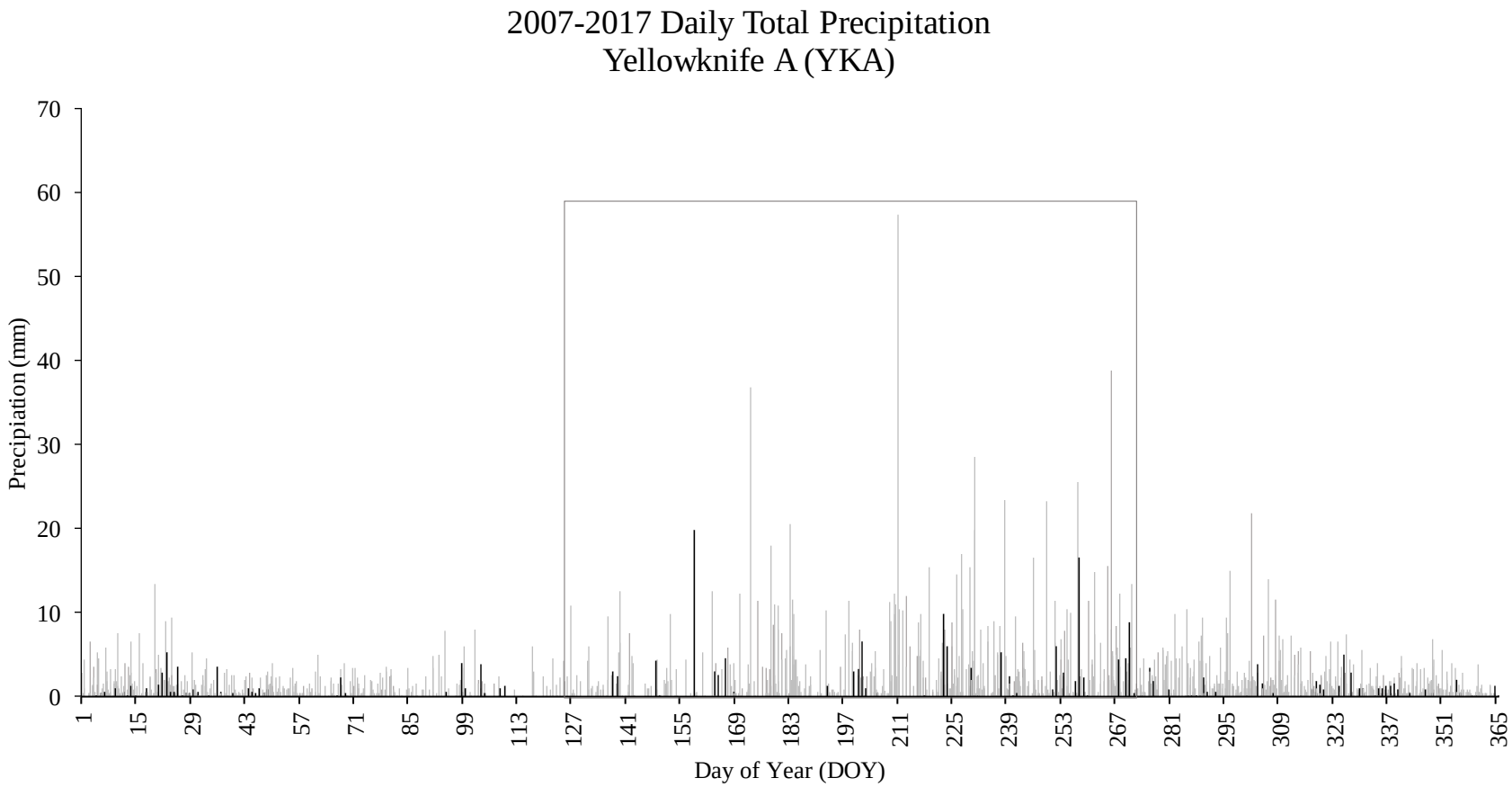

Figure 4.3. Annual Daily total precipitation 2007-2017 Yellowknife A (YKA). Previous years (2007-2016) data in grey, 2017 data in black. Grey box represents estimated annual growing season.

4.2 Microcore data

4.2.1 Timing of cell development

Average cell development for Treeville in 2017 indicated that on the first sampling date on May 5 (DOY 125) the cambial zone varied from three to seven cells, indicating the initial onset of stem rehydration and first stages of new cell production. From this observation, the timing range of cell development onset for the Treeville site in 2017 is estimated to be late May to early June. Cell counts identified first enlarging (E) cells on the May 30 (DOY 143) sampling date when daily average mean temperature was ~11ºC for the week prior to the sampling date. A site wide average of 1.1 enlarging cells was observed on the June 6 (DOY 157) sampling date when average daily temperatures ranged between 10-16°C. The first observed wall-thickening (W) was observed on the June 13 (DOY 164) sampling date, while the site wide average of 1.4 W cells was observed on the June 20 (DOY 171) sampling date. The first mature cells were observed on June 20 (DOY 171) with a site wide average of 1.1 cells (Figure 4.4). The dates marked at "onset" of phases were when site wide averages were >1 complete cell. These dates for 2017 are recorded as E: June 6 (DOY 157), W: June 20 (DOY 171), and M: June 20 (DOY 171). Mid- to late-June daily average air temperatures hovered between minimums of 5 to 10°C and daily maximum of 16 to 23°C. The transition from earlywood to latewood cell formation was observed on July 11th (DOY 192) (Figure 4.5), when daily mean air temperature was 20.8°C. Site wide average seasonal cell mature development estimated 13 mature woody cells (± 6) were produced at the end of ring formation for trees sampled in 2017. Jack pine cell growth in the 2017 season lasted an estimated 81 days from the initial enlarging xylem cell to the final sampling date on September 12th (DOY 255). Appendix Figure 1 & 2 indicates the sample depth showing the percentage (%) of missing samples due to sample structural consistency (i.e., excessive ripping and shifting of sample producing

blurry images) and sample size per sampling date. Both the raw data cell counts, and model calculations indicate that the finite end to cell production may not have been captured in 2017 (Figure 4.7).

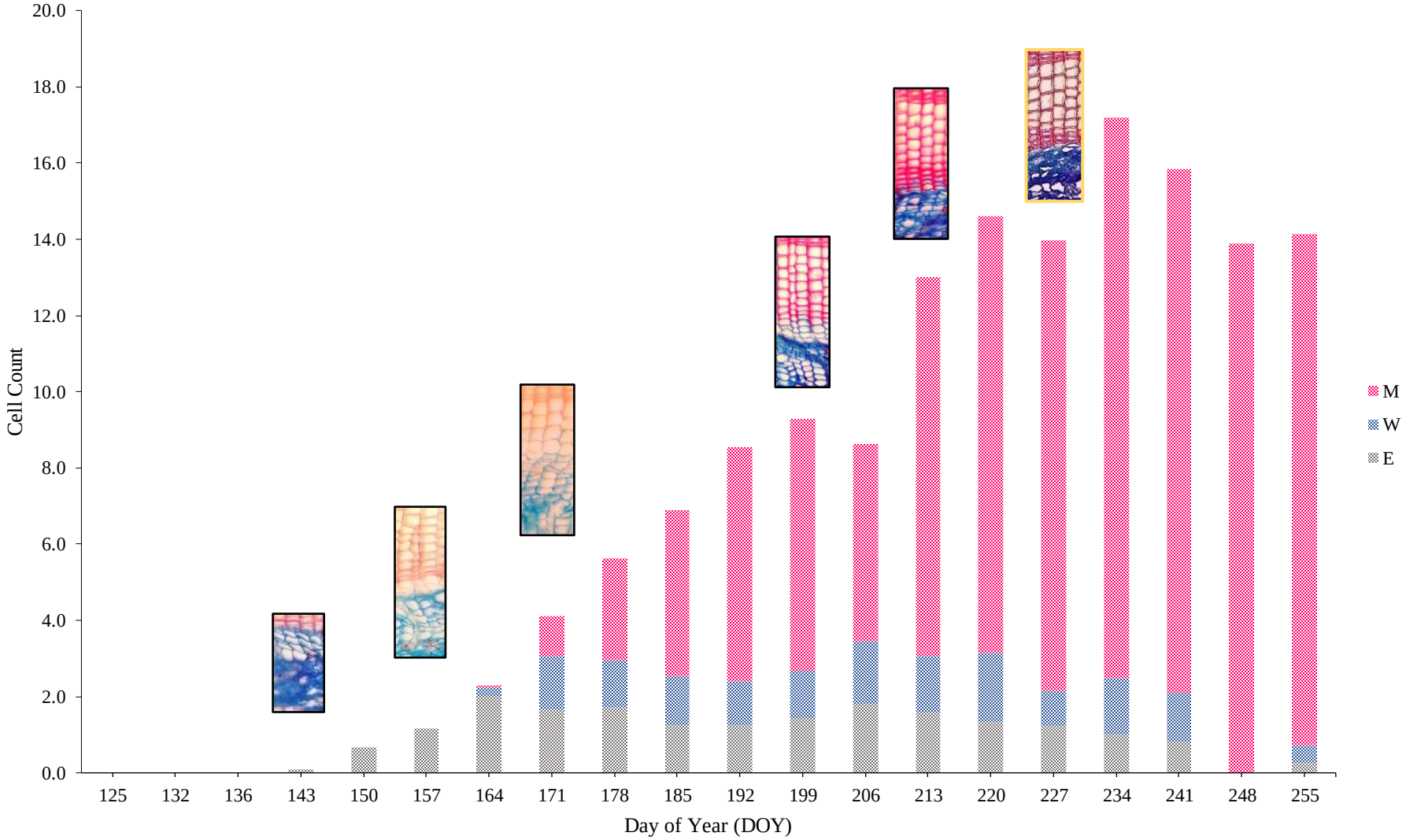

Figure 4.4. Site average weekly cell count in phases of xylogenesis for enlarging (E), wall-thickening (W), and mature (M) phases. Images from TV493 with black border, and TV500 with yellow border.

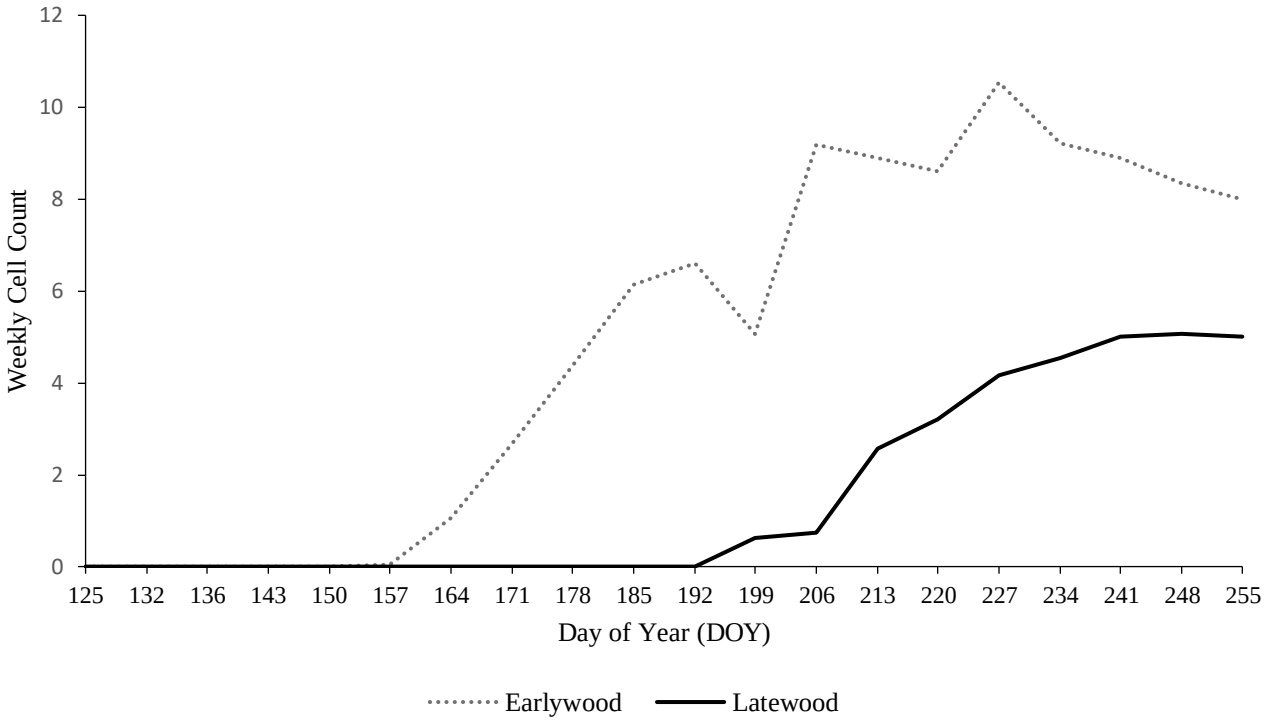

Figure 4.5. Average weekly raw cell counts for mature tracheid cell production in earlywood and latewood transitions for Treeville 2017.

Daily cell counts, calculated from the weekly microcore samples, were modelled using a combination of a generalized additive model (GAM) for C, E, and W phases and a shape constrained additive model (SCAM) for M phase, (Figure 4.6a-f). Calculations using the modeled counts indicate the wood formation dynamics and patterns of cell production throughout the 2017 growing season and the seasonal changes in the number of cells observed in the phases of xylogenesis. The number of enlarging cells (E) followed a bimodal curve, with an initial peak of average cell number on June 14 (DOY 165) with a site average of 1.7 cells in the E phase. The number of enlarging cells peaked for a second time on July 24 (DOY 205), with a site average of 1.6 cells in the E phase (Figure 4.6a; Figure 4.6d). In contrast, cell count in the wall-thickening (W) phase followed a right skewed curve where more cells were observed later in the growing season, peaking August 8 (DOY 220). The wall-thickening cells experienced rapid change in production late in June, during the period June 14 – 24 (DOY 165-175), followed by a steady rate until August 13 (DOY 225) (Figure 4.6b; Figure 4.6e). Mature cell production is estimated from the models to have begun on June 13 (DOY 164). Final samples were collected on September 12 (DOY 255), with a site average model count of a total of 18 mature cells ± 10 cells produced in the 2017 season. (Figure 4.6c; Figure 4.6f). There is a high amount of variability between studied trees for the weekly cell counts collected from the microcore samples (Figure 4.6a-c). This variability is not surprising since counts can be much different between trees based on individual tree productivity. The models are driven by the input data and variability within the dataset is captured within the model responses (Wood, 2006; Pya & Wood, 2015).

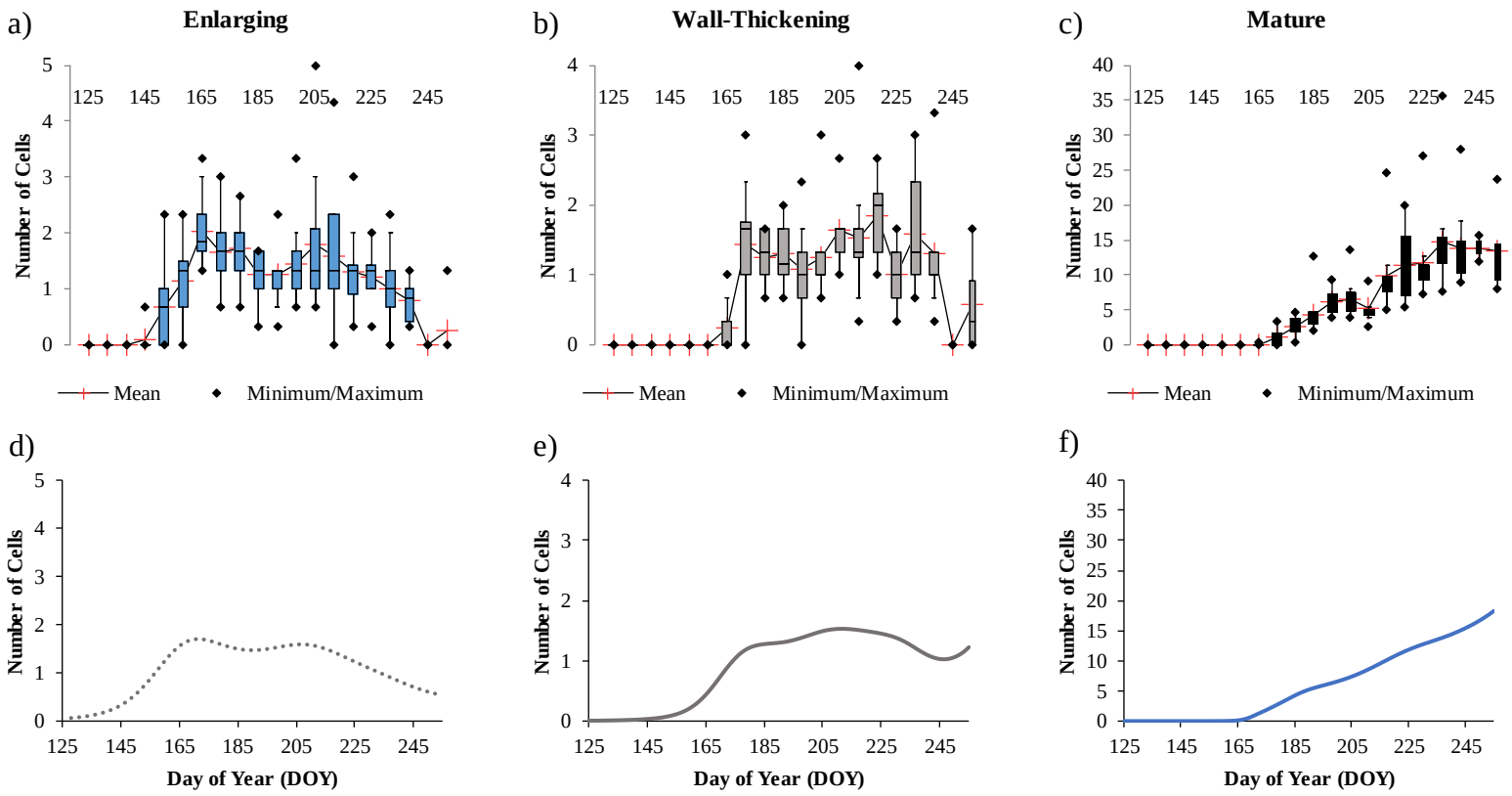

Figure 4.6. Boxplot of the number of cells from weekly sample collected (top) and their model time series using GAM (Enlarging and Wall-Thickening) and SCAM (Mature) (bottom). Box and lines represent the mean values of raw counts from three radial files for each of the 13 *Pinus bankiana* trees sampled at Treeville site in 2017.

4.2.2 Rates of cell development

For Treeville in 2017, the timing of the transition rates occurred closely between the cell phases (Figure 4.7). For enlarging cells (E average), cells had a slow increase from May 6 (DOY 126) till June 11 (DOY 162), when E cell rate per day began to increase and reached a peak in on June 21 (DOY 172), at 0.28 cells per day. Wall-thickening cell (W average) production began on June 4 (DOY 155), with their calculated rate of production peaking the same time as E cells around June 21 (DOY 172) with the same rate of 0.28 cells per day. There was a less dramatic decrease in the wall-thickening cell rate following its peak, remaining around 0.26 cells/day till July 2 (DOY 183). Mature cell production rate (M average) began increasing around mid-June reaching a peak of 0.24 cells per day July 2 (DOY 183). Rates for all phases began to drop on July 4 (DOY 185) and reached the seasonal low on July 14 (DOY 195) with rates for all phases averaging around 0.14 cells per day (E: 0.15 cell/day, W: 0.14 cell/day, M: 0.13 cell/day). Another increase in cell production rates began on July 19 (DOY 200), peaking in early august. E cell production rates peaked again August 2 (DOY 214) at 0.23 cells per day and W cell production rates peaked for a second time August 4 (DOY 216), at 0.24 cells per day. Cell development rates during this second peak were lower than the initial seasonal cell rate peak of 0.28 cells per day. Finally, M cell rates peaked again on August 5 (DOY 217), with 0.24 cells undergoing maturation per day, a similar rate to its initial peak July 2 (DOY 183), at 0.24 cells per day.

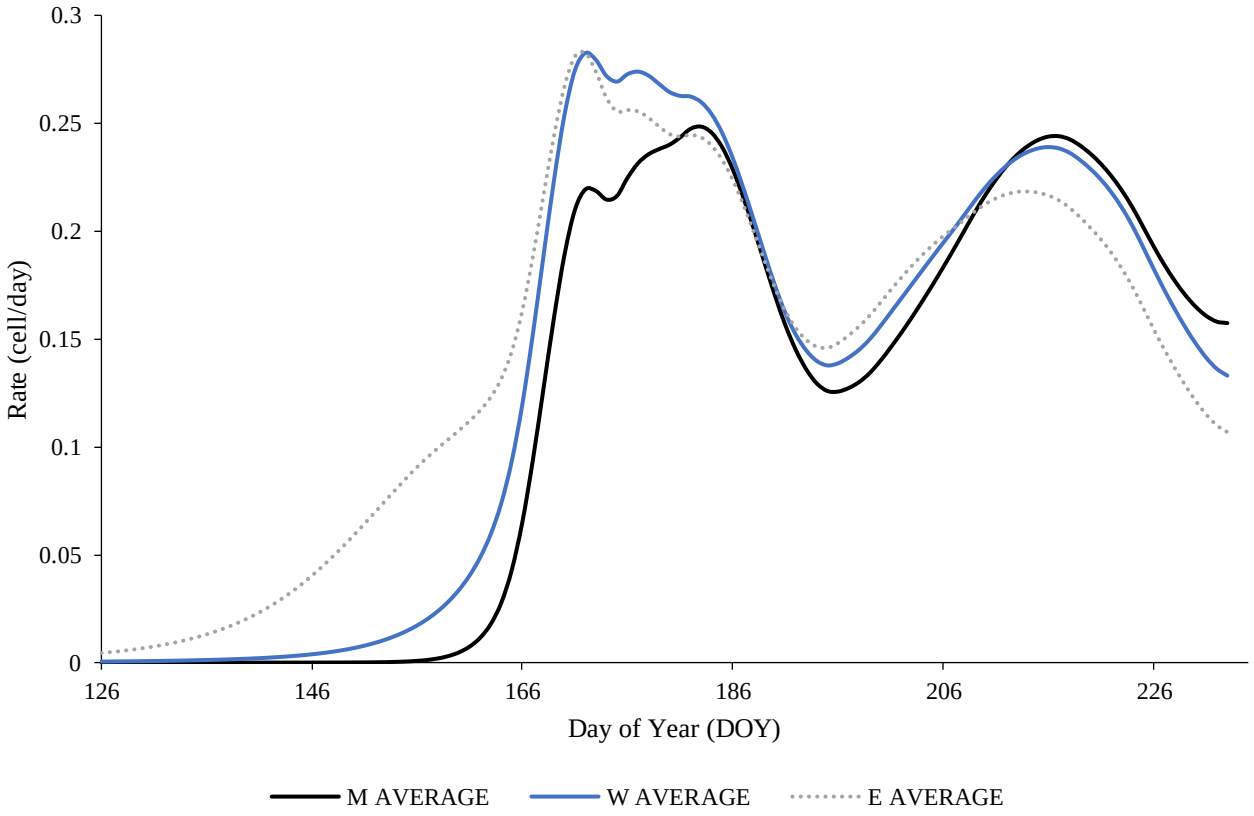

Figure 4.7. Treeville site-wide modelled cell phase transition rates for xylogenesis phases for early May to mid-August 2017 (DOY 126-233). E: entry rate of cells into enlarging phase, W: entry rate of cells into wall-thickening phase, M: entry rate of cells into mature phase.

4.2.3 Multi-year cell count & weather

Cells were counted for TV489, TV490, TV491, TV492, TV493, TV494, TV495 from 2007 to 2017. For this period, an average of 15 mature cells (±3 cells) were counted, with 2014 having the lowest mature cell count (9 cells), and 2010 and 2011 the highest mature cell count (19 cells each). To look at the influence of weather on mature cell development, individual trees were divided into two groups based on their total mature cell counts; high cell count group was established for trees which counted mature cell >15 cells and low cell group was established for mature cell counts <15 cells (Figure 4.8; Table 4.2). The high cell count group consisted of the years 2008, 2009, 2010, 2011, 2013, and 2016. The low cell count group consisted of the years 2007, 2012, 2014, 2015, 2017. The corresponding weather data for the 2007-2012 and 2014-2017 season were obtained from the Yellowknife Airport station. Weather data for 2013 was obtained from the Yellowknife Henderson station, due to lack of consistent data at the Yellowknife Airport station for 2013 (Figure 4.9a-k). The Henderson and Yellowknife Airport Mean daily temperature was highly correlated (r = 0.995), and precipitation was moderately correlated (r = 0.556). Pisaric et al. (2009) observed that June precipitation and growing season length were potential limiting factors of jack pine growth. The 2007 to 2017 monthly averages for mean temperature and total precipitation are presented in Table 4.1. To assess these hypotheses regarding annual cell counts, average total precipitation for June and the number of growing degree days (GDD)(>5^{o}C) were calculated for each corresponding year (Table 4.2). June total precipitation for the period 2007-2017 averaged 26 mm (±17.1 mm) (Table 4.1). Highest June precipitation occurred in 2008 (49.8 mm) and lowest June precipitation occurred in 2012 and 2014 (4.2 mm) (Table 4.2). Above average precipitation years occurred in 2008, 2009, 2010, 2011, 2013 and 2016. Below average June precipitation years occurred in 2007, 2012, 2014, 2015, 2017. Average yearly GDD was 139

days (±8.4 days), with over half the seasons recording higher than average GDD (Table 4.2. Lower than average GDD years occurred in 2007, 2009, 2014, and 2015. The highest number of GDD was recorded in 2012, with 148 days > 5ºC. The lowest count of GDD was recorded in 2009 with 122 days >5ºC. Trends across the 2007-2017 period for cell counts and total June precipitation are demonstrated in Figure 4.10. Correlation coefficients calculated for earlywood (EW), latewood (LW) and total mature cell counts, and total June precipitation indicate a significant positive relationship (Figure 4.11). No significant relationships between earlywood, latewood and total mature cell counts and GDD count was observed (Figure 4.11).

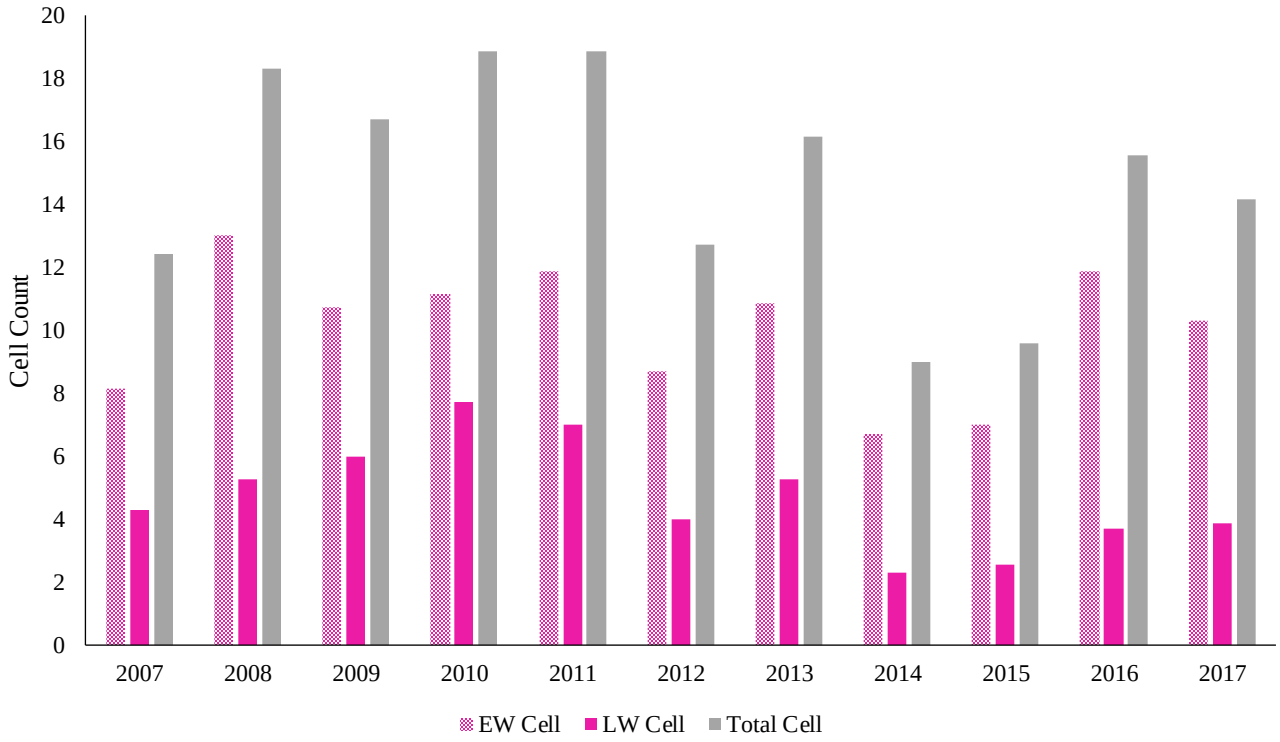

Figure 4.8. Average yearly cell counts for earlywood (EW), latewood (LW), and total cell counts for 2007-2017. Cell counts are for jack pine trees TV489, TV490, TV491, TV492, TV493, TV494, TV495 at the Treeville site.

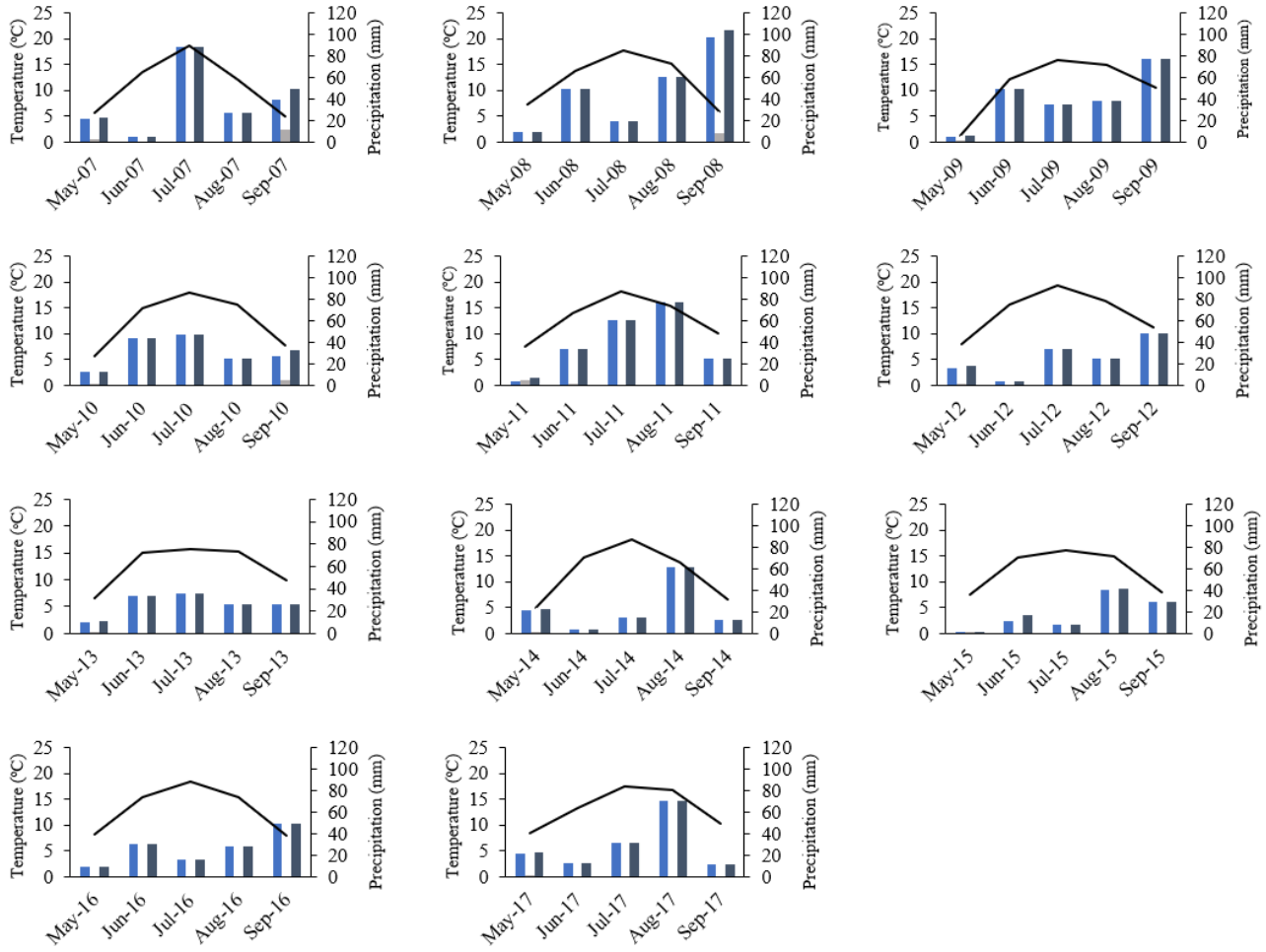

Figure 4.9. 2007-2017 Growing season (May to September) total monthly rain (blue bars), total monthly snow (grey bars), total monthly precipitation (dark blue bar); and monthly average mean temperature (black line). Data from Yellowknife Airport Station (2007-2012 & 2014-2017) and Yellowknife Henderson Station (2013).

Table 4.1 Average monthly mean temperature (ºC) and total precipitation (mm) for the period 2007-2017. Data from Yellowknife Airport Station (2007-2012 & 2014-2017) and Yellowknife Henderson Station (2013).

2007-2017		
Month	Mean Temp (°C)	Total Precipitation (mm)
May	6.4	12.9
June	14.3	25.8
July	17.6	35.4
August	15.0	43.7
September	8.4	42.1

Table 4.2 Cell counts for earlywood (EW), latewood (LW), and total mature, total June precipitation (mm), and count of GDD (>5°C) for the period 2007-2017. Shaded cells indicate higher than 2007-2017 mean values. Data from Yellowknife Airport Station (2007-2012 & 2014-2017) and Yellowknife Henderson Station (2013).

Year	EW Cell	LW Cell	Total Cell	June Precipitation (mm)	GDD Count (days)
2007	8	4	12	4.8	124
2008	13	5	18	49.8	142
2009	11	6	17	48.8	122
2010	11	8	19	43.6	139
2011	12	7	19	34.2	146
2012	9	4	13	4.2	148
2013	11	5	16	34.0	144
2014	7	2	9	4.2	133
2015	7	3	10	17.0	138
2016	12	4	16	30.6	143
2017	10	4	14	12.4	146
Mean	10	5	15	26	139
Standard Deviation	2.0	1.6	3.3	17.1	8.4

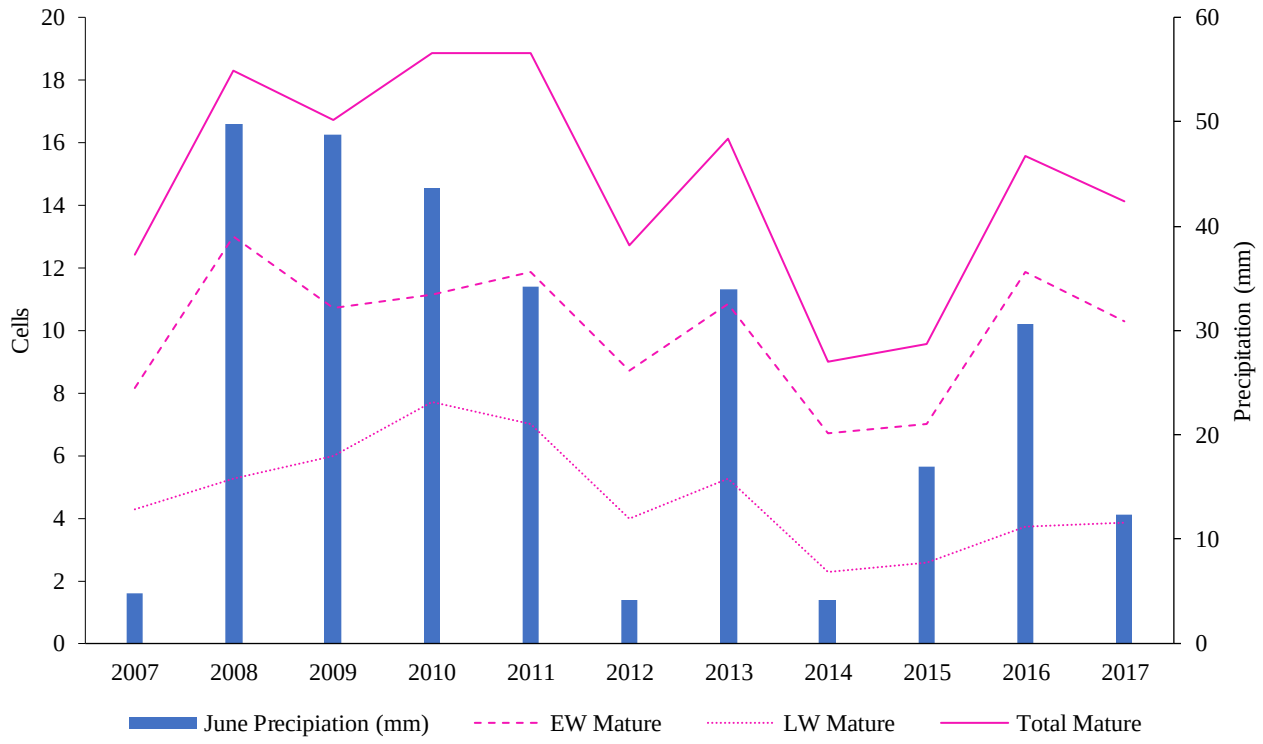

Figure 4.10. Average yearly cell counts for mature earlywood (EW), mature latewood (LW), and total mature cell counts for 2007-2017 and corresponding total June precipitation (mm). Cell counts are for jack pine trees TV489, TV490, TV491, TV492, TV493, TV494, TV495 at the Treeville site. Data from Yellowknife Airport Station (2007-2012 & 2014-2017) and Yellowknife Henderson Station (2013).

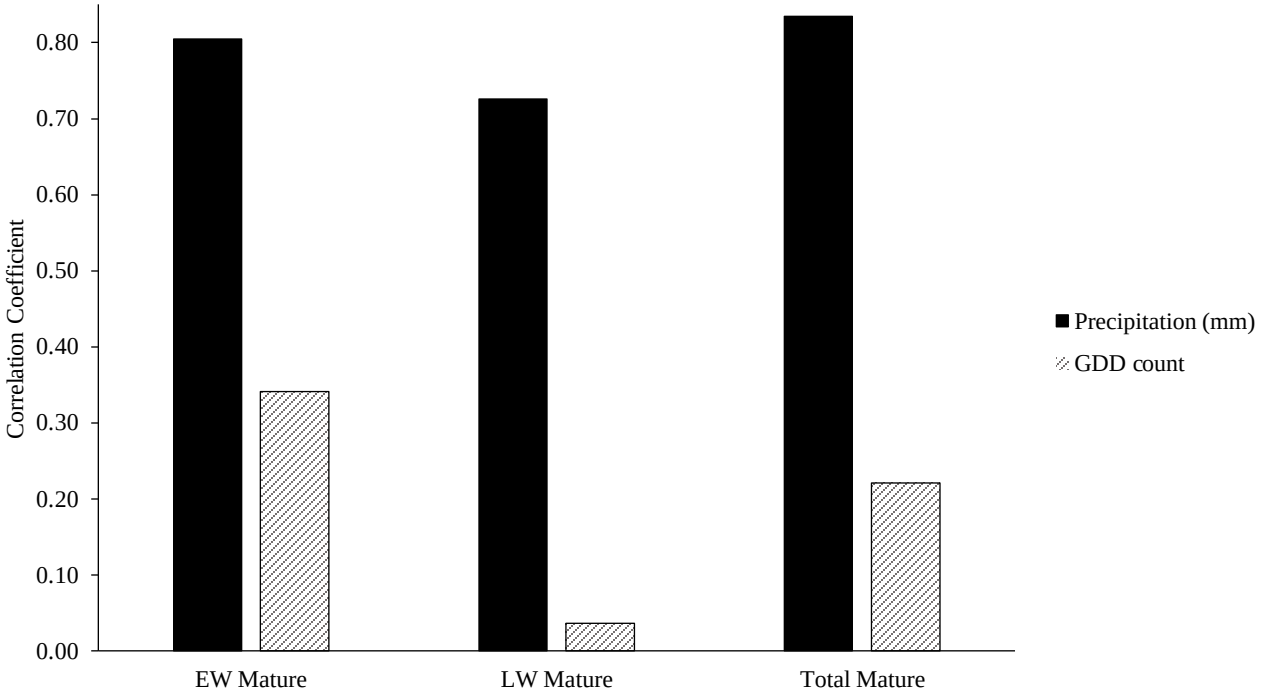

Figure 4.11. Pearson correlation coefficients between earlywood (EW), latewood (LW) and total mature cell counts for 2007-2017 and corresponding total June precipitation (mm) and annual GDD count. Solid fill bars indicate significant correlation coefficients $p<0.05$, hatched bar indicates correlation coefficients $p>0.05$.

4.3 Dendrometer data

4.3.1 Characteristics of the circadian cycle

Cycle data collected for the Treeville site is represented in Figure 4.12. The following results characterize the circadian cycle and stem radial growth throughout a single growing season for Jack pine. The *daily cycle approach* was used to define the daily fluctuations in stem size variation by calculating a daily average displacement from dendrometer signals and converting to daily averages by extracting the difference between current mean and mean values of the previous day.

Using the *stem cycle approach*, phases were defined to characterize the dynamics of stem fluctuations for the 2017 season. The median time was used to characterize the start and end times for each phase. Phase 1, the contraction phase, started around 07:30:00 and ended around 17:00:00, lasting approximately 10.80 ±10.21 hours (Figure 4.13a). Phase 2, the expansion phase, began at the end of the contraction phase and lasted approximately 17.02 ±14.94 hours, ending ~07:00:00 the following day (Figure 4.13b). Phase 3, the stem radial increment phase, occurring only when the previous day maximum is exceeded, occurred in the morning starting around 05:30:00 and ending around 08:00:00. When the SRI phase was triggered, it lasted approximately 5.97 ±6.87 hours (Figure 4.13c). Less than half of the daily cycles in the 2017 season triggered an SRI phase with a count of a total of 41 SRI phases out of 104 recorded cycles throughout the monitoring period. Phase 4, the circadian cycle lasted approximately 30.10 ±16.76 hours, beginning with the onset of the contraction phase. Table 4.3 summarizes the 2017 Treeville dendrometer sensor records and the patterns observed for the phases from May 4 to September 15 (DOY 124 to DOY 258), when the sensors were removed from the tree stems.

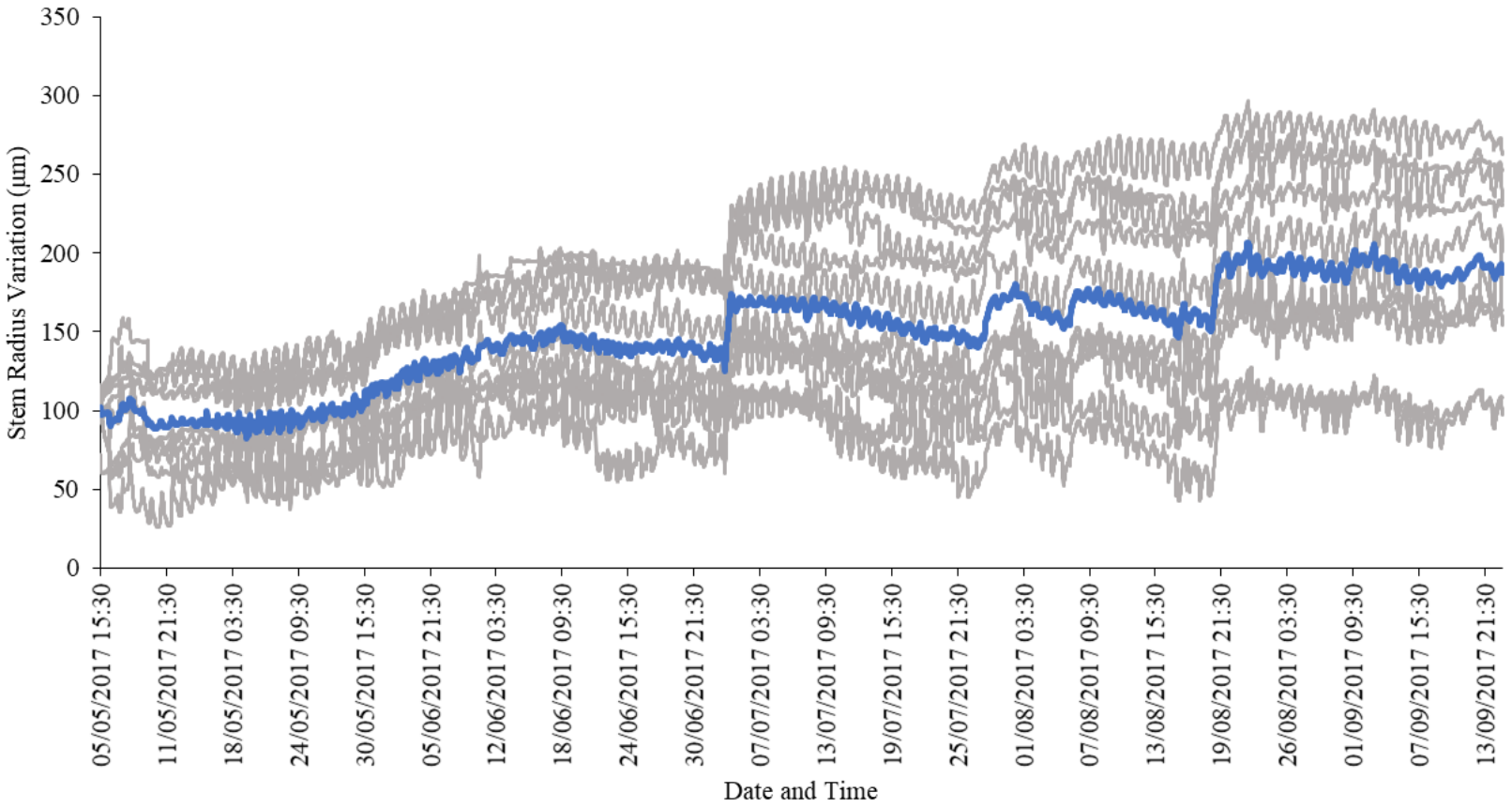

Figure 4.12. Site wide stem radius variation for May 5 to September 15, 2017 (DOY 124 to DOY 258). Individual tree responses shown as grey lines, site wide average is blue line. Site average does not include: TV490, and TV493 due to sensor failures.

Table 4.3. Summary of 2017 dendrometer phase timing, magnitude, and duration for *Pinus banksiana* at Treeville for the period of May 4 to September 15 (DOY 124-258). Phases were calculated using the Stem Cycle approach in the DendrometeR R package. Phase 1: contraction phase; Phase 2: expansion phase, Phase 3: stem radial increment phase, and Phase 4: circadian cycle. Phase 4 encompasses Phase 1 though Phase 3. Site average does not include deadwood TV487, and TV490, TV493 due to sensor failures.

Dendrometer Stem Cycle Phase Summary – Treeville 2017				
	Phase 1: Contraction	**Phase 2: Expansion**	**Phase 3: SRI**	**Phase 4: Circadian Cycle**
Mean Start Time	09:01:10	15:20:16	08:01:51	9:01:06
Mean End Time	15:20:03	08:34:04	09:04:14	8:58:57 (+1 day)
Median Start Time	07:30:00	17:00:00	05:30:00	7:30:00
Median End Time	17:00:00	07:00:00	08:00:00	7:30:00 (+1 day)
Count of Occurrence	104	103	41	104
Mean Magnitude (μm)	14.08 ±10.24	15.78 ±8.78	6.24 ±9.35	20.73 ±11.35
Minimum Magnitude (occurrences)	0.00 (187)	0.00 (1)	0.00 (58)	1.75 (3)
Maximum Magnitude (occurrences)	60.50 (1)	84.63 (1)	75.75 (1)	120.38 (1)
Mean Duration (hours)	10.80 ±10.21	17.02 ±14.94	5.97 ±6.85	30.10 ±16.76
Maximum Duration (occurrences)	0.50 (187)	0.50 (1)	0.50 (58)	9.50 (1)
Minimum Duration (occurrences)	150.5 (1)	220.5 (1)	44.50 (1)	221.00 (1)

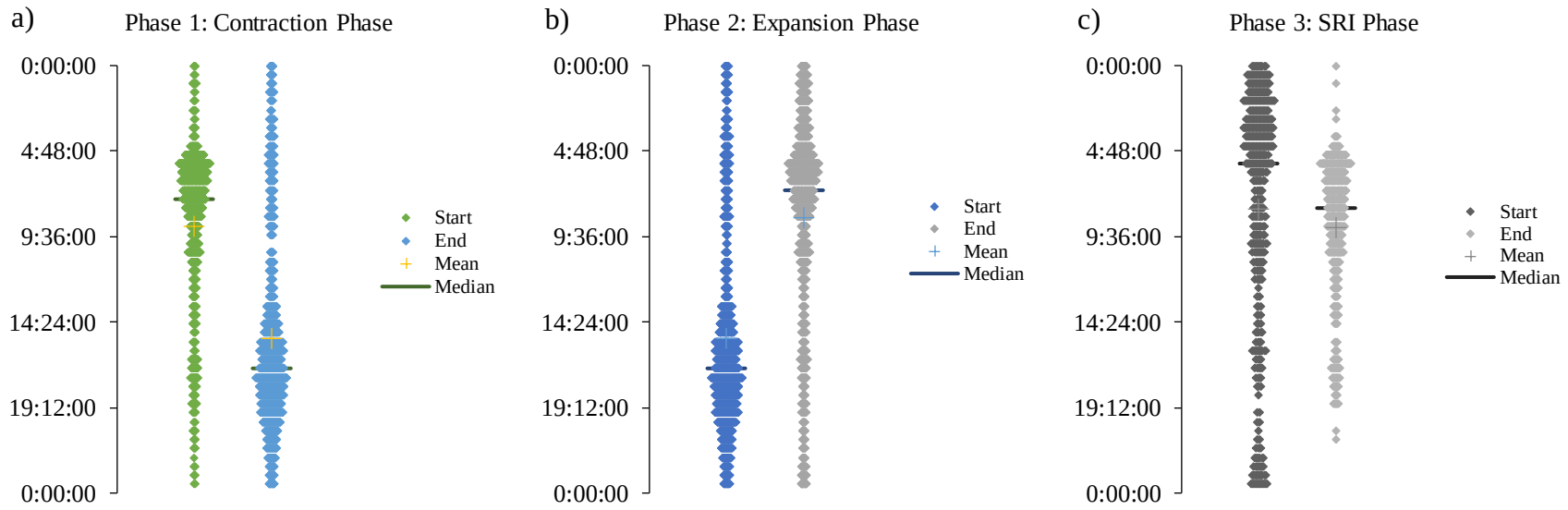

Figure 4.13. Violin plots of dendrometer phase start and end times for Treeville 2017. a) Phase 1: contraction phase; b) Phase 2: expansion phase; c) Phase 3: stem radial increment phase. Averages do not include: TV487, TV490, TV493, TV496 due to sensor failures.

Phase 3, the stem radial increment (SRI) phase, is triggered when the previous day maximum is exceeded by the current day. These exceedances are what characterizes ΔR+ cycles. Dendrometer responses and monthly frequencies of ΔR+ and ΔR- and REG and LG are plotted in Figure 4.14. Monthly frequencies of ΔR+ and ΔR- indicated lowest monthly frequencies of ΔR+ observed in August and highest monthly frequencies of ΔR+ occurring in May (54%) and June (51%) (Figure 4.14a). For the studied period from May to September, 65-85% of cycles observed throughout the study period were REG cycles (≤ 28 hrs.) and 17-35% of cycles were defined as LG (>28 hrs.) cycles. August had the lowest frequency of LG cycles (17%), and May had the highest frequency of LG cycles (35%) throughout the 2017 season (Figure 4.14b).

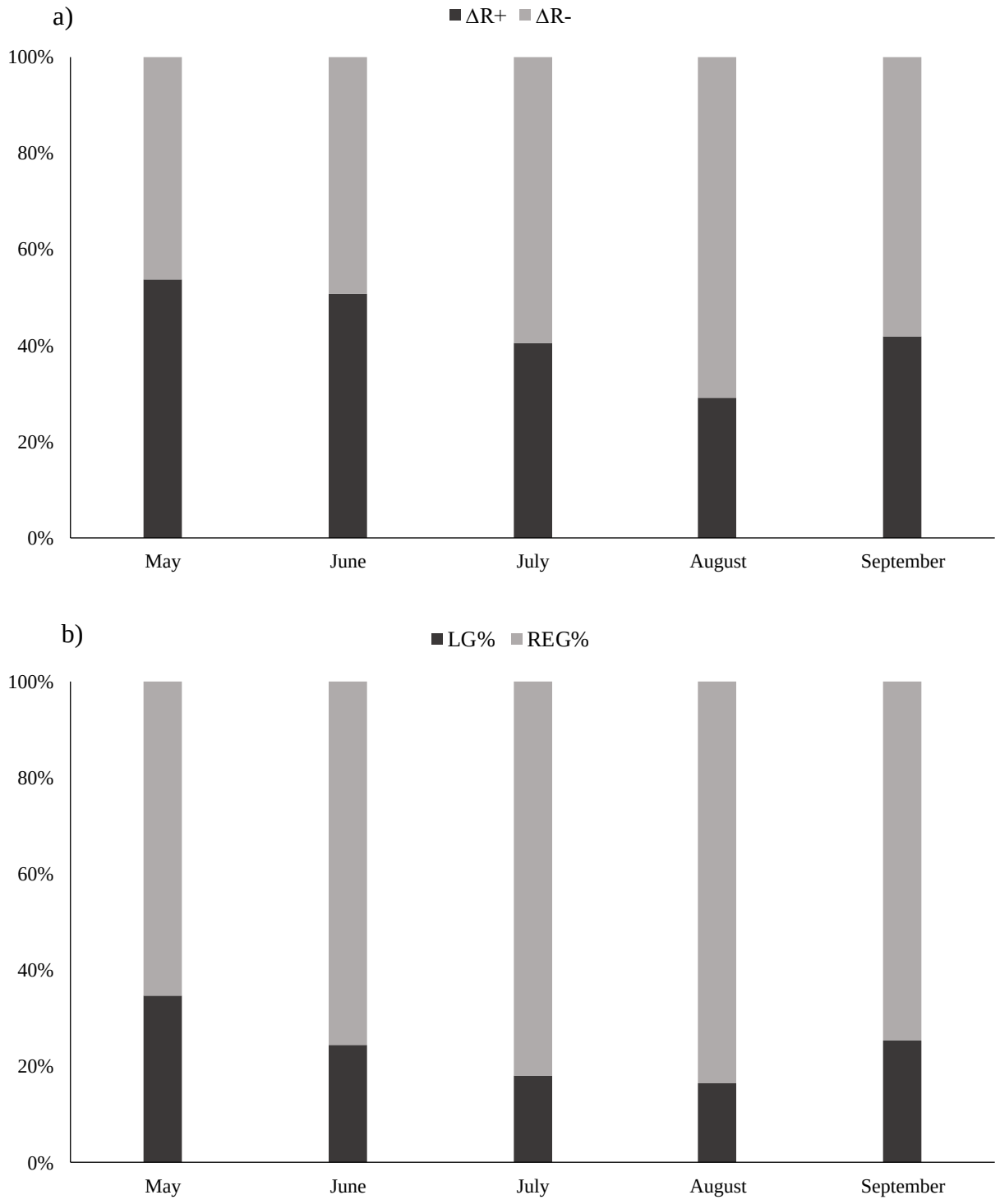

Figure 4.14. a) Monthly Frequency distribution (%) of ΔR+ and ΔR- and b) Monthly frequency distribution (%) of regular (REG) (≤28hrs) and long (LG) cycles (>28hrs) for *P. banksiana* studied at Treeville, May-September 2017. Calculations do not include: TV487, TV490, TV493, TV496.

The *daily cycle approach* was used to assess the daily stem radius variation for Jack pine trees at Treeville site in 2017. Figure 4.15 plots the daily variation in stem radial variation for each tree and site wide average for the trees monitored at Treeville from May 6 to September 15, 2017 (DOY 126 to 258). These fluctuations in stem radial size indicate timing of increased radial expansion throughout the study period. Site wide average responses recorded surges in radial size around July 4 (DOY 185), July 29 (DOY 210), August 6 (DOY 218), August 16 (DOY 228), and August 19 (DOY 231).

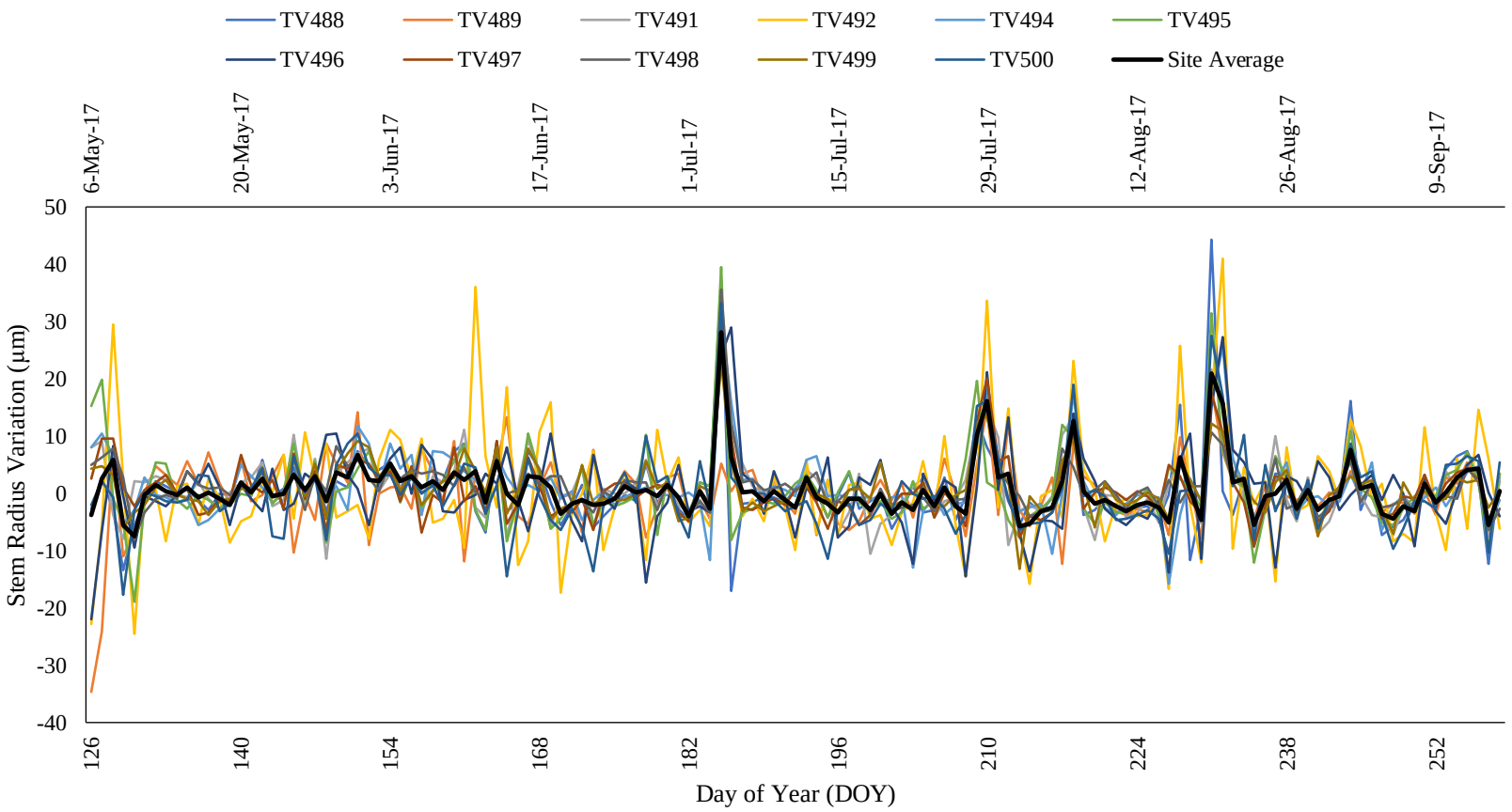

Figure 4.15. Daily change in stem radius variation for Treeville 2017. May 6 to September 15, 2017 (DOY 126 – 258). Site average results exclude: TV487, TV490, TV493.

4.3.2 Patterns of stem fluctuation & weather

The cumulative variation in stem size recorded by dendrometers indicates seasonal variation in the stem size. Figure 4.16a and Figure 4.14b illustrate daily weather variables including precipitation and temperature between overall stem fluctuations. Observed increases in stem size variation and rain events were observed on July 3, July 28, and August 19. Simple Pearson correlations were calculated to quantify the relationship between the observed daily cumulative stem radial fluctuations and daily weather variables (Figure 4.17). Maximum, minimum, and mean daily temperatures were significantly correlated with site wide daily stem fluctuations. There was no correlation between total daily precipitation and dendrometer measurements of stem size.

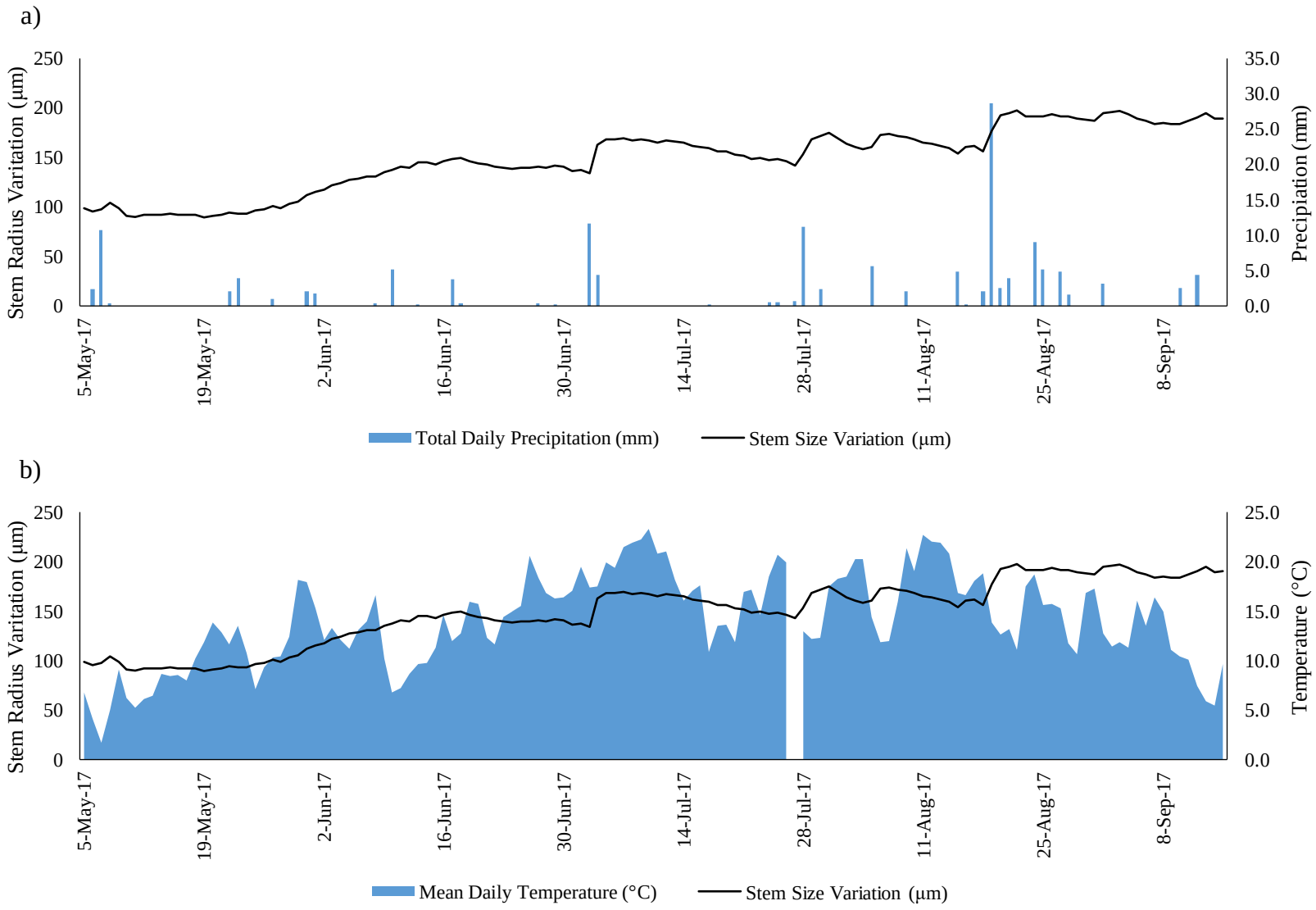

Figure 4.16. a) Cumulative site wide average stem size variation in black line and 2017 total daily precipitation (YKA) in blue bars May 5 to September 13, 2017. b) Cumulative stem size variation site wide average in black line and 2017 mean daily temperatures (°C) shaded blue area. Site average stem radial variation does not include: TV490, TV493.

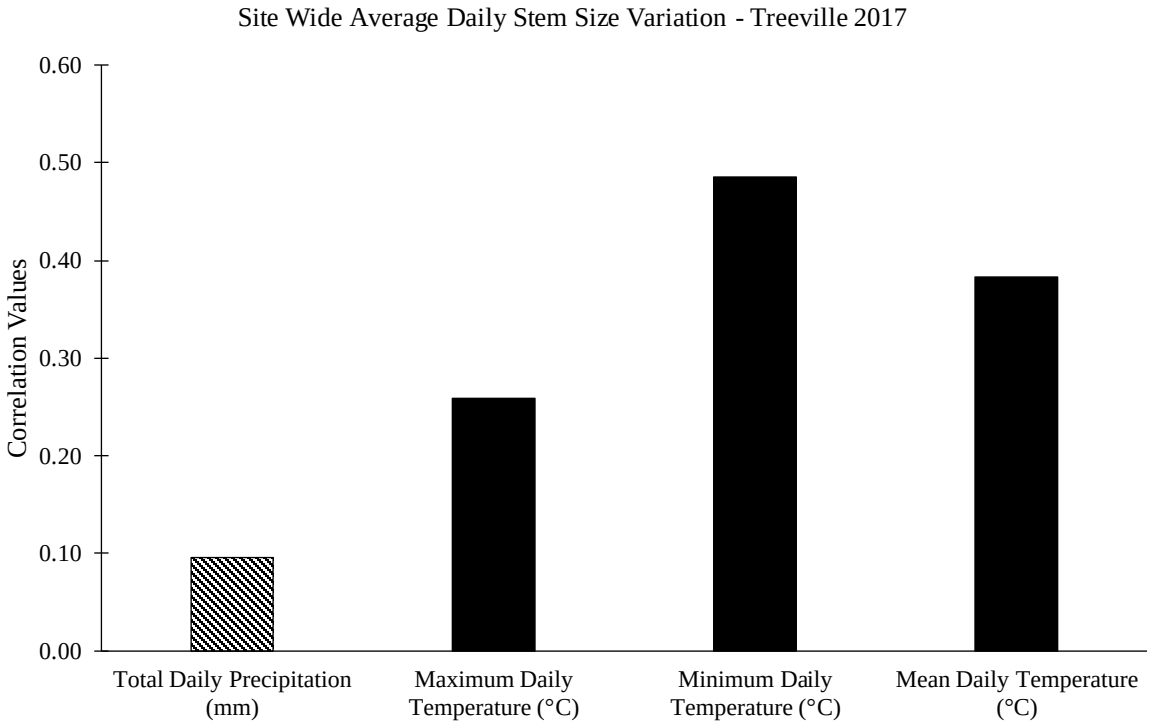

Figure 4.17. Pearson correlation coefficients between daily average stem size variation for Treeville 2017 and total daily precipitation (mm), maximum daily temperature (°C), minimum daily temperature (°C), and mean daily temperature (°C) from YKA for May 5 to September 15, 2017. Statistics do not include responses from trees: TV490, TV493. Solid fill bars indicate significant correlation coefficients $p<0.05$, hatched bar indicates correlation coefficients $p>0.05$.

Using the *daily cycle approach*, site wide daily stem radius variation (dSRV) was calculated to understand the relationship with daily fluctuations in stem radius and weather throughout the study period (Figure 4.18). High change in daily stem radius was observed on July 4, July 29, August 6, and August 20. More variation in the (dSRV) was observed after July 29. The site wide dSRV had a significant positive correlation with total precipitation ($r = 0.41$) and showed significant negative correlation with daily maximum temperatures ($r = -0.21$). Both daily mean and daily minimum temperatures showed negative relationships with dSRV, although neither were significant (Figure 4.19).

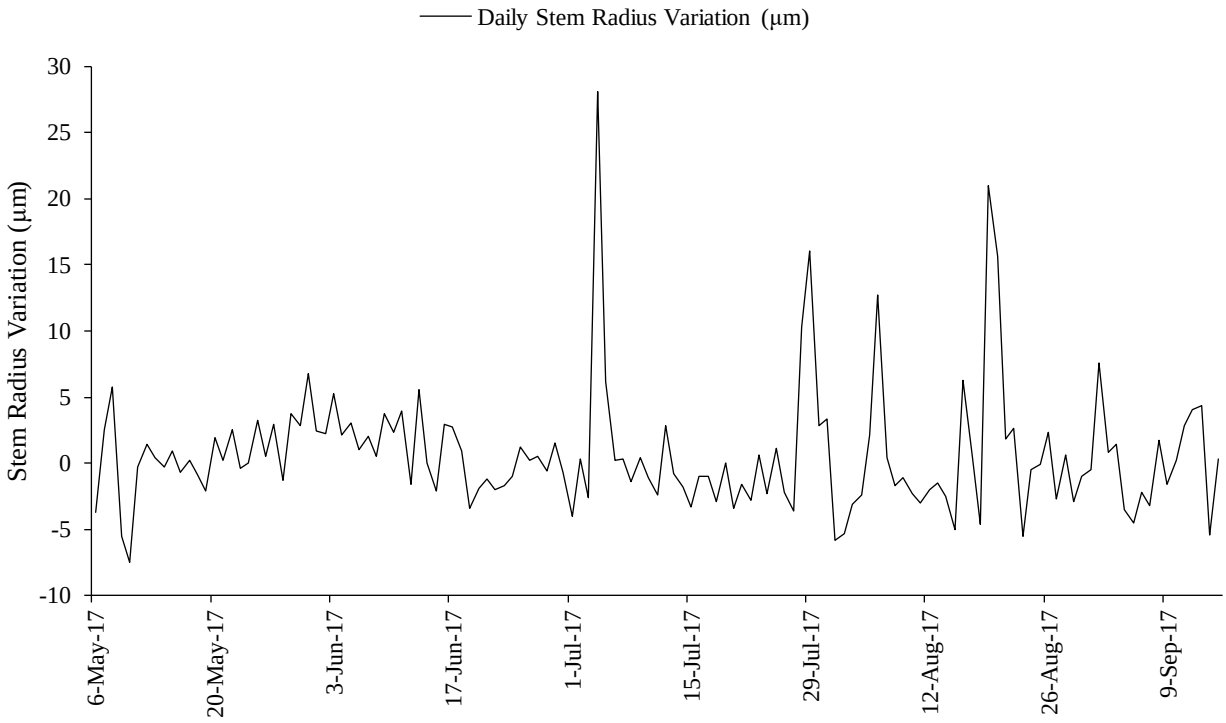

Figure 4.18. Site wide average daily stem radius variation (dSRV) as calculated using the *daily cycle approach*, extracting daily average displacement from dendrometer signals, and converting to daily averages by extracting the difference between current mean and previous day mean values. Site Average excludes: TV487, TV490, TV493.

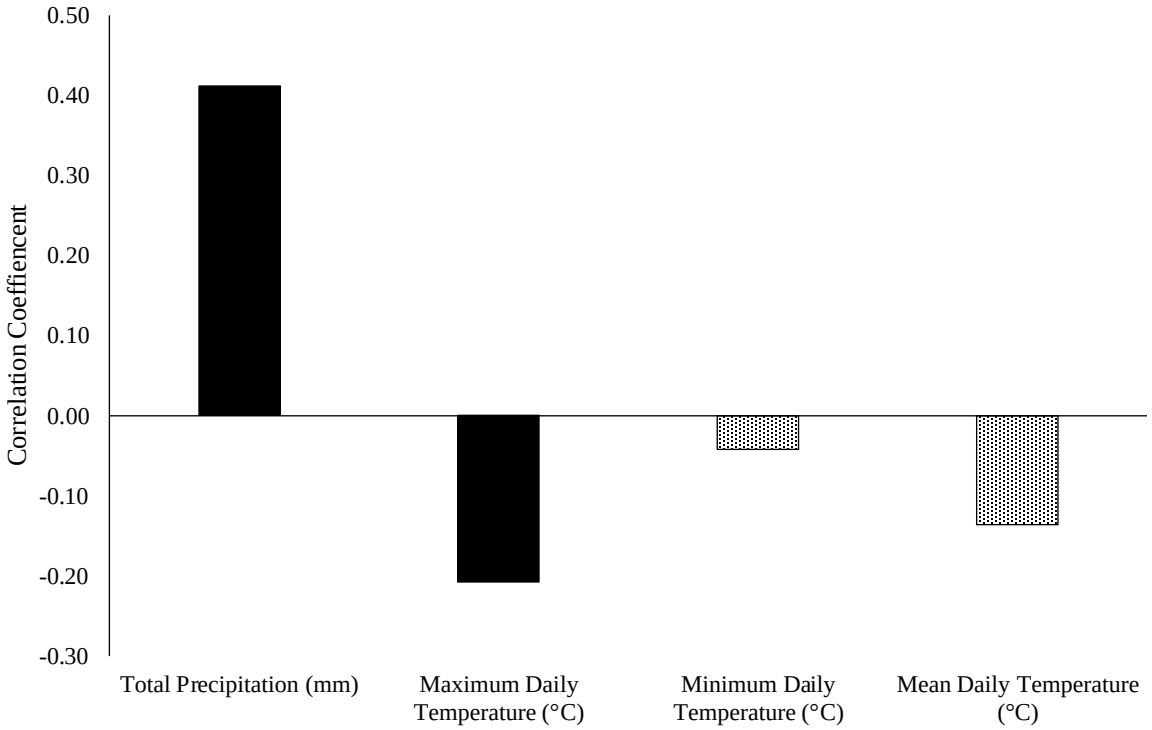

Figure 4.19. Pearson correlation coefficients between daily stem radius variation (dSRV) from Treeville and weather variables: Total precipitation (mm), Maximum Daily Temperature (°C), Minimum Daily Temperature (°C), and Mean Daily Temperature (°C), from YKA for May 6 to September 15, 2017. Solid fill bars indicate significant correlation significant correlation coefficients $p<0.05$, hatched bar indicates correlation coefficients $p>0.05$.

Phases defined under the *stem cycle approach* were measured against daily temperature and precipitation to estimate relationships between weather and phase magnitude and duration. The contraction phase overall had negative relationships with all variables. Simple Pearson correlations indicated significant negative correlations with the magnitude of the contraction phase with precipitation (r = -0.29). The duration of the contraction phase was significantly and negatively correlated with daily maximum minimum, and mean temperature (r = -0.35, -0.32, and -0.25 respectively). (Figure 4.20a). A significant positive relationship was calculated for the magnitude of the expansion period and precipitation (r = 0.21). (Figure 4.20b). Total precipitation was significantly and positively correlated with both magnitude (r = 0.55) and duration (r = 0.61) of SRI phases during the 2017 season (Figure 4.20c). The circadian cycle, made up of the contraction, expansion, and SRI phases, indicated the full cycle was most strongly related to precipitation. Results show significant negative correlation between total precipitation and the magnitude of the circadian cycle (r = -0.19) and significant positive relationships with the cycle's duration (r = 0.28) (Figure 4.20d).

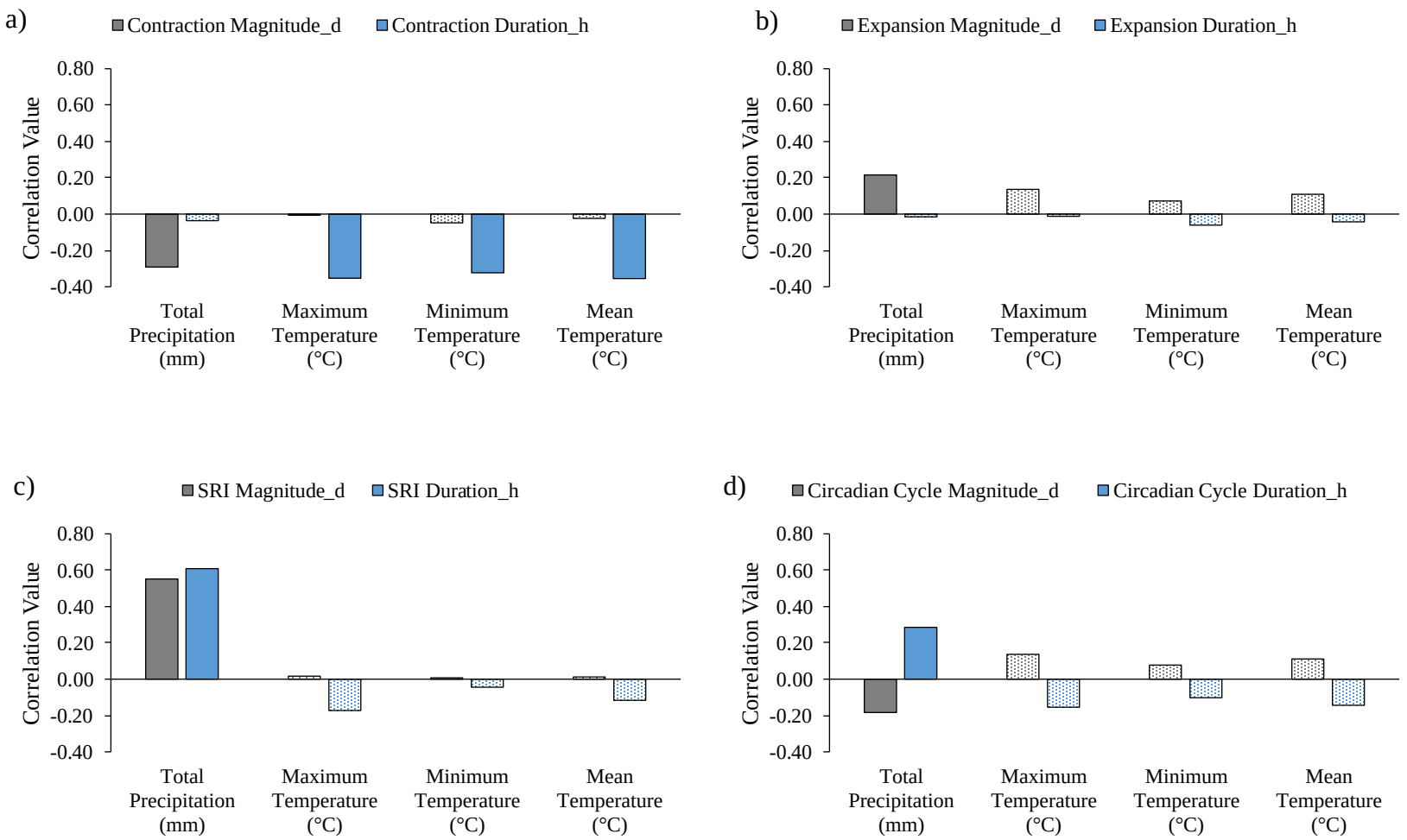

Figure 4.20. Pearson correlation coefficients between daily average magnitude and duration of stem cycle a) contraction phase, b) expansion phase, c) SRI phase, and d) circadian cycle and 2017 weather variables: total daily precipitation (mm), daily maximum temperature (°C), daily minimum temperature (°C), and daily mean temperature (°C) from YKA for May 5 to September 15, 2017. Statistics do not include responses from trees: TV490, TV493, TV496. Solid filled bars indicate significant correlation coefficients $p<0.05$, hatched bar indicates correlation coefficients $p>0.05$.

September and August both had the longest SRI phases calculated for the 2017 season, lasting an average of 7.44 and 7.58 hours, respectively. The lowest SRI phase duration average occurred in May with a duration average length of 4.58 hours (Figure 4.21a). August recorded the highest observed monthly average magnitude of 9.61 μm, compared to the lowest month (May), which recorded an average monthly magnitude of 3.70 μm (Figure 4.21b). June had the highest cumulative count of recorded SRI phases, at 126 SRI phases triggered (Figure 4.21c).

Daily averages were used to calculate Pearson correlations between daily average duration, magnitude and count of SRI phase and influences of weather variables including mean daily temperature (°C), min daily temperature (°C), maximum daily temperature (°C), and total daily precipitation (mm). Only total daily precipitation had significant positive correlation values (at 5% confidence) on the duration ($r = 0.55$), magnitude ($r = 0.61$), and count ($r = 0.25$) of the SRI phase (Figure 4.22). No significant correlations were calculated for temperature and SRI phase.

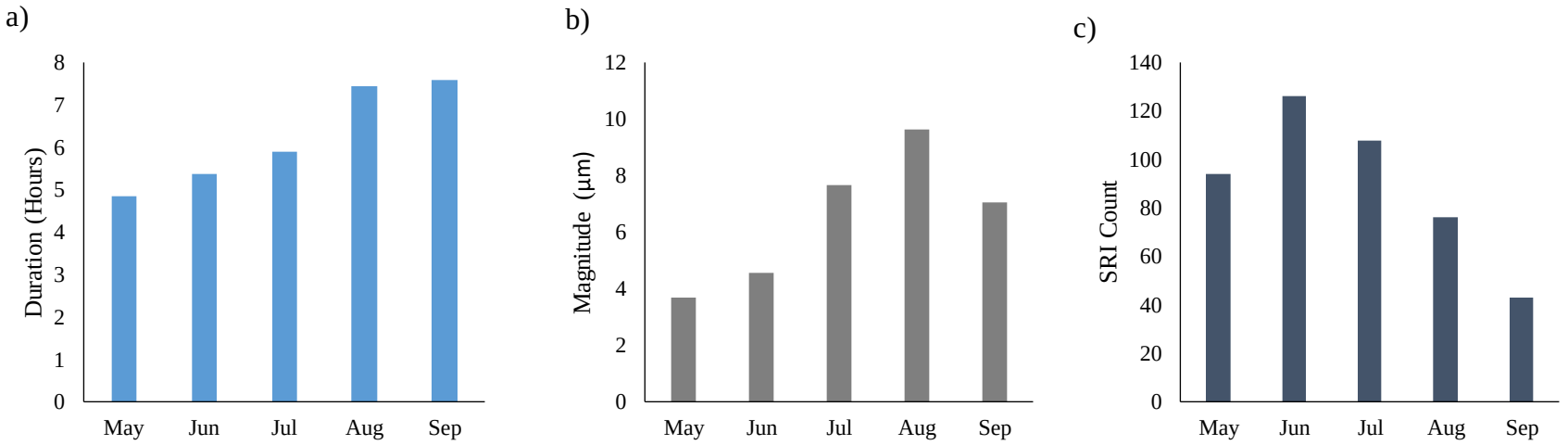

Figure 4.21. SRI phase a) monthly average duration, b) monthly average magnitude, c) count of monthly cumulative site wide occurrence of SRI phase for the 2017 season. Count and average calculations of SRI phases do not include trees: TV490, TV493, TV496.

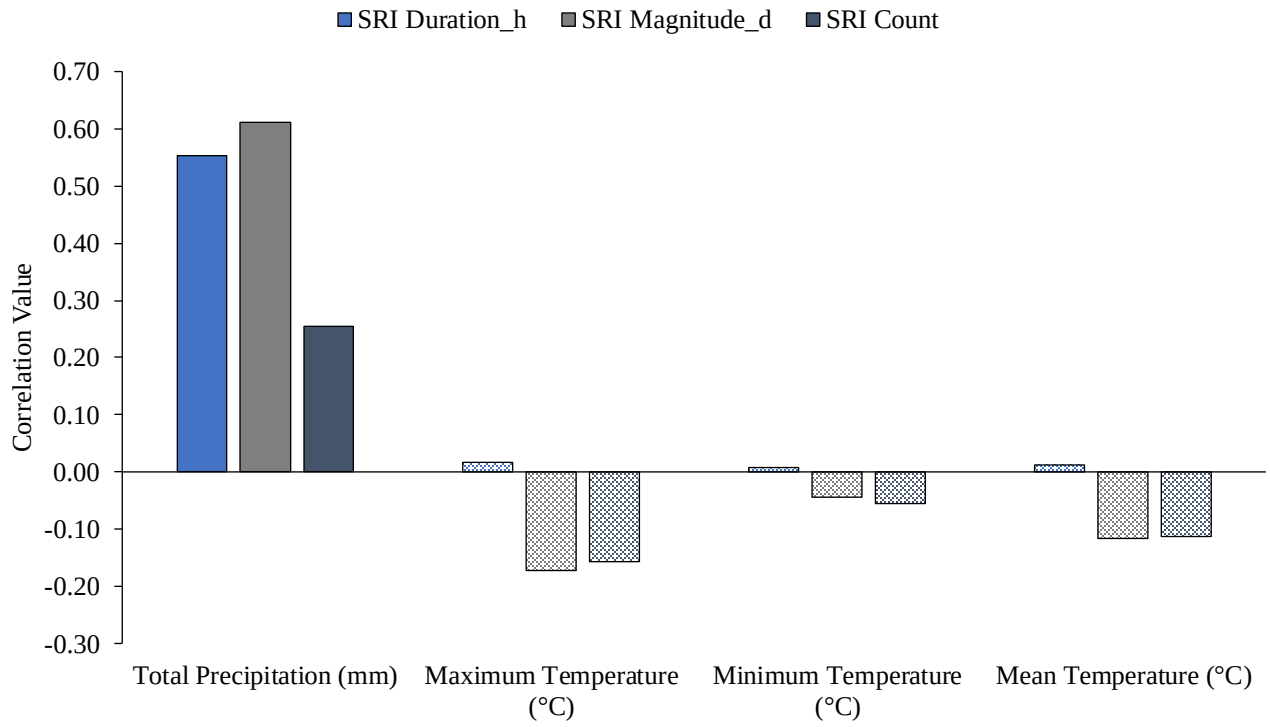

Figure 4.22. Pearson correlation coefficients between daily average duration, change in magnitude, and site wide count of SRI phase from *stem cycle approach* from Treeville and weather variables: Mean Daily Temperature (°C), Minimum Daily Temperature (°C), Maximum Daily Temperature (°C), and Total precipitation (mm), from YKA for May 6 to September 15, 2017. Solid fill bars indicate significant correlation significant correlation coefficients $p<0.05$, hatched bar indicates correlation coefficients $p>0.05$.

4.4 Method comparison

Results from both methods, microcore cell data and dendrometer stem data, were paired together to evaluate the two different types of growth information that was recorded throughout the 2017 growing season and assess the similarities between the overserved timings between the datasets. A homogeneity test, a statistical tests used to determine the timing of change in a data set, was performed in excel on the dendrometer data to determine if there was aa recorded shift in the dendrometer data slope occurred and if this timing in slope change aligned with the recorded transition between enlarging cells to wall-thickening cell development as presented in the microcore data. Figure 4.23 shows the calculated homogeneity shift across all sampled trees using a box plot to represent the spread of the shift as observed in the homogeneity test paired with the raw and modeled date of the onset of the W phase using microcore counts. A summary of these dates when the slope shift occurred in the dendrometer data and the timing of the raw and modeled date of the onset of the W phase from microcore counts is summarized in Table 4.4.

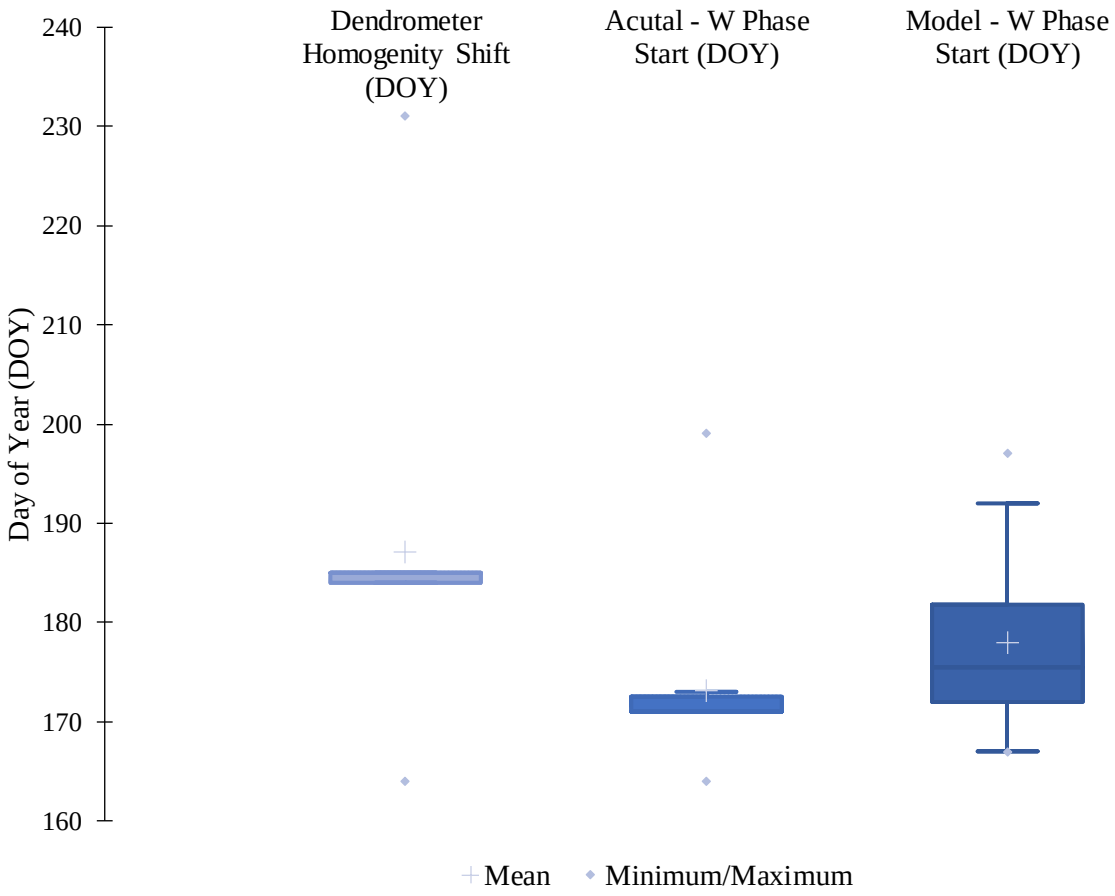

Figure 4.23. Comparison between dendrometer homogeneity shift calculation and actual and modeled wall-thickening (W) cell count phase transitions from microcore data for Treeville 2017.

Table 4.4. Summary of dendrometer homogeneity shift and microcore actual (raw) and modelled start of cell wall-thickening phase (W) at Treeville 2017. Dendrometer calculations do not include: TV490 and TV493.

Tree #	Dendrometer	Microcore	
	Homogeneity Shift (DOY)	Actual - W Phase Start (DOY)	Model - W Phase Start (DOY)
TV488	184	171	167
TV489	164	164	192
TV490	N/A	171	172
TV491	185	171	192
TV492	164	171	168
TV493	N/A	164	167
TV494	185	171	176
TV495	184	171	173
TV496	185	199	197
TV497	209	171	175
TV498	185	178	181
TV499	185	171	172
TV500	231	178	182
TV Site	**185**	**173**	**178**

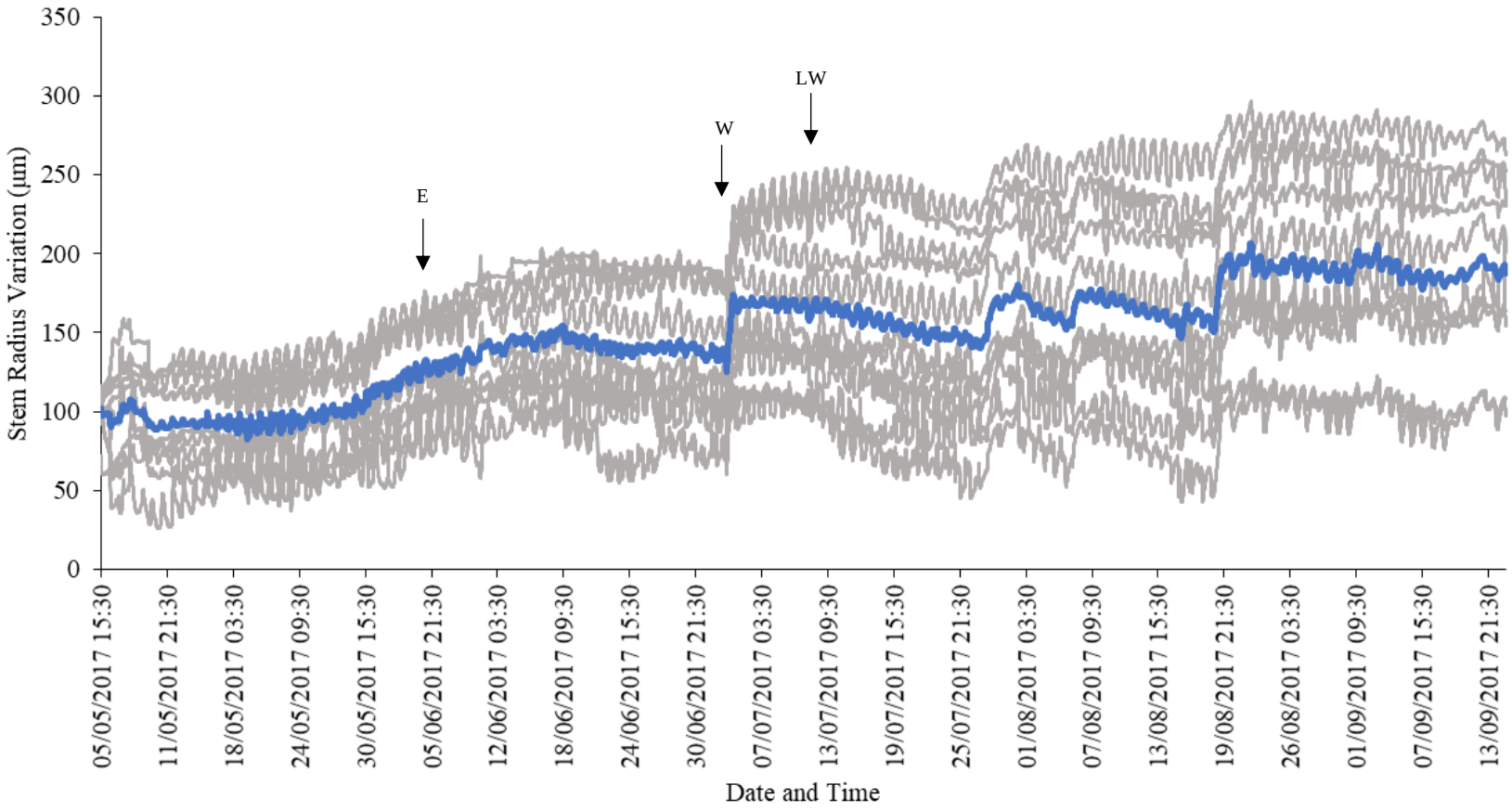

Figure 4.24. 2017 Growing season site wide stem radius variation. Individual tree responses shown as grey lines, site wide average is the blue line. Site average does not include: TV490, TV493. Black arrows denote wood formation phase timing from microcore data. E: onset of enlarging DOY 156 (June 5, 2017). W: wall-thickening transition on DOY 185 (July 4, 2017). LW: latewood transition on DOY 192 (July 11, 2017).

Site wide average homogeneity shift for dendrometer signals occurred around early July (DOY 185) although variation between trees was observed (Figure 4.23; Table 4.4). TV489 and TV492 saw shifts in dendrometer signals on June 13 (DOY 164), whereas TV500 did not see a shift in homogeneity till August 19 (DOY 231) (Table 4.4). This shift is expected to occur around the time developing cells began to enter the wall-thickening phase (W) in the xylem development process, as observed in the microcore data. For both raw and modelled microcore cell counts, the transition into the W phase began around late June 2017, raw weekly cell counts data estimated this date to occur on June 22 (DOY 173) with the model estimating June 27 (DOY 178) (Figure 4.24). A full summary of the phase transitions is shown in Table 4.4.

CHAPTER FIVE:

DISCUSSION

5.0 Introduction

Intra-annual dendrochronology research can provide information concerning the timing, duration, and pattern of wood production and tree growth within a growing season. This type of research is useful for creating an understanding of the timing of cellular development and the pattern of cell phase transition within the growing season. Assessments of the characteristics defined by intra-annual studies in dendrochronology help refine traditional dendrochronology assessments and better define drivers of tree growth. Intra-annual studies provide valuable information on the timing of cell production, and insights into what characteristics of the environment may be driving annual tree-ring production. However, it is important to acknowledge that environmental and species-specific intrinsic controls are important aspects of annual wood production and ring formation. Dendrochronological studies at intra-annual timescales create highly detailed information surrounding growth characteristics and patterns of wood production and stem growth (Rossi et al., 2008). With this greater understanding of intra-annual controls on growth, traditional dendrochronology methods can be refined and improved upon. In addition, the development of intra-annual datasets for specific species and regions will help create better projections of tree growth under current climate change estimates (Friend et al., 2019). In this study, jack pine cellular development and wood production dynamics were characterized between May and September 2017 using two intra-annual dendrochronology methods: microcores and automatic point dendrometers. The results from this thesis provide insight into the timing of xylem cell formation and seasonal characteristics of growth mechanisms. These results from the 2017 season are discussed in relation to current research on the jack pine species within southern boreal study sites. To date, no intra-annual investigations on jack pine have been performed in the boreal

forest's northern portion. The following sections discuss the findings of the research within a broader context.

5.1 Discussion

5.1.1 Cellular development

5.1.1.1 Timing of cell development

Microcore samples were collected weekly at the Treeville site during the 2017 growing season, starting on May 5 (DOY 125), and ending on September 13 (DOY 255). At the time of initial microcore collection, in early May 2017 (DOY 125), an average of 5 cambial cells were counted in the radial file. Literature for jack pine suggests that dormant cambium may contain several cells prior to the onset of growth, demonstrating the onset of cambial activity when cambial cell number increased from 6 – 8 cells to 10 – 15 cells in the beginning of May (Zhai et al., 2012). Rossi et al. (2014) observed 4-5 dormant cells in the cambium prior to seasonal reactivation, increasing to 6-10 cells at the time of cell division. Cambial cell production was not counted for the 2017 season, although according to Rossi et al. (2008), daily temperatures of 4-5°C are the most favourable for photosynthetic processes and thus xylem cell production and the onset of wood formation. Prior to the first sample date, average daily temperatures at the Treeville site were not yet consistently above the 4-5°C threshold for cambial reactivation as suggested by Rossi et al., (2008), and varied between -1.7ºC and 6.8 ºC with an average daily temperature of 2.5 ºC in the preceding week. It is unknown if the cambial cells counted in the first microcore sampling date were still dormant or newly formed cells post seasonal reactivation. Optimal temperature thresholds for onset and maintenance of growth could be lower for jack pine in this region given the short-growing season and lower seasonal temperatures. Zhai et al., (2012) noted jack pine cell development onset around 5.3 ºC for jack pine growing in lower latitudes in the boreal forest.

Research has shown that there is variability among trees and in some cases no relationship between cambial activity and threshold average temperatures (Begum et al., 2013). In addition, it is noted that other factors are important in the control and maintenance of growth, influencing the timing of the onset of cell development and subsequent cell development phase transitions (e.g., phytohormonal and or intrinsic mechanisms) (De Micco et al., 2019).

From weekly microcore cell counts it was determined that the onset of xylem cell development and enlargement occurred on the June 6 (DOY 157) sampling date and mean temperatures were 6.8°C. These temperatures recorded for this period are slightly above the critical temperatures indicated by Rossi et al. (2008) (i.e., 4-5°C) for xylem cell growth, and higher than what was observed by Zhai et al. (2012) who recorded onset of xylem cell formation at 5.3ºC. During 2017, the onset of cell formation following cambial reactivation occurred despite exceedance of temperature thresholds suggested by Rossi et al. (2008). Both Ko Heinrichs et al. (2007) and Zhai et al. (2012) found comparable results, observing the onset of cell development for studied jack pine trees in mid-May (around DOY 140) when temperatures fluctuated between 5-19°C, and cell development ~ May 7, respectively, for jack pine in lower latitudes boreal forest using microcore cell development assessment.

There was about a 2-week window observed at Treeville for the developing and enlarging cells to begin introducing a secondary wall into the newly formed xylem cells. The timing of the onset of the wall-thickening phase, and the mature phase of xylogenesis were both recorded on June 20 (DOY 171). There is a significant range of timing for the onset of the wall-thickening cell development in boreal conifers in lower latitudes, with the timing ranging around DOY 152-170, although these records did not include jack pine (Rossi et al., 2014). Zhai et al. (2012) recorded the beginning of wall-thickening in mid-May, a week following the initiation of cell enlargement.

In contrast to the overlapping of the transition between the onset of the wall-thickening and mature cell formation at Treeville, Zhai et al. (2012) observed the first mature cell was observed two weeks following the wall-thickening phase transition. In lower latitude boreal forest, the first mature cells were recorded in late May (Zhai et al., 2012). The transition between earlywood (EW) mature cells and latewood (LW) mature cells was observed on July 11 (DOY 192). Again, similar timing for the transition between earlywood and latewood was observed by Ko Heinrichs et al. (2007), marking this transition in mid to late July when temperatures hovered around 20ºC. The slowing of cell development and end of the 2017 growing season occurred during late August, with no additional cells in developing phases noted on September 5 (DOY 248). However, enlarging and wall-thickening cells were observed on the following sample collection date on September 12 (DOY 255), indicating that growth may have continued in some trees (TV491 and TV492). Due to sample processing challenges, the sample depth for the Treeville site was limited near the end of the season with less than half the samples not being included in weekly count averages on September 5 (DOY 248) and September 12 (DOY 255) (Appendix Fig.1 & 2). As a result of the limited number of samples during this portion of the sampling season, it is possible that growth was still occurring after the final sample collection date on September 12 (DOY 255). In addition, it is possible that xylogenesis may have continued beyond the final sampling collection date on September 12 (DOY 255) and until mean daily temperatures started to drop below 4-5°C around October 1 (DOY 274) if growth of trees at this site respond to daily temperature thresholds as outlined by Rossi et al. (2008). Previous research on the timing of the end of cell production for jack pine has been recorded in late August when temperatures were maintained above the 5ºC threshold with highs of 20ºC to lows of 12ºC in the days surrounding the observed end of cell production (Ko Heinrichs et al., 2007). In contrast, Zhai et al. (2012) reported the end of xylem

cell production on 9 August, when the daily mean temperature at the site was ~11.2ºC; higher than spring initiation temperatures at 5.3ºC for jack pine. Xylem cellular development at Treeville was estimated to have occurred for a period of 91 days in 2017, assuming the growing season continued to at least the final sampling date on September 12 (DOY 255). In comparison, other studies in boreal ecosystems at lower latitudes collected microcores for upwards of 200 days (De Micco et al., 2019; Cuny & Rathgeber, 2016; Rossi et al., 2016; Rossi et al., 2014; Rossi et al., 2008). Range of 90-180-day growing season lengths have been observed for boreal forest jack pine specifically (Ko Heinrichs et al., 2007; Zhai et al., 2012). If the end of the growing season occurred sometime before September 5 (DOY 248), when no new cells had been observed, the growing season length for Treeville lasted 84 days. It is noted that Rossi et al. (2016) recorded an increase of ~94 days in the length of wood formation during years with higher annual temperatures (i.e., from 83 days with a mean annual temperature of -2°C to 178 days at 12°C), indicating the increased period for wood to form under warmer conditions. Furthermore, according to Ziaco et al. (2017), year-to-year variability in the period of wood formation was from ~66 days during drought-like conditions in 2015, to ~114 days in non-drought conditions during 2016. Increased seasonal temperatures could further impact the water balance and evapotranspiration requirements for growth. The literature suggests, that in addition to temperature controls on the timing of the end of the growing season, other environmental factors, when moisture is not a limiting factor, temperature is the main control on the timing of onset of xylem formation (Rossi et al., 2008). It is possible that the length of the growing season length at Treeville would extend in response to the maintenance of temperatures above the 4-5°C threshold later in the season. If moisture is not limited, ring widths and the number of cells in the ring would increase due to a longer growing season. Additional growing season length variation information does not exist for the Treeville site to allow for direct

comparison, although the timing of cell formation completion observed at the Treeville site is similar to what was observed by Ko Heinrichs et al. (2007) and Zhai et al. (2012) for jack pine at lower latitude boreal forest sites. In general, the literature indicates that years with extended periods of xylogenesis resulted in an increase of cell production, usually as a result of longer periods of more favourable growth conditions (De Micco et al., 2019; Rossi et al., 2014). The length of the growing season is also expected to have more impact on ring width than the rate of cell production (Rossi et al., 2014). At Treeville, the site wide average was 13 mature woody cells (± 6) cells in the ring at the final sampling date on September 12 (DOY 255), which was much lower than what has been reported for jack pine in southern regions. Zhai et al. (2012) reported 81+ mature cells formed during a growing season length similar to what was observed at Treeville. Despite similar season lengths, the rate of cell production was much higher compared to Treeville. With a much longer growing season length of ~180 days, Ko Heinrichs et al. (2007) reported 141±47 cells in the tree ring for jack pine at a southern boreal forest site. These observations indicate that growing season length, as well as cell production rates result in differences in the number of cells observed in the annual ring. The controls of weather on both the length of the season and the rates that are recorded are important for understanding the productivity of trees at specific sites.

5.1.1.2 Rates of cell development

Growth rates for the 2017 season were calculated using a generalized additive model (GAM) on the enlarging and wall-thickening cell phases, and a shape constrained additive model (SCAM) on the mature cell phase. The models estimated daily cell counts from weekly microcore counts. In general, it was observed during the 2017 growing season at Treeville, xylem cell differentiation demonstrated synchronicity, and in some cases overlapped completely between

phases, with cells still in developing and enlarging phases while cells began to transition into both wall-thickening and mature phases of xylogenesis. The timing observed at Treeville, has been demonstrated in other conifer stand assessments in the boreal forest, with the wall-thickening phase following close behind enlarging cell onset (Rossi et al., 2014). From the 2017 assessment of cell production rate, two periods of rapid development as expressed by the number of new cells developing in each phase of xylogenesis were observed. The first period of rapid development occurred June 21 – July 2, 2017 (DOY 172 to 183), and the second peak around July 19 (DOY 200). The initial increase in cell development rate was higher (~0.28 cells/day) than the second phase (~0.24 cells/day). The first date for rapid cell development observed in 2017 coincided with the longest day of the year (June 21). A similar timing for rapid cell production was also by Ko Heinrichs et al. (2007), indicating the date of greatest growth on June 27 (DOY 178) and cell production on June 28 (DOY 179). In addition, Zhai et al. (2012) recorded the period of rapid cell development to occur in June for jack pine, at a rate of 1.22 cells/day, much higher than the rates observed for jack pine at Treeville. It is also important to note the stand age of the trees studied in the 2017 season at Treeville site. The average tree age for sampled trees was 150-200 years old and cell production rates (xylogenesis) has previously been documented to change throughout the lifespan of the tree. Rossi et al. (2008) demonstrated that the timing of xylogenesis was 2-3 weeks shorter in 40–80-year-old trees compared to old trees (220+ years), leading to lowered cell production rate in old trees. The timing of the period of rapid cell development has been associated with the timing of increased seasonal photoperiod (Zhai et al., 2012; Ko Heinrichs et al., 2007; Rossi et al., 2006). Zhai et al. (2012) found a significant positive relationship between air temperature and xylem cell formation. The timing of both increased seasonal air temperatures and photoperiod contributed to the increased growth rate observed during this period (Zhai et al.,

2012). In the Yellowknife region specifically, results from long-term dendroclimatic assessment indicated a growth relationship between jack pine and June precipitation has been identified (Pisaric et al., 2009). It is possible, based on the literature, that both photoperiod length as well as the environmental factors (e.g., temperatures and precipitation) that meet the threshold requirements for this species are what influenced the timing of the periods of rapid growth seen during 2017. Based on the literature and the timing of the peak growth rate observed in 2017 microcore data, there is indication that June is an important period for growth. June may present both optimal temperature and increased daylength optimal for growth and June precipitation has been observed to be limiting for growth. The interactions between these weather variables impact the rates at which cells are developed during this period. Multi-year intra annual microcore data has yet to be presented for this species in this region. To assess these trends on a longer-term scale, cells were counted in 2017 dating back to 2007 to assess the relationship between weather and cell count at the Treeville site specifically.

The cause for the second peak in cell development rate adds to the complexity of the discussion surrounding the trends observed in the 2017 data. Two arguments are presented for this second increase. First, this could be an accurate depiction of how the trees were growing during the 2017 season, and there was an actual response to an input that resulted in an increase in cell production during that time. Increases in the observed precipitation in mid to late August may have triggered a growth response resulting in an increase in cell production rate. An observed increase in the dSRV in the dendrometer data occurred during the second peak of increased cell production rates, around July 28. Additional years of investigation will aid to assess the responsiveness of jack pine to precipitation and if similar observations are made year to year. Jack pine growth is limited by precipitation (Pisaric et al., 2009), so it is possible that precipitation events during the

latter half of growing season could trigger an additional period of rapid growth. However, this response has not been documented in this region and for this species. Alternatively, the second peak in cell development rate observed in the data could be due to the responsiveness of the model. Previous research found that these types of models respond to slight changes in cell counts during the phases of xylogenesis (Cuny et al., 2013). Further investigations into this model's use on trees producing low annual cells are needed to determine if its responsiveness is overestimating cell development rates.

Further to these observations for the timing of cell/day rate, it was observed that there was similar timing between the maximum growth rates for enlarging, wall-thickening, and the mature cell phases of xylem production. Again, the first noted peak for cell rate increase was noted to occur around the timing of longest seasonal photoperiod. The synchronicity of the timing of phase rate increase may occur as a result to growth requirements of northern plants with short growing seasons. This synchronicity has also been demonstrated for jack pine at lower latitudes in the Canadian boreal forest (Rossi et al., 2014). In contrast, for longer seasons (200+ days) as observed with Cuny et al. (2013) the observed peaks in growth rates of enlarging and wall-thickening phases did not synchronize, with enlarging cell rates peaking around ~May 30 (DOY 150) and wall-thickening cell rates not peaking until around ~September 7 (DOY 250) for three conifer species [*Picea abies*, *Pinus sylvestris*, and *Abies alba*]. It is possible that with longer growing seasons, more time can be allocated to the enlarging phase prior to the initiation of wall-thickening prior to the reduction in nutrient availability during the season. In lower latitude boreal forest, Zhai et al. (2012) saw at least 1 week between the transition of phases from enlarging to wall-thickening (1 week transition period) and wall-thickening to mature (2-week transition period) for jack pine. The timing of the wall-thickening phase onset occurs as part of the programmed mechanisms of the

cell development process, and the addition of cellulose and lignin to the cell wall for structural requirements of the tree stem, although this mechanism is currently understudied. It is known that the deposition of cellulose and lignin into the cell wall is controlled by the accessibility of soluble sugars (Cartenì et al., 2018).

5.1.1.3 Multi-year cell development & weather

Based on the literature, and the results of the 2017 cell counts, it is apparent that weather conditions in June are important for cell development for jack pine in Yellowknife. Microcore analysis for the 2017 growing season indicates an increased rate of cell production in June that corresponds to increasing daylength. This result is consistent with previous research in lower latitudes of the Canadian boreal forest (Zhai et al., 2012; Ko Heinrichs et al. 2007). Zhai et al. (2012) concluded that the length of the growing season is an important determinant for the number of cells produced in tree rings. This reactivation and maintenance of cellular development is understood as temperature controlled and is believed to represent an estimated threshold of 4-5ºC (Rossi et al., 2014; Rossi et al., 2008; Rossi et al., 2007). A similar range for spring reactivation and seasonal temperature thresholds for growth have been suggested for jack pine by Zhai et al. (2012). Zhai et al. (2012) noted cellular differentiation in jack pine at spring temperatures of 5.3ºC. At Treeville in 2017, onset of cell development was noted when air temperature reached ~6.8 ºC. It has been documented that more variation occurs in the timing of the onset of cell development compared to the end of the season, suggesting that temperature control on cell development is more flexible in spring compared to the end of the growing season (Zhai et al., 2012; Vaganov et al., 2006). To test the results observed in 2017 on a multi-year scale, cell counts were counted on collected microcores for the period 2007 to 2017, with the goal of assessing the relationship

between weather and yearly cell counts. Weather influences were tested using seasonal growing degree days (GDD) when mean daily temperatures exceeded >5ºC and June total precipitation.

Growing degree days >5ºC for the period 2007-2017 did not vary extensively from one year to the next. Seasons with above average GDD counts (i.e., GDD >5ºC) occurred during 70% of the sampled years. On the other hand, only 2007, 2009, 2014, and 2015 had lower than average GDD counts. When comparing GDD groups and cell counts, there are 3 years that are not consistent between the two groups. Both 2012 and 2017 recorded higher than average GDD (>5ºC), but both years were represented by below average cell counts (< 15 annual mature cells). This result suggests that regardless of increased seasonal GDD's, limited June precipitation during both these years (4.2 mm and 12.4 mm, respectively) reduced the total mature cell development for the season. Correlation coefficients between annual mature cell counts and GDD counts did not identify a significant relationship between these groups. These results are consistent with the previous research indicating warm temperatures are a driving factor of jack pine growth only when moisture requirements are met (Malliet et al., 2022). In addition, Malliet et al. (2022) suggested short-term temperature increases in response to projected climate warming will result in increased growth for jack pine if moisture is not limited. The results for the 2007-2017 cell counts indicate comparable results for Treeville that when moisture is limited, jack pine growth is expected to be reduced.

Years with above average "high" cell count group (>15 annual mature cells) included 2008, 2009, 2010, 2011, 2013, and 2016. Years with below average "low" cell count group (<15 annual mature cells), included the years 2007, 2012, 2014, 2015, and 2017. The above average "high" precipitation group (>25 mm) included 2008, 2009, 2010, 2011, 2013, and 2016. Below average "low" precipitation (<25 mm) group included 2007, 2012, 2014, 2015, and 2017. The groups form

for the high cell count group and the high June precipitation group (>25 mm) were identical groupings, with 2008, 2009, 2010, 2011, 2013, and 2016 being in both groups. A significant positive correlation (r = 0.72 to 0.84) was observed between EW, LW, and total mature cell counts and total June precipitation, demonstrating the strong relationship between the observed annual mature cell production and June precipitation throughout the 2007-2017 period. The similarity in the group reiterates the relationship noted between the importance of June precipitation on cell count and ring width as demonstrated by Pisaric et al. (2009). When the opposite groups are formed for low June precipitation group and low cell count group, there is again no difference between groups. These results demonstrate that June precipitation impacts yearly cell counts, supporting what has been reported in the literature.

It is noted that additional influences on cell development outside of what is discussed here are expected, knowing that multiple factors can control cell development (e.g., nutrient availability, sunlight, phytohormonal regulation, etc.). The analysis of the 2007-2017 period and corresponding weather demonstrates the importance of June precipitation and season length, represented by number of GDD >5ºC. Increases in seasonal GDD >5ºC may offset low June precipitation, as seen in 2017, but in most cases years with reduced June precipitation led to lower-than-average total mature cells developing, regardless of increased GDD >5ºC counts. It is apparent that moisture is a limiting factor for seasonal mature cell count, as demonstrated by the high cell count group occurring in years with the highest June precipitation for the 2007-2017 period.

5.1.2 Dendrometer signals

Automatic point dendrometers were installed on 13 trees at the Treeville site in 2017, and these sensors collected data on 30-minute timestamps from May 5 (DOY 125) to September 29,

2017 (DOY 272). Dendrometers continuously measure the contraction and expansion of the tree stem. Dendrometer data from 2017 was transformed using both the *stem cycle approach* and the *daily cycle approach* (Deslauriers et al., 2003; Deslauriers et al 2007). The *daily cycle approach* was used to assess the daily change in the stem size, referred to as the daily stem radius variation (dSRV). The dSRV can be used to interpret daily water movement within the tree stem. In general, there was a positive correlation between daily variation and precipitation and negative correlations with maximum daily temperatures. Year-to-year comparisons of the relationships between weather variables and the variation in the measured dSRV values can provide insights on both the dynamics of water movement within the stem, and seasonal stem growth. The stem cycle approach was applied to determine the unique characteristics of the jack pine circadian cycle at the Treeville site and investigate potential environmental controls of growth during the 2017 growing season.

5.1.2.1 Characteristics of the circadian cycle

The use of the *stem cycle approach* allows for a deeper analysis of the trends recorded in the dendrometer signals in relation to weather conditions and the timing and lengths of the circadian cycle and the phases. The *stem cycle approach* divides the circadian cycle into 3 phases including contraction (Phase 1), expansion (Phase 2), and stem radial increment/SRI (Phase 3). The characteristics of the timing and duration of the phases included in the full circadian cycle (Phase 4), provide information on the daily responses and timing of irreversible stem fluctuations and seasonal stem growth. The circadian cycle at the Treeville site in 2017 lasted on average 30.1 hours. On average, the contraction phase lasted 10.80 hours with the phase being triggered ~7:30 lasting until 17:00, when the expansion phase began. The expansion phase lasted ~17.02 hours until 7:00 the following day. The trends observed in the 2017 showed similar timings to dendrometer results from research in lower latitudes (Quebec boreal region) using two conifer

species [*P. abies* and *L. decidua*]. In their study, Deslauriers et al., (2007) suggested contraction phase began around 08:00 to 09:00, and expansion phase commenced mid-afternoon between 15:00 and 18:00. These timings were similar to those observed at Treeville. Due to the longer photoperiod in the Yellowknife region, the contraction phase was lasting longer in response to the longer seasonal daylight hours experienced in higher latitude regions. At Treeville, when the SRI phase was observed, it typically was recorded in the morning starting ~05:30:00 and ending around 08:00:00, lasting around 6 hours when triggered. In contrast, Deslauriers et al. (2007) found the SRI phase was triggered later in the evening from 23:00 to 02:00. It is unclear as to why there is an opposite timing calculation of the SRI phase at Treeville. Despite the climate in the boreal region of Quebec being similar to climatic conditions experienced at Treeville, with seasonal lows of -22°C in January and seasonal highs of 24°C in July, there are differences in the phase timing observed at Treeville, most notably in the timing of the SRI phase. The characteristics of the timing of these phases observed at Treeville may confirm the concept of plasticity and variability in the responses observed in different tree species at regional scales.

5.1.2.2 Patterns of stem fluctuation & weather

Overall, daily minimum temperatures had the strongest positive correlation with the site wide daily average stem size variation, and precipitation had no correlation on the daily average stem size variation. When transformed using the *daily cycle approach*, total daily precipitation was positively correlated with daily stem variation, and maximum temperatures had a negative correlation with daily stem variation. These two signals indicate that precipitation is what drove the increase in stem size in response to the movement of water in the tree stem (swelling), while the highest daily temperatures were responsible for reducing the stem radial size. The relationship between these two variables depicts the relationship between the tree and evapotranspiration

impacts to the stem sizes. In summary, these results show the strong influence that water availability has on jack pine situated on rocky outcrop habitat.

Analysis of the data transformed using the *stem cycle approach* did show that there were significant negative relationships between total daily precipitation and the daily magnitude of the circadian cycle and significant positive relationships with the duration of the circadian cycle. This may be an indication of jack pine sensitivity to precipitation inputs due to the environmental conditions that jack pine grow (e.g., none to thin soil depth, rocky outcrops). Dendroclimatology research in the Yellowknife region demonstrated that growth of jack pine is limited by the amount of precipitation during June (Pisaric et al., (2009). In addition, Maillet et al., 2022 showed strong annual relationships between jack pine and precipitation in southern Canada boreal forest. Ziaco & Biondi (2018) found that precipitation had the strongest control on the occurrence of the SRI phase, demonstrating that trees growing in mesic conditions were successful in utilizing large precipitation events to trigger growth. However, the Ziaco and Biondi (2018) study was undertaken in the hyperarid Mojave region which has a much different climatic setting compared to the Treeville site, although comparisons still provide insights on the utilization of water in trees in moisture limited habitats. The literature surrounding jack pine response to the environment hypothesizes that due to the environment that jack pine is typically found (i.e., rocky outcrops and well drained areas), that jack pine is restricted in regard to available water and thus demonstrates a unique response to precipitation, similar to the responses of trees growing in warmer and drier regions (Ziaco & Biondi, 2018; Maillet et al., 2022). The trends observed in the 2017 data at Treeville are similar to the timing observed in Deslauriers et al. (2007) in respect to the responses to precipitation and the occurrence SRI phases during the season.

The SRI phase was observed 41 times out of the 104 circadian cycles recorded during the 2017 season. Based on the literature of when the SRI phases are triggered, it is expected that variation in environmental inputs (i.e., precipitation) influences the amount of SRI phase recorded during a season (Ziaco & Biondi, 2018). To further investigate the patterning of SRI phases and variation in the duration of circadian cycles, long (LG) and regular (REG) cycles were assessed. Monthly Frequency distribution (%) of ΔR+ and ΔR- were also assessed but the trends for these data were similar to observations of the distributions of LG and REG cycles for the 2017 season, and do not provide additional insights into the seasonal trends. The stem cycle approach allows for the circadian cycle length to vary daily as opposed to assuming a 24-hour cycle when using the daily cycle approach. These variations occur in response to the lengthening or shortening of phases in the circadian cycle, as well as whether an SRI phase occurs. Cycle length variation within the growing season provides an illustration of the variation that exists during the growing season. To observe trends of the variation in the lengths of the growing season, cycles were divided into two groups, REG, and LG cycles. REG cycles are defined as cycles lasting a maximum of 28 hours and LG cycles are defined as those surpassing 28 hours. The frequencies of REG and LG cycles during the growing season were used to assess the variability of the circadian cycle length throughout the study period. For the 2017 season at Treeville, 77% of cycles were characterized as REG cycles and 23% LG cycles. May had the highest frequency of observed LG cycles, which aligns with the timing of stem rehydration and the onset of enlarging cell formation at the start of the growing season. June had higher rates of longer cycles than what was recorded in July and August, corresponding to the switch from early cell development and formation of new cells to wall-thickening and lignification (later in June). Lowest observed frequency of both ΔR+ and LG cycles were observed in August, with an increase in frequency observed in September. Similarly,

data from automatic band dendrometers on balsam fir in the boreal regions of Quebec, where an increased frequency of LG cycles was observed at the start and at the end of the season, and lowest during mid-season observations (Deslauriers et al., 2007). The increased frequency of LG cycles observed at Treeville in May is a combination of both onset of growth as well as spring rehydration of the stem. Deslauriers et al. (2007) indicated the variation in LG and REG cycles throughout a full year of study, including overwinter dynamics, indicated confusion may exist when relying solely on dendrometer signals for the interpretation of growth onset due to the dynamics of water uptake as snow melt occurs. Similar to what was recorded during 2017 at Treeville, Malliet et al. (2022) indicated precipitation was the main driver of the changes observed in stem radius during the season. Other studies using dendrometer measurements also indicated the difficulty of accurately determining the start of cambial onset and wood formation versus spring rehydration when relying solely on dendrometer signals (Cocozza et al., 2016). It is noted that LG cycles recorded at the beginning of the season may be related to stem rehydration versus the onset of wood formation. It is suggested that dendrometer analyses are paired with cellular development analysis, like microcores, to better define seasonal onset of stem growth.

5.1.3 Summary

5.1.3.1 Onset of growth

The onset of the development of newly formed xylem cells began in late May to early June for the 2017 season, with June 6 (DOY 157) marking the onset of cell formation at the Treeville site. This transition began when daily average air temperatures hovered around 6.8°C. The results from the Treeville site indicated similar timing of cell development onset as observed for jack pine literature in southern boreal forest sites (Zhai et al., 2012; Ko Heinrichs et al., 2007). Zhai et al., recorded onset of cell development to occur at 5.3ºC at their southern boreal study site. In addition,

the average daily air temperature around the time of the onset of xylogenesis aligned with the cell development temperature thresholds of 4-5ºC (Rossi et al., 2008; Rossi et al., 2007; Ko Heinrichs et al., 2007). The higher seasonal frequencies of ΔR+ at the start of the season in May signaling spring rehydration and water movement in the stem in early season (Deslauriers et al., 2007). The highest seasonal frequencies observed in June can be attributed to water movement in the stem and radial increase due to the onset of xylem cell formation and the period of rapid growth.

5.1.3.2 Main period of growth

An initial period of rapid growth was recorded on June 21 (DOY 172), at around 0.28 cells per day for all phases of xylogenesis, mature cell development rate was slightly lower at 0.26 cells per day. The timing observed at Treeville aligned with the seasonal longest photoperiod during the summer solstice, which occurs annually on June 21. This timing of rapid growth observed at Treeville was consistent with the timing of rapid growth around longest photoperiod day as observed by Zhai et al. (2012), rates peaking in June, and Ko Heinrichs et al. (2007), increased rates of cell production on June 28. It is not surprising that the longest photoperiod would allow for increased growth due to its relationship with photosynthesis. Given temperatures are optimal for growth, above 4-5ºC during that period. It has also been demonstrated that precipitation, specifically June precipitation, is important for growth. Pisaric et al. (2013) indicated June precipitation as a limitation for growth using historical ring width analysis. This relationship was tested for total mature cell counts from 2017 dating back to 2007. It was evident for years when June precipitation was low there was a reduction in final cell count. Recognizing that other factors may limit or enhance growth possibilities (e.g., timing of cell development onset, seasonal nutrient availability, phytohormonal controls, etc.). Increased seasonal GDD did not outweigh the growth response to reduced precipitation for this period, specifically in June, suggesting that temperature

controls for growth providing moisture is not limited. A similar observation was made by Malliet et al. (2022) suggesting that warmer temperatures are only favourable for growth when it does not limit moisture or exasperate evapotranspiration rates. The dendrometer data also recorded a strong relationship between precipitation and stem radius change observed at the Treeville site, most notably in the occurrence of the SRI phase, ΔR+, and LG cycles during the study period. Highest SRI phases frequency was observed in June, aligning with the period of rapid growth observed in the Treeville site. The timing on the onset of wall-thickening phase occurred around the June 20 (DOY 171) sampling date, the transition of allocation of efforts from the strictly producing new enlarging cells to adding efforts to produce a secondary wall to the newly formed cells was observed in the slope change in the dendrometers as demonstrated by the homogeneity test. The change in slope recorded in the dendrometers occurred on July 4 (DOY 185) signaling of the change in growth mechanisms within the tree stem in response to the onset of the wall-thickening phase on June 20 (DOY 171). The frequency of both ΔR+ cycles and LG cycles were lowest in both the month of July and the month of August. Signaling the physiological change in xylem formation from a new cell development to the addition of secondary wall and maturation of cells (Deslauriers et al., 2007). This period highlights slower cell development leading up to the cessation of cell formation, which marks the end of the growing season.

5.1.3.3 End of growth

The end of the growing season was estimated to occur in late August to early September prior to the 5 September (DOY 248) sampling date when no more cells were observed in the development phases of xylogenesis. This timing is consistent with the literature for jack pine in lower boreal forest sites, estimating the end of wood formation in August. A site average of 13±6 cells were recorded in the 2017 season. Zhai et al. (2012) noted end of seasonal growth on 9

August, when temperatures were ~11.2ºC. Ko Heinrichs et al. (2007) observed cessation of cell development in late August. For 2017, the growing season was on the lower end of what has been observed for jack pine at 84 days. Ko Heinrichs et al. (2007) reported growing season lengths upwards of 180 days with ~150 cells in the yearly ring in lower latitudes of the Canadian boreal forest. Zhai et al. (2012), at a study site in a southern Canadian boreal forest site, reported similar growing season length at 91 days, but final seasonal cell count was more than 6 times the amount observed at Treeville in 2017. This is most likely due to the increased rate of cell production, 1.22 cells per day, compared to the lower rates of cell production, 0.28 cells per day, recorded at Treeville in 2017 (Zhai et al., 2012). The results from the microcore analysis at the Treeville site provided insights into the characteristics of the growing season in comparison to what has been observed in the literature. The use of both methods for characterizing the timings observed in cell production and stem circadian cycle provided insights into how jack pine is responding to its environment at its northern growth limits, as well as provided the opportunity to compare the timing of these events to the literature. In particular, the analysis of the data from 2007 to 2017 highlighted the relationship between annual cell counts and June precipitation.

Within the dendrochronology field, there is discussion whether the data from dendrometers could be used to replace the more labour intensive microcore data to examine growth responses (Ko Heinrichs et al., 2007; Mäkinen et al., 2008). The comparison of the two datasets for the 2017 season demonstrates some similarities, and with additional years of analysis may allow the replacement of one method (dendrometers) over the other (microcores). At this time, the recommendation would be to continue both methods to accurately define how the signals are being expressed within each data set.

5.2 Conclusion

Microcore data from the 2017 season provided new insights into the onset, duration, and end of the formation of woody cells of jack pine at the Treeville site near Yellowknife, NT. The information collected from the microcore dataset provides a great baseline understanding of xylogenesis timing, including observations of the periods of rapid cellular development. Discussion around the timing observed in the 2017 season indicates the physiological responses, especially the timing of the day with the longest (photoperiod). Intra-annual research such as presented in this thesis offer two major contributions to our understanding of the global climate. First the detailed understanding of how weather contributes to the formation of wood can help produce a better understanding of climate-growth relations for jack pine enabling more robust reconstructions of past climatic conditions for northern regions where instrumental climate records are of short duration. In particular, the hydrological variability for this region. Second, the information collected from intra-annual datasets, in the greater context of current climate change projections, will deepen our understanding of the physiological response of tree growth under changing climate conditions with regards to carbon allocation. At the Treeville site, it was noted that onset of cell formation began when daily average air temperature increased above 5^{o}C, comparable to the threshold temperatures proposed by Rossi et al., 2008. This is a good indication that under warming conditions that the onset of cell formation may begin to occur earlier if favourable conditions occur earlier in the season, as well if favourable growing conditions extend beyond the normal seasonal end date which was observed later in August. There was some nuance to the trends in the 2017 season due to microcore processing errors and thus definitive calculations of the end of the growing season are not conclusive. Most of the annual $\Delta R+$ and LG cycles were recorded in the early part of the season, most of which could be explained by the strong relationship

between cycle lengths and precipitation as well as relationship between stem swelling and wood formation. As discussed, the trends observed in the 2017 season do point to a strong relationship between stem radial fluctuations and precipitation, supporting previous research hypothesizing the important relationship between jack pine growth and water availability. Again, results within the larger body of literature for jack pine growth relationship to precipitation, the results recorded in the 2017 dendrometer data are not surprising (Malliet et al., 2022; Pisaric et al., 2009). Strong correlations between cycle lengths and the occurrence of SRI phases were observed. However, despite the dendrometer signals having strong correlations with precipitation, temperature has the largest control on timing of cell production, especially for spring growth reactivation. For this species it is expected that when evapotranspiration requirements are met temperature has the most important impact on the rate of cell production and the amount of wood formed during the year due to the impacts of growing season length and the productivity of the period of rapid growth. In the dendrometer signaled that temperature only had a correlation with length of the contraction phase in 2017. The timing of cell production demonstrated the relationship between the timing of increased cell development and the longest photoperiod occurring during the annual summer solstice on June 21.

The relationship between the timing of xylogenesis and the dendrometer data was assessed by examining the timing of the homogeneity (slope) change, which occurred on July 4 (DOY 185) in relation to the timing of cell wall-thickening phase which occurred on June 22 (DOY 173). The signal of the change in growth priorities, from developing cells to wall-thickening cells was observed in the 2017 data. Overall, the information collected from both methods provides insights into the 2017 growing season and the timing of growth. To further understand how jack pine grows in this region, additional years of data collection are suggested. The literature has demonstrated

that growth is variable among species and sites, putting emphasis on the importance of developing specific climate growth relationships for all trees to assess the characteristics of growth during the season to better understand our past, using dendrochronology climate reconstructions and future, by having better estimations of tree growth response under changing climatic conditions.

CHAPTER SIX:

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

The overarching goal of this research was to collect baseline information on jack pine growth and responses to weather. This information will help better understand the drivers of jack pine growth. A deeper understanding of the intra-annual dynamics of jack pine growth can aid in creating more robust reconstructions of climate using dendroclimatology methods and assist in creating better forecasting of tree growth responses under current climate change projections. More specifically, the aim of this research was to characterize xylogenesis and stem radial fluctuations for a single growing season using microcores and dendrometers. The three objectives proposed at the outset of this research and associated conclusions for each are described.

Objective 1. Identify the timing of onset and cessation of wood formation (xylogenesis) seasons, the timing of xylem cell phase transitions, and highlight period(s) of rapid seasonal cell development using microcores. Identify potential controls for growth considering current literature for jack pine.

The timing of onset of cell development was determined using microcores and analysis of cell development. Onset of cell development at Treeville occurred on June 6 (DOY 157) when mean temperatures were 6.8°C. This is slightly warmer than threshold temperatures (4-5ºC) proposed by Rossi et al. (2008) for the onset and maintenance of cellular development. Zhai et al. (2012) recorded onset of cell development for jack pine in southern boreal forest occurred ~7 May, about a month earlier than at Treeville when mean temperatures were ~5.3ºC.

At Treeville, there was a 2-week period between the onset of the enlarging phase to the onset of the wall-thickening phase. In comparison, Zhai et al. (2012) observed a 1-week transition phase from enlarging cells to the beginning of wall-thickening in mid-May.

Cellular development rates at Treeville indicated a period of rapid growth coinciding with the period of highest photoperiod on June 21, which is consistent with the other jack pine growth studies (Ko Heinrichs et al., 2007; Zhai et al., 2012). Cell production rates during the period of rapid growth at the Treeville site were much lower than what occurs in southern boreal forest study sites. In comparison to the cell production rate at Treeville of ~0.26 cells/day, Zhai et al. (2012) reported rates of 1.22 cells/day during the period of rapid growth.

Assessment of annual cell counts from 2007-2017 indicated a relationship with June precipitation. The extended analysis between 2007-2017 indicates that higher cell counts were correlated with increased June precipitation at Treeville. This result is consistent with annual ring-width data for jack pine in the Yellowknife region, where growth was highly correlated with total June precipitation (Pisaric et al., 2009). The relationship between total June precipitation and annual cell count suggests the importance of moisture requirements for growth in addition to temperature thresholds. Recent findings by Malliet et al. (2022) indicate that warmer seasonal air temperatures are only favourable for growth when moisture requirements are also met.

The cessation of wood formation at the end of the growing season was not well defined for the 2017 season due to sampling errors. The end of the growing season for Treeville is estimated to occur during late August to early September when no more cells were counted in developing phases of xylogenesis on 5 September (DOY 248) sampling date. These results are consistent with other studies on jack pine growth, indicating end of seasonal growth occurs in early August (Ko Heinrichs et al., 2007; Zhai et al., 2012). The length of the 2017 growing season at Treeville was

84 days. This is similar to the growing season length observed by Zhai et al. (2012) at ~90 days for jack pine growing in the southern Canadian boreal forest. The number of cells produced at the end of the season at Treeville was much lower than what has been observed for jack pine in lower latitudes of the boreal forest, with a site average of ~13 mature cells at Treeville. Zhai et al. (2012) reported close to 150 cells in a similar length growing season (~90 days), compared to 84 days for Treeville. This difference is attributed to the lower cell development rates recorded at the Treeville site.

Objective 2. Determine the timing of jack pine circadian cycle and seasonal stem cycles using dendrometers.

Circadian cycle dynamics indicated that the contraction phase occurred in the morning lasting till evening when the expansion phase began. The timing of cycle dynamics at Treeville is similar to estimates from study sites in more southern boreal forest sites in Canada, with slightly longer contraction phases being observed at the Treeville site. In contrast to the SRI timing observed at Treeville in 2017, Deslauriers et al. (2007) found SRI phases occurred in the evening at sites in Northern Quebec. The SRI phase was triggered in 39.4% of daily cycles in 2017, most of which occurred in May, June, and September.

As expected, temperature and precipitation had impacts on the recorded variation in stem size. In general, stem size variation was mainly impacted by temperature, however, when transformed into cycle phases, temperature was negatively correlated with the sitewide daily stem radius variation, and precipitation was positively correlated.

Analyzing results from the *stem cycle approach*, the SRI phase had a strong positive correlation with precipitation throughout the growing season and no correlation with temperature.

These results are consistent with findings presented by Malliet et al., (2022) for jack pine in Saskatchewan. Higher ratios of ΔR+ were observed during seasonal re-hydration, during the time of rapid cell development, and after cell growth ended. Temperature had no significant effects on the occurrence SRI phase, only showing significant negative correlations with the magnitude and duration of contraction phase.

Objective 3. Evaluate the challenges and benefits of microcores and dendrometer data to assess jack pine growth in the northern environment.

Microcore weekly cell counts were used to assess the timing of xylem cell phase transition during the 2017 season and provide insights into how weather, particularly temperature, is a controlling factor for the onset and maintenance of cell development. Higher precipitation demonstrated a strong relationship with seasonal cell counts and an increase in the frequency of SRI phases.

Microcore analysis provided information on the period(s) of rapid growth during the 2017 season. The peak of cells/day rate was observed in late June, coinciding with the longest photoperiod of the year (and growing season). The peak of cells/day was also synchronous with June precipitation which was previously suggested to be an important growth-controlling factor (Pisaric et al., 2009). Dendrometer measurements showed that the longest circadian cycles were observed at the start of the growing season as a result of both stem rehydration in early May and eventual onset of xylogenesis and the development of enlarging xylem cells. Dendrometer data was not used to specifically identify the timing of rapid growth as expressed by the dendrometer measurements, although the frequency of SRI phases, LG/REG, and ΔR+/ΔR- cycles throughout the season coincided with changes in wood formation processes identified in the microcore analysis.

Using multi-year mature cell development counts, a relationship between annual mature cell counts and June precipitation was observed. Similarly, a positive relationship was observed in dendrometer responses to precipitation throughout the 2017 season. In particular, the SRI occurrences during the season showed relationships with precipitation events which is in agreement with previous dendrochronological climate reconstructions using jack pine in the Yellowknife region (Pisaric et al., 2009).

Literature suggests the change in the dendrometer responses can indicate the transition from enlarging cells to the onset of the wall-thickening phase and development of the secondary wall (Deslauriers et al., 2003, 2007). Dendrometer measurements identified a site wide slope change in radial displacement measurements on July 4 (DOY 185). This shift recorded in the dendrometer data aligned with the timing of wall-thickening cell development onset on June 22 (DOY 173). The use of dendrometers to estimate this timing was reasonably accurate for the 2017 season, demonstrating potential use of dendrometer measurements to detect this transition without the use of microcores. However, there was significant variation in the timing of this shift in the dendrometer data compared to the variation in microcore data for the onset of the wall-thickening phase. It is clear, despite the labour required for microcores, that they are more accurate in defining periods of cell development than what is observed in the dendrometer signals. In previous research, the growth period in dendrometers was defined using the change in slope of the dendrometer measurements throughout the season (Deslauriers et al., 2003, 2007).

6.2 Recommendations for future research

A single year of data provides a baseline understanding of the timing and characteristics of jack pine growth during the growing season of 2017 in Yellowknife, Northwest Territories. The

recommendations for future research, and recommendations for the use of these methods are detailed below.

The aim of this research was to characterize xylogenesis and stem radial fluctuations for a single growing season. The use of microcores and dendrometers were successful in providing baseline information on the growth characteristics of jack pine in Yellowknife, Northwest Territories during the 2017 study period. Recommendations for modifications to the methods used in the study, as well as recommendations for future or continued research, are important for the advancement of the understanding of jack pine growth in this region. Based on the results and findings of this research the following recommendations are made:

Recommendation 1:

Modification of the processing of microcore samples. The microcoring technique outlined by Wegner (2013) used an epoxy glue to secure microcore samples to the wooden holder for processing using a microtome. It was noted that during this thesis the use of the gluing technique resulted in occasional rotation of the microcore samples during the drying period of the glue, and thus accurate transverse sections were not always possible. This resulted in blurry, sometimes unusable samples. In addition, the friction of the glue on the microtome blade occasionally caused tearing of microcore samples. It is recommended to modify the methods by Wegner (2013) to reduce the impacts of glue on the sample. A solution could be to use glue only on the base of the sample to reduce the drag of glue on the microtome blade.

Recommendation 2:

Assess the use of the GAM when calculating rates of cell production with low total annual cell count. During the 2017 growing season, cell/day rate calculations indicated two peaks during

the growing season. The initial increase in cell development rate aligned with results from previous research (e.g., Cuny et al., 2013; Ko Heinrichs et al., 2007; Zhai et al., 2012), recording highest rates of cell production around the time of longest seasonal photoperiod day (e.g., summer solstice). The second increased rate of cell production observed at the Treeville site was not consistent with what has been depicted in the literature. Speculation as to how the GAM responds with low cell count, and the potential overestimation in response, may explain the observed second increase in cell development. Without a comparison for this site, it is difficult to tie these values to actual biological increases in cell production. Additional sampling years will aid in identifying year-to-year trends for this species in this region and the suitability of the GAM for locations with low annual cell development.

Recommendation 3:

Expand the study period to (1) fully capture the onset of wood formation, including cambial reactivation, prior to the onset of xylem cell formation and subsequent cell development, and (2) fully capture the end of the growing season (e.g., all trees no longer producing cells in developing phases of xylogenesis). Lengthening the study period while using both dendrometer and microcore data will ensure both start and end of season data is captured.

Recommendation 4:

A multi-year study should be carried out to further assess patterns of growth and better evaluate weather and environmental controls on the mechanisms of seasonal production of wood. Longer-term studies can develop a better understanding of the biological mechanisms of tree growth as they relate to the interpretation of climatic signals contained in tree rings (De Micco et al., 2019; Friend et al., 2019). Multi-year studies also permit year-to-year comparisons between

phenological phases of cell growth. For example, comparisons can be made of the timing of initial xylem phase onset, phase transitions, and the timing of periods of rapid growth. In a single study year, the timing of these events can be discerned, but it is not certain how well they characterize these parameters from one year to the next. Carrying out a multi-year study will more accurately define the timing of xylem phase initiation and cessation throughout the growing season and will be critical for defining important temperature controls for onset of growth, rates of cell development and transitions between phases, similar to what has been defined by Rossi et al. (2008) for conifer species in lower latitudes of the boreal forest.

Recommendation 5:

Perform a similar study of jack pine growth at additional sampling locations throughout the northern portion of the boreal forest. Research suggests that variability exists between species, locations, and seasons (Rossi et al., 2008). To fully capture this variability, it is recommended to assess jack pine growth across a variety of locations.

Recommendation 6:

Researchers seeking to fully define weather and climatic controls on the growth of jack pine within a northern context should continue to use both microcoring and dendrometer techniques to have a full assessment of the complexity of wood formation and tree growth. This thesis used a combination of two proxy methods to assess wood formation processes and stem growth of jack pine. The microcoring technique, although more laborious, provided detailed information concerning wood formation and xylogenetic processes during the growing season. Automatic point dendrometers provided insights on the radial fluctuations of the stem, including identifying the typical diurnal cycles and responses to weather of jack pine during the study period.

Dendrometer signals may oversimplify the growth processes and therefore this method is not recommended to be used independently of microcores (Deslauriers et al., 2007; Cocozza et al., 2016; Ziaco & Biondi, 2018).

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APPENDICES

Appendix I: Sample Depth

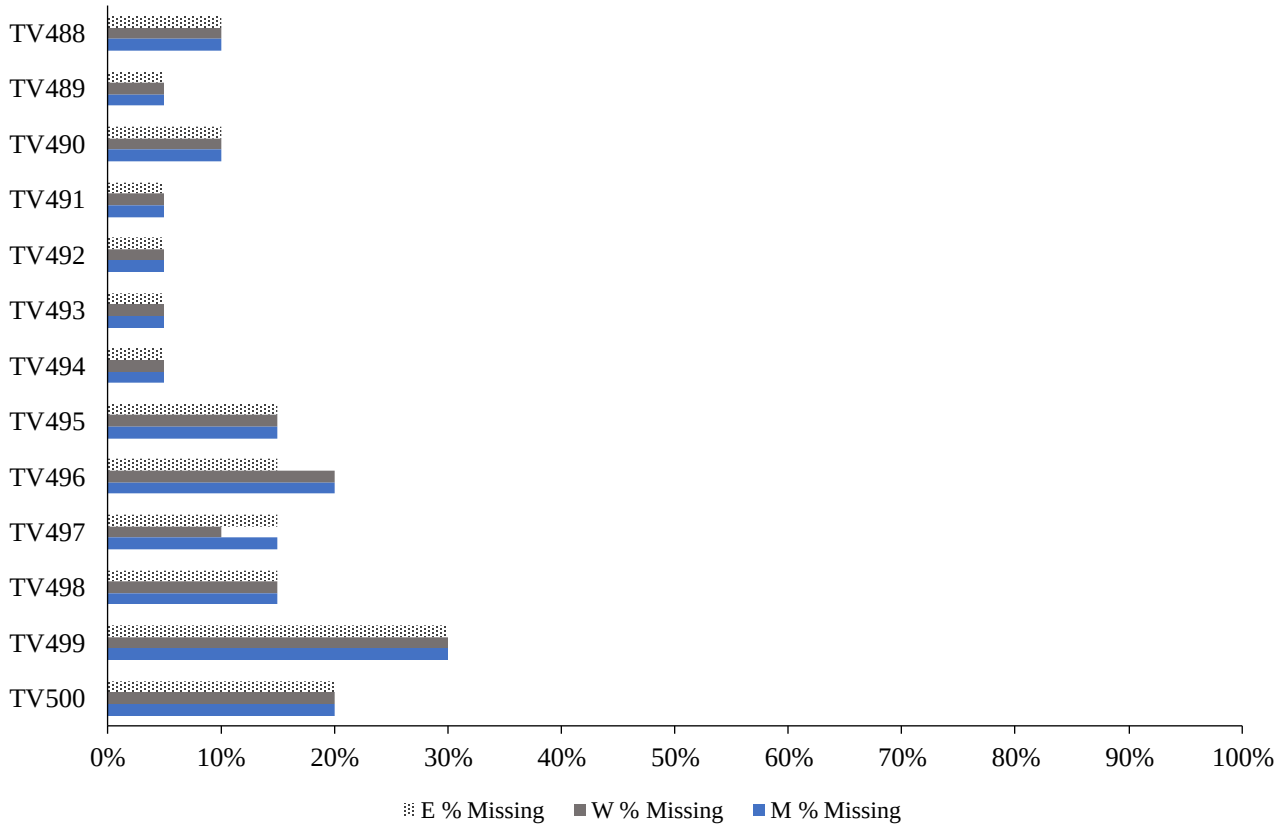

Figure A.1. Percentage of missing microcore samples for each individual tree. Bars depict the percentage (%) of missing counts for each tree, listed by their identification code number, due to sample structural consistency.

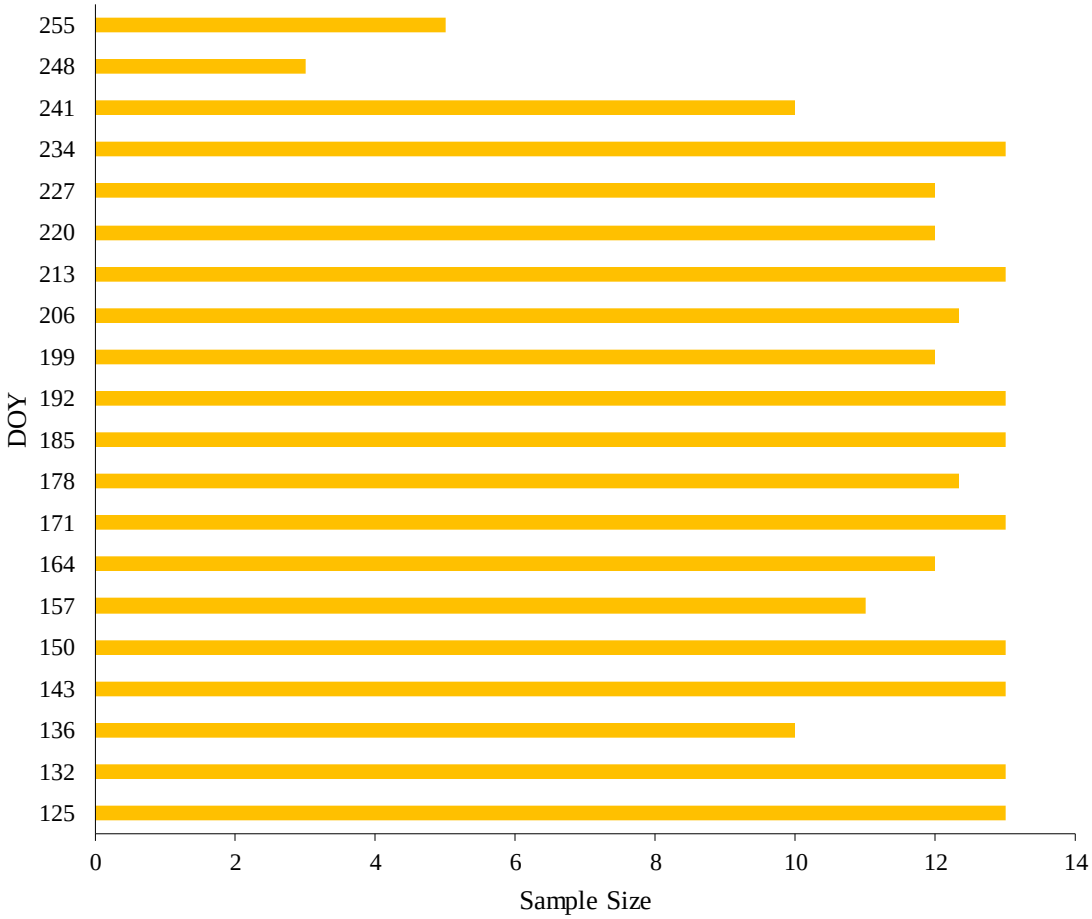

Figure A.2. Microcore sample size by sampling date Day of year (DOY) for the 2017 season.