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Abstract

The boreal region of Europe has seen a notable increase in spring temperatures which affects the onset of transpiration. Freeze-thaw temperature cycles are characteristic of early spring, but transpiration is difficult to measure under these conditions. Sap flow sensors can estimate transpiration in trees by using the relationship between wood thermal properties (volumetric heat capacity and thermal diffusivity) and stem water content. Rapid temperature changes that occur during freeze-thaw cycles are known to introduce error in these calculations, and the relationship between stem water content and thermal properties needs validation across temperature gradients to produce reliable estimates of transpiration in spring. The purpose of this study is to achieve the following research aims: 1) Establish a relationship between changes in water content and volumetric heat capacity of three boreal tree species: birch, pine and spruce. 2) Establish a relationship between changes in volumetric heat capacity and thermal diffusivity of the three boreal tree species. 3) Identify whether heat pulse sap flow sensors can reliably estimate thermal properties within a temperature range of -15 to 25ºC. 4) Use point dendrometers to determine the role of stem water content in diameter fluctuations during freeze-thaw cycles. The results showed a temperature-dependent limit to reliable measurements of stem water content using current sensor methods. Thermal properties can be related to water content, but require parameterization near the freezing threshold and for rapid temperature change. Stem expansion from ice formation does occur during freezing, and should be taken into account when using diurnal cycles of stem diameter change to mark the onset of spring transpiration. This study contributes to understanding whole-tree water use and measurements of transpiration during shifting spring conditions, with implications for measuring the effect of climate change on forest functioning.

Keywords: boreal forest, stem water content, sap flow, thermal properties, transpiration, freeze-thaw

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Abbreviations

BOKU	Vienna University of Natural Resources and Life Sciences (Universität für Bodenkultur Wien)
ET	Evapotranspiration
K	Thermal Diffusivity of Sapwood
Ө	Volumetric Water Content
ρc	Volumetric Heat Capacity
FDR	Frequency domain reflectometry
HPM	Heat pulse method
HRM	Heat ratio method
MHR	Maximum heat ratio
TDR	Time domain reflectometry
T	Transpiration
ΔT	Change in temperature
SLU	Swedish University of Agricultural Sciences

1. Introduction

1.1   The boreal forests

Boreal forests are the second largest biome on Earth, located at high latitudes between 45° and 70° and representing roughly one-third of the global forest cover (Bonan, 2008; Bradshaw et al., 2009; Olson et al., 2001). The dominant species in the boreal forests of Sweden are Norway Spruce (*Picea abies*), Scots Pine (*Pinus sylvestris*), and Silver birch (*Betula pendula*) (Soja et al., 2007). Boreal forests are important regulators of global water and energy fluxes, and store an estimated 30% of terrestrial carbon (Bonan, 2008; Bradshaw & Warkentin, 2015; D. Chen et al., 2018). The boreal region of northern Europe is expected to experience a faster rate of climate change than temperate regions, and a notable increase in winter and spring temperatures (Bonan, 2008; X. Chen et al., 2015; Kjellström, 2004; IPCC, 2013). The persistence of snow cover in boreal forests produces a strong cooling effect through albedo, and changes in the seasonal timing and duration of snowpack is likely to have a major impact on global climate and carbon cycles (D. Chen et al., 2018; Kropp et al., 2022; Moen et al., 2014).

1.2   Hydrology of the boreal forest

Boreal forests are characterized by short growing seasons, cold winter temperatures, and long persistence of snowpack in spring (Baldocchi et al., 2000). The accumulation of snow over winter and gradual release during spring drives the water balance of boreal forests, and the ecosystem is adapted to these strong seasonal patterns (Gutierrez Lopez & Laudon, 2023; Kropp et al., 2022; Nehemy et al., 2023). Changing climate conditions in the region have resulted in earlier spring onset and have begun to decouple the timing and relationships between components of forest water balance such as snowmelt, discharge, storage, and evapotranspiration (ET) (Gutierrez Lopez & Laudon, 2023; Pierrat et al., 2021). This is predicted to have a strong impact on boreal forest hydrology, productivity and ecosystem services, and may lead to feedbacks in regional and global climate (Gutierrez Lopez & Laudon, 2023; Hasper et al., 2016).

As temperatures rise, an increase in days above freezing during early spring will likely result in freeze-thaw cycles (Bonan, 2008; Kjellström, 2004). Naturally occurring freeze-thaw cycles are a key characteristic of boreal forests, which drive the slow snowmelt in spring. A seasonal shift in their occurrence could disrupt the water balance of boreal forests, with negative impacts on water storage and discharge in spring due to early melting (X. Chen et al., 2015; Gutierrez Lopez & Laudon, 2023; Kropp et al., 2022; Zona et al., 2022). As boreal forest species are highly reliant on the seasonal patterns of freeze-thaw and gradual snowmelt, effects of climate change on these ecosystems are likely to be driven by these changes in spring timing and conditions (Chan & Bowling, 2017).

1.3 The role of trees in boreal forest hydrology

Evapotranspiration (ET) in trees represents two different components of water flux in forest ecosystems, with the transpiration (T) component controlled by plant physiological processes, i.e. stomata, and the evaporation (E) component driven primarily by environmental conditions, i.e. the vapor pressure deficit (Kozii et al., 2020). This means the two components of ET are likely to have different responses to changing environmental conditions, which will alter the proportion of T/ET, and subsequently alter which component plays a greater role in the water balance under specific conditions (Gutierrez Lopez & Laudon, 2023; Kozii et al., 2020). Boreal ecosystems experience strong seasonal variation in the relative importance of different water balance components (Kozii et al., 2020). During the growing season, when ET is the dominant driver of ecosystem water flux, T represents an average of 40% of annual ET in boreal forests (Gutierrez Lopez & Laudon, 2023; Kozii et al., 2020).

The transition between winter and spring in boreal forests can have variable timing, and this is expected to become even more variable as winter conditions become more unstable due to regional warming (Kjellström, 2004). Conifer-dominated forests lack a phenological demarcation between the growing season and dormant season, so there is a potential for rapid shifts between dormant and transient states in response to environmental conditions (Barnard et al., 2018). It has been shown that photosynthesis and transpiration in boreal conifer trees can continue during warmer periods in winter (Baldocchi et al., 2000; Sevanto et al., 2006; Turcotte et al., 2011). Furthermore, the increasing air temperatures and resulting freeze-thaw conditions of spring transition likely drive the initial onset of spring photosynthesis for boreal conifers (Pierrat et al., 2021). This suggests that an increase in the number of above-freezing winter days could have substantial implications for forest ecosystem functions, annual carbon uptake, and hydrologic partitioning.

There is still a lack of knowledge about tree water use in ecosystems which experience winter dormancy and the partitioning of ET during the winter and spring transition (Nehemy et al., 2023; Pierrat et al., 2021). Therefore, measurements of tree water use and transpiration in boreal forests during the seasonal transition are an important part of addressing this knowledge gap. Studies which focus on winter and the spring transition may improve predictions of climate change on boreal forests (Chan & Bowling, 2017). Measuring transpiration and water usage in the conditions that characterize the transition between winter and spring would improve our understanding of water use and partitioning in boreal forests, and the potential impact of climate change on regional ecosystem functioning.

1.4   Water content in green stems

Water content inside living stems is an important aspect of whole tree water use and transpiration, as water is transported and stored in the sapwood and phloem (Steppe, Sterck, et al., 2015). Stem water storage contributes to ET even under conditions of sufficient soil water (Matheny et al., 2015; Steppe, Sterck, et al., 2015; Zweifel et al., 2001), and can be heavily depleted during daily transpiration, especially for large trees (Hao et al., 2013; Lu et al., 2017; Matheny et al., 2015; Phillips et al., 2003). Warm days with high evaporative demand during winter and spring can drive ET in boreal forests, but is often limited by root uptake and lack of water availability in frozen soils (Baldocchi et al., 2000; Pierrat et al., 2021). During photosynthesis in early spring, in the absence of unfrozen soil water, trees must rely on water stored in the stem or extract meltwater through foliage (Harpold et al., 2015; Sevanto et al., 2006; Zweifel et al., 2001). Water storage in the stem and bark is an important buffer to prevent xylem cavitation in these conditions (Hao et al., 2013; Matheny et al., 2015; Zweifel et al., 2001), and photosynthesis can also occur in tree stems as an additional buffer for periods of low foliar gas exchange and promoting embolism repair (Berry et al., 2021).

The water stored in tree stems can vary between species and individual trees due to differences in wood properties, and environmental factors such as soil water availability (Matheny et al., 2015). Stem water content can be estimated with direct and indirect approaches (Berry et al., 2021; López-Bernal et al., 2012; Matheny et al., 2015; Sevanto et al., 2006). Direct stem water content measurements involve measuring gravimetric water loss using weighing lysimeters, while indirect approaches can use either time domain reflectometry (TDR) or frequency domain reflectometry (FDR) (such as TEROS12 by Meter Group). Weighing lysimeters are expensive and can be inconvenient to use, and consequently indirect options are commonly preferred (López-Bernal et al., 2012; Lopez, 2012; Matheny et al., 2015; Vandegehuchte & Steppe, 2012).

Additionally, water content also results in short term variations in stem size (Drew & Downes, 2009), which is relevant for measurements of tree productivity and carbon assimilation, as it might affect growth estimates based on radial expansion of stem circumference. Further changes in stem water content influence wood properties and it is known to influence sap flow measurements (Vergeynst et al., 2014), since both thermal dissipation and heat pulse sap flow methods rely on the thermal properties of wood. For example, decreases in stem water content have been shown to increase the maximum temperature difference used as a reference in heat pulse methods (Vergeynst et al., 2014), which result in increases in measured sap flow rates (Zweifel et al., 2001). Nonetheless, changes in stem water content are not often considered in calculations of sap flux (Vergeynst et al., 2014). López-Bernal et al., (2012) demonstrated that water content calculated from heat pulse sensors has a strong correlation with gravimetric measurements at high water contents, but diverged as moisture content decreased. This suggests that calibration is required to improve measurements under environmental conditions which result in changes in stem water content, such as freezing and depleting of internal water storage.

While methods for estimating stem water content are well-established, there are limited works that focus on stem water content during the winter-spring period (Irvine & Grace, 1997; Nehemy et al., 2022; Pierrat et al., 2021). Consequently, there is a need for studies which can measure the water content of green stems at low and rapidly changing temperatures to improve our understanding of whole-tree water use during winter and spring conditions, and the potential implications of seasonal shifts on forest functioning.

1.5 The influence of water content and thermal properties on sap flow estimates

Measuring sap flow in trees is used to estimate transpiration and water use across many ecosystem types (Green et al., 2003; Mencuccini et al., 2019; Smith & Allen, 1996; Vandegehuchte & Steppe, 2013b). Most studies on sap flow focus on the growing season, excluding winter conditions (Chan & Bowling, 2017; Graf et al., 2015; Kozii et al., 2020). Springtime sap flow conditions feature rapid temperature change around the freezing point, which result in freeze-thaw cycles. Under such conditions, thermal properties can change significantly and affect the measurement of water content in the wood, which in turn affects estimates of sap flow and consequently tree transpiration (Chan & Bowling, 2017; Lopez et al., 2021; Peters et al., 2018). Sap flow methods that rely on heat pulses and wood thermal properties such as the heat ratio method (HRM) or maximum heat ratio (MHR) method (Lopez et al., 2021), are known to be more accurate (see Section 1.6.4) But some thermal

properties are often assumed for these methods, or general values are assigned to several species, potentially resulting in errors in sap flow estimates. To improve measurements of sap flow and properly assess winter and springtime transpiration, there is a need for proper estimates of thermal properties which will lead to better stem water content measurements (Lopez et al., 2021).

HRM and MHR are optimal for measuring slow, reverse, and zero flows, and are best for extreme environments like high latitude boreal forests (Burgess et al., 2001; Green et al., 2003; Lopez et al., 2021; Vandegehuchte & Steppe, 2013b), where low power consumption is highly desirable. However, current algorithms for calculating sap flow are not designed to deal with the fast changes in temperature commonly observed in boreal forests, and may be unable to produce accurate representations of whole tree water uptake when temperatures fluctuate around the freezing threshold (Lopez et al., 2021; Peters et al., 2018). One reason why many methods fail during fast temperature changes, is that thermal properties such as volumetric heat capacity (ρc) and thermal diffusivity (K) also change as the sap crosses the freezing point. Thermal diffusivity is measured as the time required for wood to equilibrate changes in temperature, and volumetric heat capacity is measured as the amount of heat that can be stored during changes in temperature, without causing phase change (Hrčka & Babiak, 2017). Volumetric heat capacity is a key parameter used in the equations to estimate sap flow using heat pulse methods, and is linearly proportional to the volumetric water content (Figure 1) and thermal diffusivity of sapwood (Vandegehuchte et al., 2012, 2015). Consequently, precise estimations of these thermal properties at different sapwood temperatures and water contents are crucial for sap flux density calculations (Green et al., 2003; Lopez et al., 2021; Steppe et al., 2006; Vandegehuchte et al., 2012; Vergeynst et al., 2014).
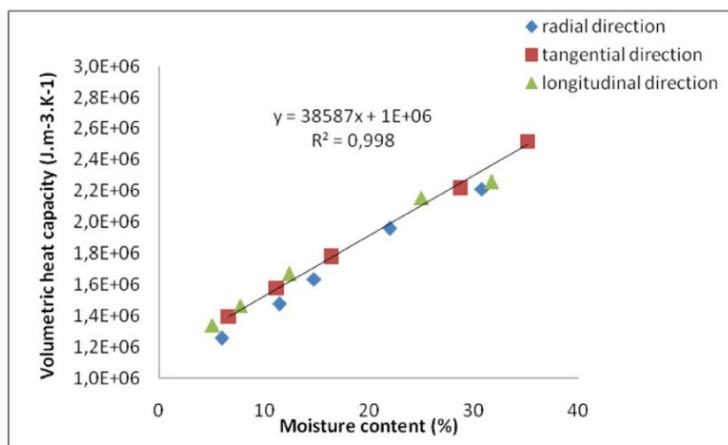
Figure 1. The typical relationship observed between volumetric water content (Ѳ) and volumetric heat capacity (ρc) in sapwood exhibits a linear correlation above the freezing point. Below the freezing point, this relationship breaks down (see Figure 2).

Note. From Mvondo, R. R. N., Damfeu, J. C., Meukam, P., & Jannot, Y. (2020). Influence of moisture content on the thermophysical properties of tropical wood species. Heat and Mass Transfer, 56(4), 1365–1378. https://doi.org/10.1007/s00231-019-02795-8. Copyright 2019 by Springer Nature.

Volumetric heat capacity and thermal diffusivity of sapwood are relatively stable at temperatures above freezing, but these characteristics change sharply at the freezing threshold (Figure 2) (Burgess et al., 2001; Green et al., 2003; Lopez et al., 2021; Vandegehuchte et al., 2012). This shift is attributed to the lower density and higher thermal conductivity intrinsic to ice, as well as the heat released during exothermic phase change from liquid water to ice (Fukusako, 1990; Vasheghani Farahani et al., 2020). The thermal conductivity of ice also depends on the freezing rate, with faster rates of freezing associated with higher thermal conductivities (Bonales et al., 2017). Furthermore, the freezing (and subsequent thawing) of sap in trees causes irregularities such as directional changes in sap flow, and is influenced by many factors such as xylem structure, sap chemistry, the rate of temperature change across the freezing threshold, and the formation of embolisms (Bonales et al., 2017; Graf et al., 2015; Hao et al., 2013; Lopez et al., 2021; Steppe, Vandegehuchte, et al., 2015; Vergeynst et al., 2014).
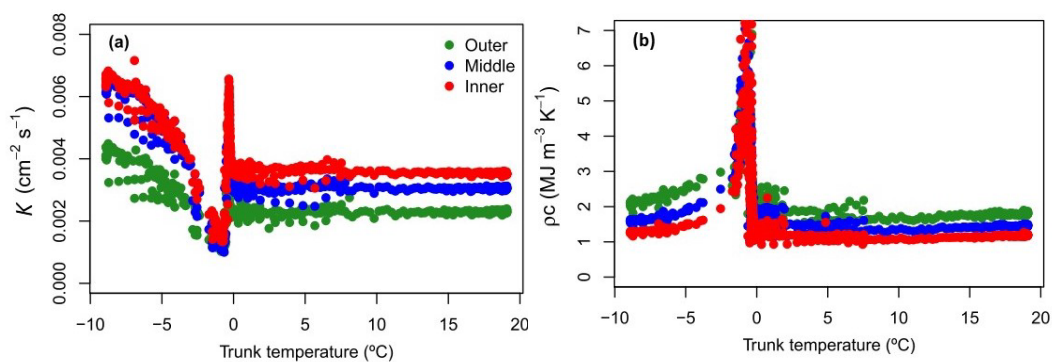
Figure 2. (a): The commonly observed relationship of thermal diffusivity (K) in sapwood is stable at temperatures above 0°C, if water content remains constant. As temperature crosses the freezing threshold, the phase change causes a shift downward in K, then changes at a nonlinear rate as temperature decreases. (b): If water content remains constant, volumetric heat capacity (ρc) in sapwood is stable at temperatures above 0°C. As temperature crosses the freezing threshold, the phase change causes a shift upward in ρc which then changes at a nonlinear rate as temperature decreases. Values of ρc across the freezing threshold at varying water contents currently lack validation. Calibration is needed to determine if reducing water content during freeze-thaw cycles will cause ρc to return to its original curve at 0°C, or if changing water content will create a new ρc function.

Current sensor methods to estimate water content in porous medium, including TDR and FDR, need to be validated for living stems across the freezing point of sap. If the relationships can be validated for these conditions, it would expand the range of possible measurements to include below-freezing temperatures, and improve estimations of water use and transpiration during winter and spring conditions.

Considering the rapid changes in winter conditions and the onset of spring freeze-thaw cycles in boreal forests, and the fact that few studies have addressed the problems of measuring water content and sap flow across the freezing threshold, with this study I aim to validate measurements of stem water content via the relationship between water content and thermal properties, through a cut-log experiment in controlled conditions.

1.6 Methods and challenges in measurements of water content in green stems

1.6.1 Gravimetric measurements of stem water content

Gravimetric measurements are considered the most reliable method to measure water content in porous medium such as soil or wood, as they are a direct measurement calculated based on differences in mass, and are not affected by temperature (Bryla et al., 2010; Burgess et al., 2001; López-Bernal et al., 2012). However, gravimetric measurements are labor intensive and typically require destructive sapling (López-Bernal et al., 2012; Nasta et al., 2024). Weighing lysimeters are highly accurate instruments for gravimetric measurements of water content (Bryla et al., 2010; Evett et al., 2009). However, weighing lysimeters can be affected by irregularities in the representative sample location due localized to variations in sample properties (Bryla et al., 2010; Evett et al., 2009; Green et al., 2003). Additionally, weighing lysimeters are expensive and often very large, which makes them difficult to acquire and use (Lopez, 2012; Vandegehuchte & Steppe, 2012). As gravimetric measurements of water content are more accurate, but less convenient, they are commonly used for validating indirect methods for measuring water content (Burgess et al., 2001; Clearwater et al., 2009; Hao et al., 2013; López-Bernal et al., 2012; Lu et al., 2017; Vandegehuchte & Steppe, 2012).

1.6.2 Frequency domain sensors

Frequency domain reflectometry (FDR) sensors are an indirect method for measuring water content that are increasingly used to measure stem water storage in trees (Matheny et al., 2015). This method uses an electromagnetic field, measuring the change in frequency of the wave emitted as it propagates through porous medium. The change in frequency measured by the receiving end is read as mV by the sensor, and converted to water content by the sensor manufacturer's formula, or customized formulas developed for specific parameters. Higher attenuation in the amplitude of waves measured by the sensors indicates higher water content, and the intensity of the electromagnetic signal produced by the sensor determines the range of the field of measurement. FDR sensors such as

CS655 (Campbell Scientific, Logan, Utah, USA), ECH20 (Meter Group, Pullman, WA, USA), and TEROS (Meter Group), typically consist of two or three needles, one which emits the electromagnetic signal, and the others which receive it. FDR sensors are convenient for continuous field measurements because they are durable, low-cost, and consume little power, and can have probe lengths of as little as 9.5cm, which is useful for measuring stems of various diameters. However, other studies have suggested that longer sensors can be useful for minimizing wounding effects in proportion to the field of measurement (Hao et al., 2013; Matheny et al., 2015).

There are limitations to measurements of water content using FDR methods, as they are strongly affected by factors which influence the electromagnetic properties of porous medium, such as salinity, chemical composition, and especially temperature. The dielectric permittivity of water increases with temperature, which affects the readings of sensors based on electromagnetic properties (Nasta et al., 2024). It has been suggested that the accuracy of FDR sensors may be improved through species-specific calibration (Steppe, Vandegehuchte, et al., 2015), but temperature corrections for this method remain an ongoing area of investigation (Nasta et al., 2024).

1.6.3 Time domain sensors

Time domain reflectometry (TDR) is an older method for measuring water content using principles of emitting an electromagnetic pulse, similar to FDR methods, but rather than measuring changes in frequency, the principle behind TDR methods is based on the time differential between emitting the electromagnetic pulse and the pulse bouncing off the receiving probe. The time required for the pulse to propagate between emitting and receiving probes is mainly affected by the surrounding medium, especially water content, and since electromagnetic pulses propagate faster in air than in water, a slower propagation indicates higher moisture content (Dahlen et al., 2015; Irvine & Grace, 1997). Sensors such as the SoilVue10 (Campbell Scientific) and E20/20N step TDR (AEA Technology, Inc., Carlsband, CA, USA) can measure variable depths, although it has been suggested that shorter probe lengths are more suitable for measuring water content in trees than those used for soil, as the majority of water is stored in recently produced sapwood (Irvine & Grace, 1997). TDR sensors can be expensive and require calibration, and are severely affected by chemical properties and temperature for the same reasons as FDR sensors (López-Bernal et al., 2012; Nadler et al., 2006).

1.6.4 Thermal properties sensors

Thermal properties sensors such as the TEMPOS thermal properties analyser (Meter Group) measure thermal properties such as ρc and K, and do not measure water content. These sensors use the transient line heat source method, an unsteady

state method used for measuring thermal properties in porous medium (Vasheghani Farahani et al., 2020). In this method, a dual needle probe is frequently used, where heat is emitted from one needle of the probe, and the rate of temperature increase is measured by the other. Heat is emitted for a specific duration according to the manufacturer (e.g. 10-20 seconds), then the temperature increase and over the following time of measurement duration is used to interpret ρc and K of the sample (TEMPOS User's Manual). However, these sensors are affected by certain conditions, such as moisture content of the sample, and temperature crossing the freezing point. The rate of temperature increase is affected by water content and the thermal properties of wood. While the manufacturer claims the TEMPOS sensor is capable of measuring thermal properties below the freezing point of water, freezing is an endothermic process and as ice forms the heat released by phase change can affect the measurements. Given that stems do not freeze uniformly (see section1.6.7), temperature changes can affect readings of thermal properties far above and below the freezing point.

Heat pulse-based sap flow sensors can estimate water content using thermal properties. The two most common sap flow sensors use heat dissipation and heat pulse methods. Heat dissipation methods use a dual needle probe to maintain a constant heat. Then the temperature differential is measured between the heater probe and the reference probe, and as sap moves through both reference and heater probes, the difference in temperature can be converted to sap flux density (Granier, 1985, 1987). However, the thermal dissipation method heats the sapwood, maintaining this temperature, effectively altering natural patterns of freezing and thawing. Additionally, there are no existing equations to convert temperature differences from heat dissipation sensors into water content (Chan & Bowling, 2017; Clearwater et al., 1999; Vandegehuchte & Steppe, 2012, 2013a; Vergeynst et al., 2014).

Heat pulse-based sap flow sensors emit a short pulse of heat, and the temperature is traced above and below the heater source. The temperature rise after the pulse can be used to estimate how fast the pulse of heat travels through sapwood. Consequently, such data can also be used to estimate thermal properties as seen in Equation 1 (Lopez et al., 2021). Given that they have similar configuration, many sap flow sensors could be used to estimate thermal properties (Vandegehuchte & Steppe, 2013a), however, there are few studies that have developed such validations (Lopez et al., 2021). Similar to other thermometric methods, such as the TEMPOS, these measurements can be affected by temperature, especially around the freezing point of water. There are studies have introduced equations for temperature corrections on estimates of sap flux density (Vandegehuchte et al., 2015), but validation is lacking for temperature corrections on estimations of thermal properties and water content using these sensors. For many sap flow studies, a single value for thermal properties and water content is often assumed for an entire

season, and it is highly desirable to develop methods for reliably estimating these values using heat pulse sensors.

1.6.5 How temperature influences thermal properties in porous mediums

The thermal properties of porous mediums change with temperature, largely due to the changes occurring in the water inside these substances (Vasheghani Farahani et al., 2020). Ice has a higher thermal conductivity than water, and therefore heat propagates faster through ice (Fukusako, 1990; Vasheghani Farahani et al., 2020). The sudden changes in thermal properties associated with exothermic and endothermic phase change result in irregularities in measurements based on these thermal properties. Additionally, the rate of freezing reflects the rate of energy loss from water molecules, which influences the geometric structure of ice as it forms, and as a result has an effect on its thermal properties (Bonales et al., 2017; Vasheghani Farahani et al., 2020). This means that the temperature itself and the rate of change across the freezing threshold need to be considered in sensor measurements using thermal properties.

1.6.6 How temperature influences the propagation of electromagnetic waves and pulses in porous medium

Measurements of water content using sensors based on electromagnetic waves and pulses are strongly affected by temperature, as the dielectric permittivity of water increases with higher temperature (Nasta et al., 2024). Temperature gradients that occur during measurement result in inaccuracies in the attenuation measured by these types of sensors, due to the changes in the electromagnetic properties and the resulting difference in the waves produced. As water freezes, the change in molecular structure during phase change affects how the electromagnetic wave travels through porous medium, and since ice has a higher thermal conductivity than water, the wave propagates faster through the medium and attenuation is higher (Bonales et al., 2017; Fukusako, 1990). As a result, the wave becomes nearly invisible to sensors using electromagnetic properties, causing them to significantly overestimate the water content.

1.6.7 How stems freeze

Tree stems do not freeze instantly, but instead have a freeze front that is directional from the source of the cold temperature. As sap freezes and expands within vascular tissues, this forces the remaining liquid to move away in order to equilibrate. As such, a tree which freezes from the top-down will result in sap flow in the downward direction, and likewise a tree which freezes from the bottom-up should demonstrate a positive sap flow direction (Moore et al., In Review).

However, most cold fronts in nature reach the tree radially, and freezing occurs from the bark and outer parts of the sapwood towards the center (Graf et al., 2015). The extracellular space in trees, known as the apoplast, where water transport is facilitated, freezes before the cells themselves (Lintunen et al., 2017). It has also been shown that fiber cells freeze first at a slower rate, before the vessel which freezes quickly, and that the reverse occurs during thawing (Graf et al., 2015). As a result, it is believed that apoplastic water freezes and expands due to ice formation, while the tissues themselves shrink from the negative water potential this causes (Lintunen et al., 2017; Zweifel & Häsler, 2000). The exothermic heat of thawing and endothermic heat of freezing can cause sap movement inside the tree even when ambient temperatures remain constant, and consequently sap flow can occur at temperatures far above or below the freezing point of water (Moore et al., In Review). The position of sensors relative to the freezing nuclei influences magnitude and direction of flow measured, and consequently it can be challenging to provide a whole-tree perspective on the freezing process. Thus, determining the actual freezing point of sap is a topic of ongoing investigation.

1.7   Stem water content and diameter fluctuations

Changes in stem diameter are the most accurate ways to estimate tree growth and biomass accumulation (Améglio et al., 2001; De Swaef et al., 2015; Drew & Downes, 2009; Zweifel et al., 2010). However, other factors can influence changes in stem diameter, especially during seasonal transition at the onset of winter and spring, (Améglio et al., 2001; Sevanto et al., 2006; Zweifel et al., 2001). For example, Zweifel et al., (2016) differentiated between stem expansion due to changes in water storage and expansion caused by tree growth during the growing season, yet it remains unclear to what extent periods of transpiration in spring would influence these patterns in stem diameter fluctuation (Mayr et al., 2006; Mencuccini et al., 2017; Nehemy et al., 2022; Zweifel & Häsler, 2000). There is a need for studies which incorporate the role of ice formation in partitioning stem diameter fluctuations driven by spring transpiration, from growth and shrinkage due to phase changes in xylem (Fatichi et al., 2016; Lintunen et al., 2017; Nehemy et al., 2023; Steppe et al., 2006; Turcotte et al., 2011).

The influence of winter and spring transpiration and freeze-thaw cycles on radial stem fluctuations remains an understudied component of whole-tree water usage (Nehemy et al., 2023; Zweifel et al., 2006; Zweifel & Häsler, 2000). The freezing and thawing of tissues leads to sudden changes in stem diameter, which can impact tree growth (King et al., 2013; Sevanto et al., 2006; Zweifel et al., 2010; Zweifel & Häsler, 2000). Daily amplitudes in stem expansion from freeze-thaw activity are much smaller than those from transpiration in temperate forests (King et al., 2013), but not tested in boreal forests, therefore precise measurements from point

dendrometers are needed to measure radial stem expansion at high temporal resolution (Drew & Downes, 2009).

During the growing season stem diameters have diurnal cycles of expansion and shrinkage driven by transpiration during the day, which depletes stem water storage, and recharge from soil water at night (Matheny et al., 2015; Steppe, Vandegehuchte, et al., 2015; Zweifel et al., 2001). In winter, these diurnal cycles of stem diameter fluctuations become decoupled from transpiration, and air temperature becomes the primary driver of stem expansion (Améglio et al., 2001; King et al., 2013; Lintunen et al., 2017; Sevanto et al., 2006; Zweifel & Häsler, 2000). The shift from temperature-driven to transpiration-driven diurnal cycles of stem diameter changes is considered one of the phenological demarcations of transpiration onset in spring, and is often used to determine the range of measurements for estimating annual tree growth (Nehemy et al., 2023). Previous studies have suggested that stem diameter of forest trees decreases in winter, and attribute this shrinkage to a negative water potential formed inside living cells as ice is formed (Lintunen et al., 2017; Zweifel & Häsler, 2000). However, other studies have found that ice formation in tree stems can cause diameter increase of up to 9% due to expansion associated with phase change from liquid water to ice (Améglio et al., 2001; Lintunen et al., 2017).

In this study, I will measure radial fluctuations in non-transpiring stems during freeze-thaw cycles to distinguish the role of ice expansion from diurnal patterns driven by environmental conditions. The results from this study can be useful in distinguishing the effect of freeze-thaw cycles for partitioning of radial stem growth, and improve calibration for measurements of winter and spring transpiration. Additionally, I expect that this study will lay out a strong foundation for furthering the study of stem water content, which currently lacks validations between thermometric and gravimetric measurements, particularly at cold temperatures.

1.8   Purpose and Hypotheses

1.8.1   Research Aims

In this research project, I have four aims:

Research Aim 1: Establish a relationship between changes in gravimetrically-derived water content and volumetric heat capacity (ρc) of three boreal tree species: birch, pine, and spruce.

Rationale: Measuring water content in green stems is very important for estimating sap flow (Vergeynst et al., 2014). However, most studies follow one of two approaches: use a single value for the entire season, which leads to large errors, or require additional equipment which leads to increased costs. Sap flow methods

can estimate thermal properties (Vandegehuchte et al., 2012), which have shown a linear relationship to volumetric water content in other porous mediums (Vasheghani Farahani et al., 2020). Consequently, there is a strong interest to test whether thermal properties such as volumetric heat capacity can be well correlated to water content in green stems.

Research Aim 2: Establish a relationship between changes in volumetric heat capacity and thermal diffusivity of the three boreal tree species.

Rationale: Thermal diffusivity is used to estimate sap flow, as a parameter for calculating how fast a pulse of heat is moving inside the wood (Lopez et al., 2021). Volumetric heat capacity and thermal diffusivity are important parameters for calculating stem water content, and establishing the relationship across the freezing threshold will enable estimates for transpiration during winter and springtime conditions.

Research Aim 3: Identify whether heat pulse sap flow sensors can reliably estimate thermal properties in green stems within a temperature range of -15°C to 25ºC.

Rationale: Thermal properties are known to change with temperature, which influences measurements of sap flow (Vandegehuchte et al., 2015). Thermal properties can be estimated using destructive means, or using expensive equipment (e.g. the TEMPOS sensor, by Meter Group). However, according to heat conduction-convection equations used to estimate sap flow, it should also be possible to estimate thermal properties using the same sap flow sensors, but with a slightly different data analysis (Lopez et al., 2021). Consequently, it is important to test whether sap flow sensors can reliably estimate thermal properties, and more importantly thermal properties crossing the freezing point of sap**.** Rising temperatures in boreal forests will increase the occurrence of freeze-thaw events, making it more challenging to reliably estimate sap flow and stem water content across the freezing point of water.

Research Aim 4: Use point dendrometer data to determine the role of stem water content in stem diameter fluctuations during freeze-thaw cycles in the three boreal species.

Rationale: Point dendrometers measure tree growth through changes in stem diameter at a micrometer resolution (Drew & Downes, 2009). They are often used for determining the start of transpiration during the growing season (Nehemy et al., 2023). Stem growth is important to estimate forest productivity and biomass accumulation. Stem expansion due to other factors, such as freezing and thawing of wood tissues, can affect measurements of stem growth and stem water recharge during spring (Daudet et al., 2005; Sevanto et al., 2006; Zweifel et al., 2016).

1.8.2 Hypotheses

Considering that the relationship between water content and heat capacity in porous mediums has been established for temperatures above freezing, for my first research aim, I hypothesize that:

1. It is possible to establish a relationship between volumetric water content and volumetric heat capacity to reliably estimate water content at below freezing temperatures

Given that ice has a higher intrinsic heat capacity than water, for my second research aim, I hypothesize that:

2. Volumetric heat capacity of sapwood increases as stem water crosses below the freezing point.

Since sap flow calculations are based on the relationship between stem water content and thermal properties, for my third research aim, I hypothesize that:

3. Heat pulse sap flow sensors can reliably estimate thermal properties and stem water content, as long as there is no sap flow occurring.

Previous studies on live trees have shown that stem water content and sapwood freezing influence measurements of stem diameter, therefore, for my fourth research aim, I hypothesize that:

4. Expansion from ice formation will result in increased diameter at decreasing temperatures. Higher stem water content will be correlated with higher diameter fluctuations.

2. Methods

2.1 Experimental Setup

For this study I conducted a cut-log laboratory experiment where I subjected non-transpiring tree logs to repeated freeze-thaw cycles, between ambient temperatures of -18°C to 25°C. Nine logs of approximately 20 cm in diameter and 40 cm in length were collected, with three replicates of each species: Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and Silver birch (*Betula pendula*). The logs were collected from the Svartberget Experimental Forest in the boreal forest region of northern Sweden. The Svartberget site is a 100-year-old mixed stand comprised of approximately 68% Scots pine, 20% Norway spruce, and 12% Silver birch, with tree heights around 20m (Peichl et al., 2024)

Logs were equipped with one heat pulse sensor, consisting of three needles and three measurement depths, one frequency domain water content sensor at a depth of 9.4cm (TEROS 12, Meter Group, Munich, Germany), and one point dendrometer (Nakton, Zweifel Consulting, Oetwil am See, Switzerland). Additionally, I monitored thermal properties – conductivity, diffusivity, and volumetric specific heat capacity – with a TEMPOS thermal properties sensor (Meter Group) equipped with SH-3 sensors at a depth of 3cm (Figure 3). Heat pulse and water content sensors were placed on logs 1-8, and point dendrometers were placed on logs 1-6 (Table 1). Log 9 was not equipped with sensors and was used as a control for gravimetric water loss to test if sensor placement produces overestimates in water loss. Heat pulse sensors, water content sensors, and point dendrometers were connected to an automated data logger (CR1000X, Campbell Scientific, Logan, Utah, USA), and a multiplexor. Thermal properties were measured with the handheld TEMPOS sensor. Data from the sensors (with exception of the TEMPOS handheld device) were collected with the automated logger every 15 minutes, and one cycle of freezing and thawing was considered one measurement cycle. Thermal properties were measured using the TEMPOS sensor every 30 minutes for a complete freezing and thawing cycle on three logs, for at least one replicate of each species (Table 1).

The logs were placed in the freezer (-18°C) in the Forest Ecology and Management Department at the Swedish University of Agricultural Sciences (SLU)

in Umeå, Sweden, for a few days in order to freeze, then removed from the freezer and allowed to thaw. When removed from the freezer, each log was weighed as an independent measurement of gravimetric water content using a scale. Additionally, the logs were put outside for the period from March 21-24 for measurements that reflect typical rates of freezing and thawing experienced in boreal forests during spring onset. After April 1, 2024 the logs were left for several weeks at room temperature to measure thermal properties as moisture content decreases under stable conditions.

Figure 3. Log equipped with point dendrometer, heat pulse sap flow sensor, TEROS water content sensor, and TEMPOS thermal properties sensor (left). Log weighed on scale with point dendrometer attached for measuring gravimetric water loss (right).

Table 1. Experiment logs and sensors

Log	Species	Diameter (cm)	Heat Pulse	TEROS	Nakton	TEMPOS
1	*P. sylvestris*	22.4	Yes	Yes	Yes	Yes
2	*P. abies*	20.1	Yes	Yes	Yes	No
3	*B. pendula*	19.9	Yes	Yes	Yes	No
4	*P. sylvestris*	21.1	Yes	Yes	Yes	Yes
5	*P. abies*	20.7	Yes	Yes	Yes	Yes
6	*B. pendula*	22.2	Yes	Yes	Yes	Yes
7	*P. sylvestris*	20.3	Yes	Yes	No	No
8	*P. abies*	21.3	Yes	Yes	No	Yes
9	*B. pendula*	20.0	No	No	No	No

2.2 Data Processing and Analysis

Stem water content was estimated using one frequency domain sensor (TEROS), two thermometric methods (TEMPOS and heat pulse), and all were validated using gravimetric measurements. Data from all sensors were processed in JMP Pro (SAS Institute Inc.) and RStudio (R Core Team). Thermal properties from the TEMPOS sensor were calculated following transient line heat source method (Fukusako, 1990; Vasheghani Farahani et al., 2020). Water content measured by the TEROS sensors was calculated using manufacturer's specified equations for FDR methods, described in Section 1.6.2 (Dahlen et al., 2015; Hernández-Santana & Martínez-Fernández, 2008). Gravimetric estimates of water loss in the logs was calculated through difference in mass over time, and wood density reference values were obtained from Fundova et al., (2018), Wilhelmsson et al., (2002), and Dobrowolska et al., (2020).

Heat pulse sensors were processed to extract actual values of K and ρc. This was done using the process described in Lopez et al., (2021), based on the heat cohesion-convection equation (Carslaw HS, 1947; Marshall, 1958; Vandegehuchte & Steppe, 2012). For these sensors, measurements were taken for 20 seconds of initial temperature, and 100 seconds after the pulse. Initial temperature was used to estimate average initial temperature, and temperature drift. The temperature rise (ΔT) was estimated by subtracting initial temperature from all temperature data after the pulse. Estimates for ρc and K were obtained fitting Equation 1 to the observed ΔT (1), where ρc and K were the parameters to be predicted. Equation 1 was fitted in RStudio using the package LME4. Once initial parameters of ρc were obtained, Equation 1was fitted once more, using initial parameters. ρc estimates were then used to estimate water content with the MHR method, as described in Lopez et al., (2021). The MHR method uses the thermal properties derived from heat pulse sensors (Equation 1) to estimate volumetric water content (Θ), based on the linear relationship between ρc and Θ described in Campbell et al., (1991) to solve for Θ (Equation 2). Values of thermal heat capacity, diffusivity, and water content calculated from the heat pulse sensors were then averaged between the three sensor depths to create a merged data set for each log.

Equation 1. Formula used to find values of K and ρc above heater probe using best fit curve, using MHR methods described in Lopez et al., (2021)

$$(1) \quad \Delta T_u = \frac{q}{4\pi K t} Ei(\frac{\rho c}{4K} \frac{(x_u + V_h t)^2}{t})$$

$$(2) \quad \Delta T_d = \frac{q}{4\pi K t} Ei(\frac{\rho c}{4K} \frac{(x_d - V_h t)^2}{t})$$

Equation 2. Formula used to solve for Ө using MHR methods described in Lopez et al., (2021) based on linear relationship between ρc and Ө established by Campbell et al., (1991)

$$(3) \quad \theta_v = \frac{\rho c - \rho_w c_w}{\rho_s c_s}$$

Raw point dendrometer readings were converted from mV to mm of displacement following manufacturer specifications, and calibrated by establishing the zero-growth line (Zweifel et al., 2016) based on the first stable measurement from each sensor. Displacement as percentage of annual growth was calculated using a reference value of 2mm/year, which is considered an average annual growth for the Svartberget Forest (ICOS Sweden unpublished data).

3. Results

3.1 Research Aim 1: Stem water content

Stem water content and water loss during the freeze-thaw cycles was calculated using gravimetric measurements, TEROS FDR sensors, and heat pulse sap flow sensors.
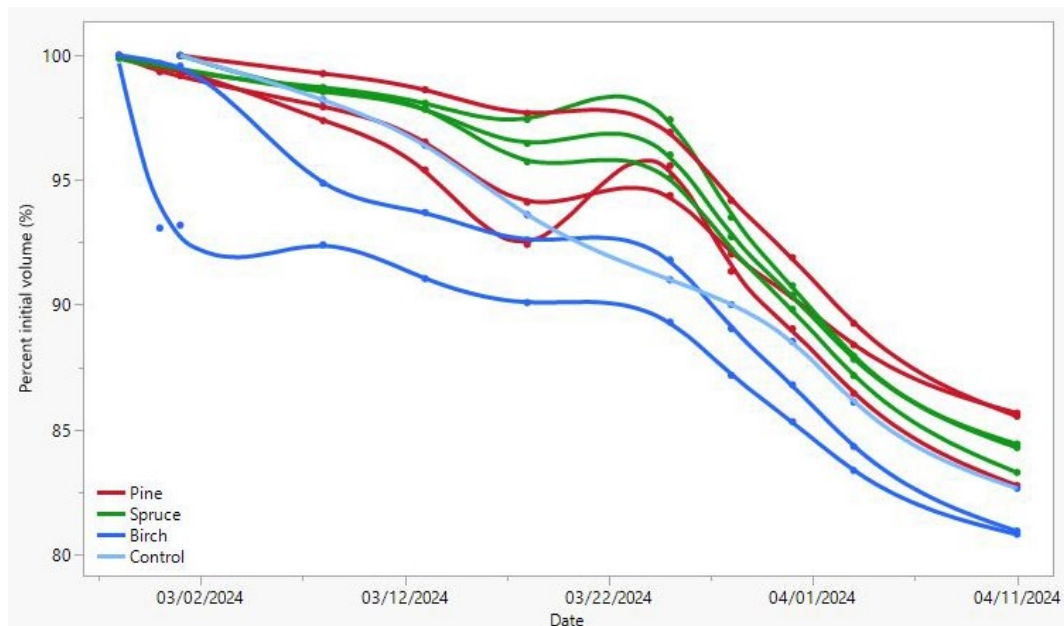
Figure 4. Gravimetric water loss represented as percent of initial mass for all experiment logs during freeze-thaw cycles.

Measurements of gravimetric water loss over the course of the freeze-thaw cycles show that trees of all species exhibit a similar rate of water loss (Figure 4). The most water loss during freeze-thaw cycles occurred in the Silver birch logs, particularly at the beginning of the cycles. After the freeze-thaw cycles were discontinued on April 1, 2024, all logs show a stabilization in the rate of decrease in gravimetric water content. Log 9, indicated in a lighter shade of blue (Figure 4), was not equipped with sensors and was used as a gravimetric control, demonstrating that sensor placement did not interfere with gravimetric measurements of water loss. With advanced stages of drying, cracks began to form in the wood of some of the logs, particularly in Log 6 (Silver birch), which developed a large crack that

neared the sensor location by the end of the study period. From February 26 Feb to April 11 the logs lost between 14.3% and 19.2% of their initial mass, with a mean of 16.6% (±1.8%). Mean water loss by tree species was 15.35% (±1.6) for Scots pine, 16.01% (± 0.6) for Norway spruce, and 18.55% (±1.0) for Silver birch. Log 3 (Silver birch) showed the most water loss at 19.2%, and Log 7 (Norway spruce) had the lowest at 14.5%.

3.1.1   Water content measurement thresholds

Water content from the TEROS sensors during freeze-thaw cycles shows that measurements of moisture content are only reliable above a certain temperature, around 5°C as measured by the sensor itself, after which the readings from the sensors follow changes in temperature (Figure 5). The maximum values of water content measured during thawing decreased over time (Figure 5), demonstrating that the total water content of the logs was decreasing over the course of the freeze-thaw cycles. The period around March 21-24, 2024 where temperatures fluctuated around the freezing point corresponds to the time when the logs were placed outside to measure typical seasonal conditions, and show that the TEROS sensors can still produce reliable estimates of water content under these conditions. However, fast temperature changes result in false water content readings.
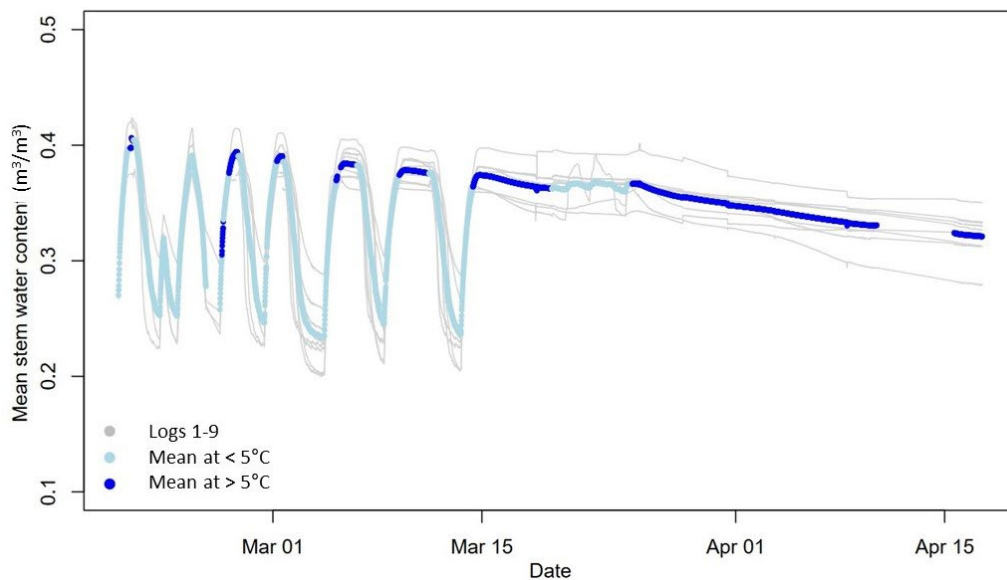

Figure 5. Volumetric water content (m³/m³) measured by TEROS sensors for freeze thaw cycles. The temperature range where sensors produced reliable measurements (>5°C) is indicated in dark blue, and the temperature range where sensors become unreliable (<5°C) is indicated in light blue.

There is a temperature-dependent threshold past which the TEROS sensors are unable to produce reliable measurements of moisture content. This can be seen in the hysteresis curves for each species where volumetric water content readings start to change at a certain temperature (Figure 6). The two hysteresis curves correspond to the respective processes of freezing and thawing. The curve on the left represents the freezing process, while the curve on the right represents the thawing process. There is a clear hysteresis with temperature, showing that the TEROS sensors function at low temperatures until approximately -4°C, and as temperatures rise the TEROS sensors only begin working properly around 5°C. The hysteresis appears to occur at approximately the same temperature for all species during the thawing process, while during freezing the sensors in Scots pine appear to become unreliable at a few degrees warmer than those in Norway spruce and Silver birch (Figure 6).
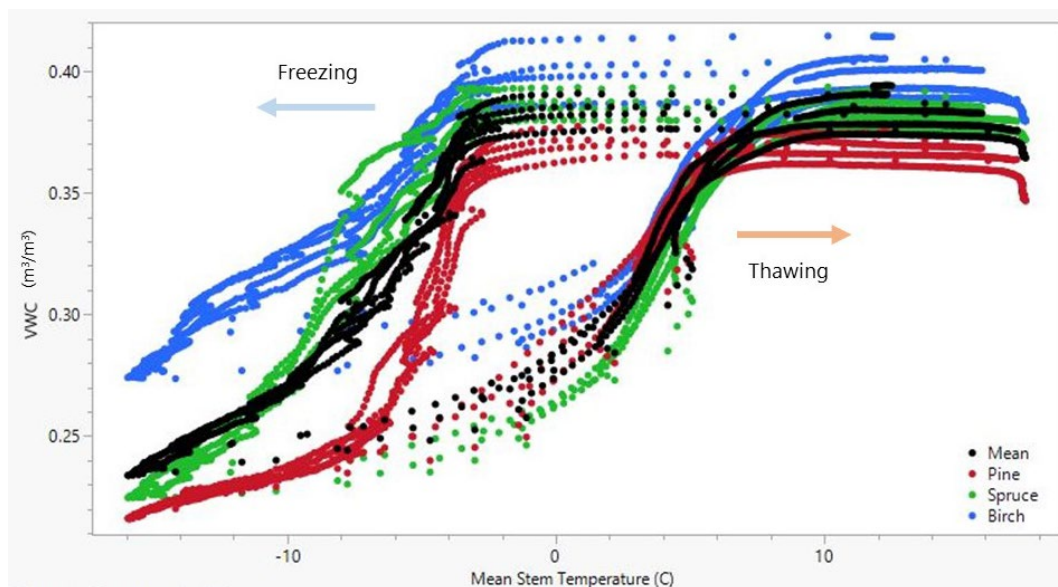
Figure 6. Volumetric water content (m³/m³) from TEROS sensors by species mean across the temperature range of freeze-thaw cycles shows hysteresis curves during freezing and thawing.

3.1.2 Heat pulse sensors and water content
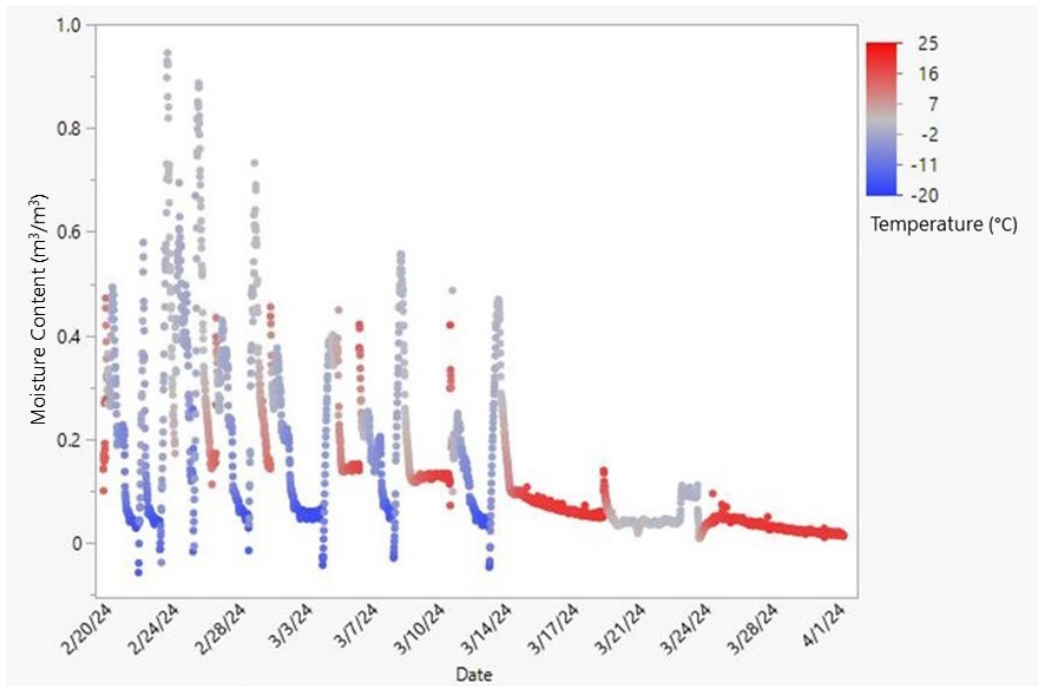
Figure 7. Moisture content (m³/m³) measured by sap flow sensors during freeze thaw cycles.

Moisture content measurements from the heat pulse sap flow sensors show that the sensors become unreliable at temperatures near the freezing threshold (Figure 7). This is shown by the spike in readings during the freeze-thaw cycles at temperatures approximately between -5°C and 7°C, where the sensors appear to produce false readings at low temperatures below -5°C. Measurements taken by the sap flow sensors at the temperature range for which they able to show water loss in
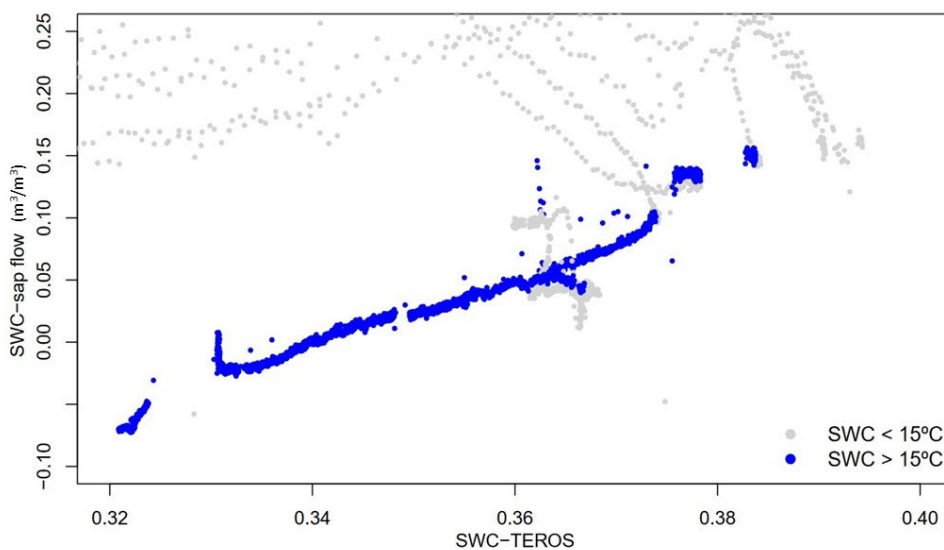
Figure 8. Comparison of stem water content (SWC) (m³/m³) measured by TEROS and heat pulse sap flow sensors show linearity at temperatures above a threshold of 15°C.

the logs over time can be considered reliable as they are able to estimate expected trends in moisture content (Figure 7).

The stem water content measured by the heat pulse sap flow sensors (Figure 8) correlates linearly with measurements from the TEROS sensors at temperatures above the threshold for both sensors, indicated in Figure 5 and Figure 7. Although there is an offset in values, the linear relationship shown in Figure 8 demonstrates that in the absence of sap flow, the heat pulse sensors are comparable to the TEROS sensors, and can be calibrated to reliably estimate water content within these conditions.

3.2 Research Aim 2 and 3: Water content and thermal properties

The heat pulse sap flow sensors maintained linearity in relating ρc and water content using current algorithms across the entire temperature range (Figure 9). However, there is a high temperature-dependent threshold for reliable measurements of K from the heat pulse sap flow sensors of around 19°C (Figure 9), below which measurements of K are unreliable. At very low temperatures below the threshold the sensors failed to establish a relationship between moisture content and K, which may indicate that the linearity shown for ρc was maintained using generalized values from the model used in calculation (Equation 1). Most of the extreme outliers for values of K occurred in measurements taken near the freezing threshold. For measurements above this threshold, the calculated water content and thermal diffusivity can be related and follows the established pattern (Figure 9).
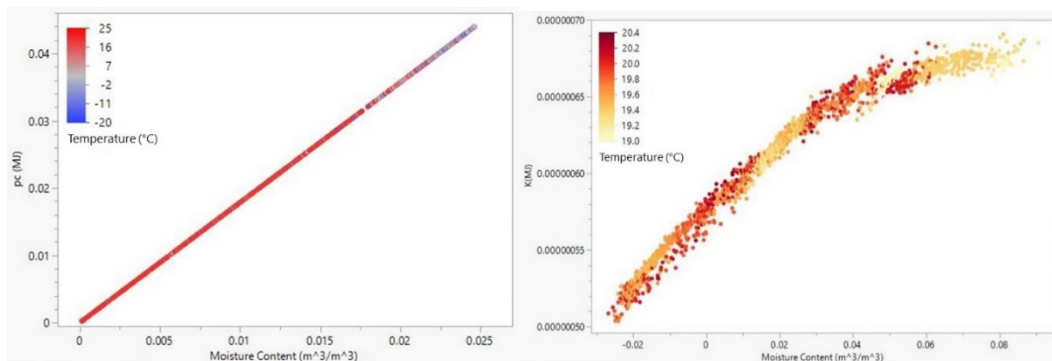
Figure 9. Left: Sap flow sensors maintain linearity in the relationship between calculated water content and volumetric heat capacity (ρc) for the entire temperature range. Right: Relationship between calculated water content from heat pulse sensors and thermal diffusivity (K) above a threshold of reliability at 19°C.

The TEROS sensors also showed a temperature-dependent threshold for measuring thermal diffusivity comparable to that of the sap flow sensors, with reliable measurements beginning around 18°C (Figure 10). Unlike measurements from the sap flow sensors, the TEROS sensors were not able to maintain the

relationship for volumetric heat capacity across the entire temperature range, and only produced reliable measurements at temperatures above the threshold of 18°C (Figure 10).
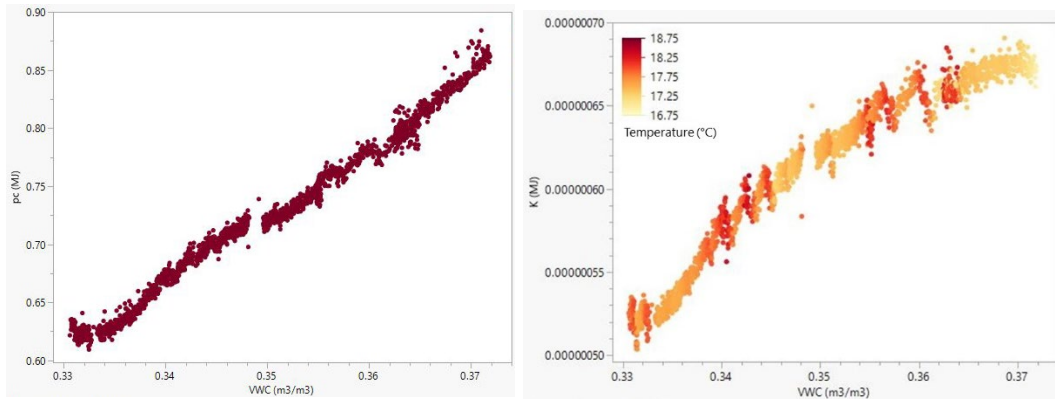
Figure 10. Left: Relationship for TEROS volumetric water content (VWC) and ρc from heat pulse sap flow sensors show linearity for temperature range above 18°C where readings are reliable. Right: Relationship of TEROS VWC to K from sap flow sensors show linearity for temperature range above 18°C where readings are reliable.

Data from both the heat pulse sensors and the TEMPOS thermal properties analyzer reflects the established linear relationship between ρc and temperature which have been validated above the freezing point (see Figure 2), with stable values until the freezing threshold, then a strong increase at the point of phase change. Below freezing, ρc values measured by both sensor methods decreased at a nonlinear rate that begins to stabilize around temperatures of -6°C (Figure 11). At temperatures below freezing, ρc measured by both sensors appears to stabilize at a level below those of above freezing values.
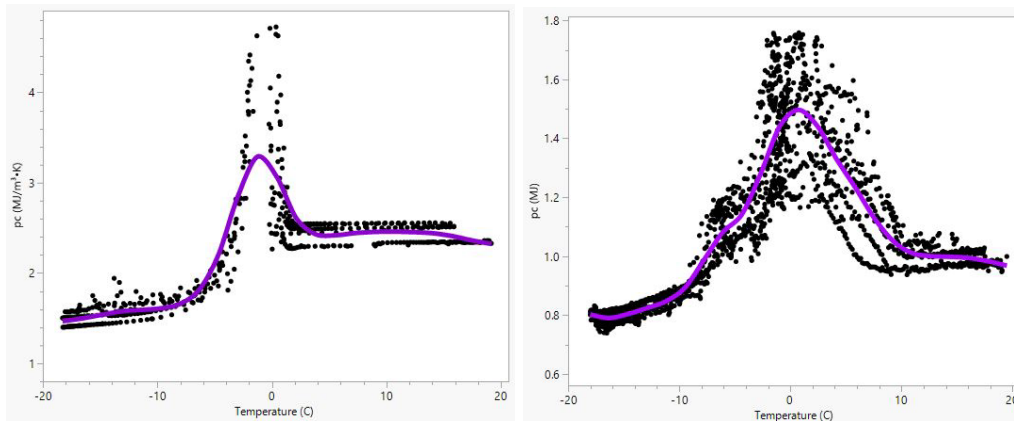
Figure 11. Left: Relationship of volumetric heat capacity (ρc) from TEMPOS sensor with temperature from TEMPOS sensor. Right: Relationship of volumetric heat capacity (ρc) from heat pulse sensors with temperature from heat pulse sensors.

The relationship between thermal diffusivity and temperature measured by heat pulse sensors and TEMPOS (Figure 12) reflects the established pattern across the entire temperature range. Thermal diffusivity increases sharply at the freezing point, then stabilizes at temperatures of approximately -5°C with values higher than those measured at temperatures above freezing.
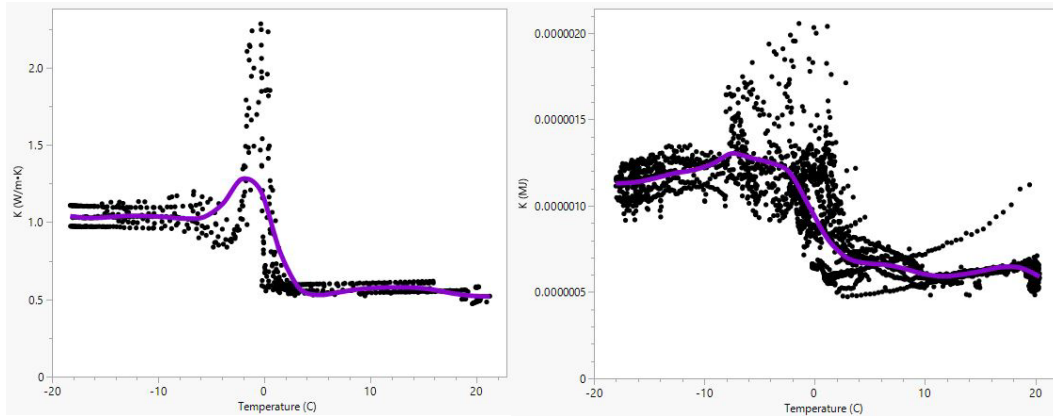
Figure 12. Left: Relationship for thermal diffusivity (K) and temperature measured by TEMPOS sensors. Right: Relationship for thermal diffusivity (K) and temperature measured by heat pulse sensors.

3.3   Research Aim 4: Radial stem expansion

Radial fluctuation patterns during the freeze-thaw cycles differed by species, with Scots pine and Norway spruce logs showing a persistent shrinkage over time as water content in the logs decreased, while this shrinkage was less pronounced in Silver birch (Figure 13). The magnitude of stem diameter changes for all species decreased with time as log water content decreased (Figure 13). As expected, the patterns of shrinkage and expansion follow the temperature changes from the freeze-thaw cycles.
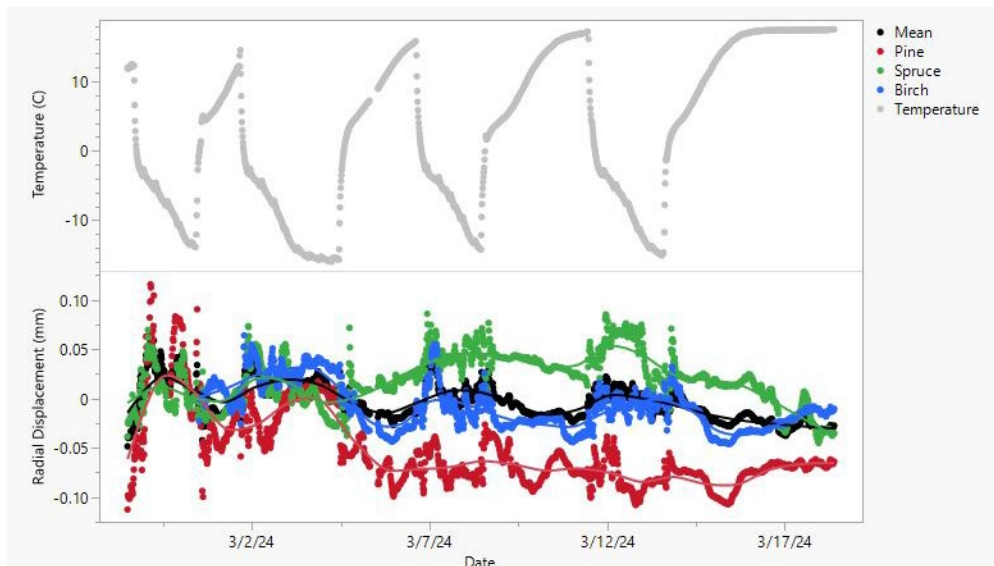
Figure 13. Stem diameter change (mm) by species mean with temperature during freeze-thaw cycles.

Radial displacement of the logs measured by the point dendrometers shows an increase in stem diameter as temperatures decrease and cross the freezing threshold, and a decrease in diameter as temperatures rise (Figure 14). There appears to be two small peaks of stem expansion during the freezing process (Figure 14), one
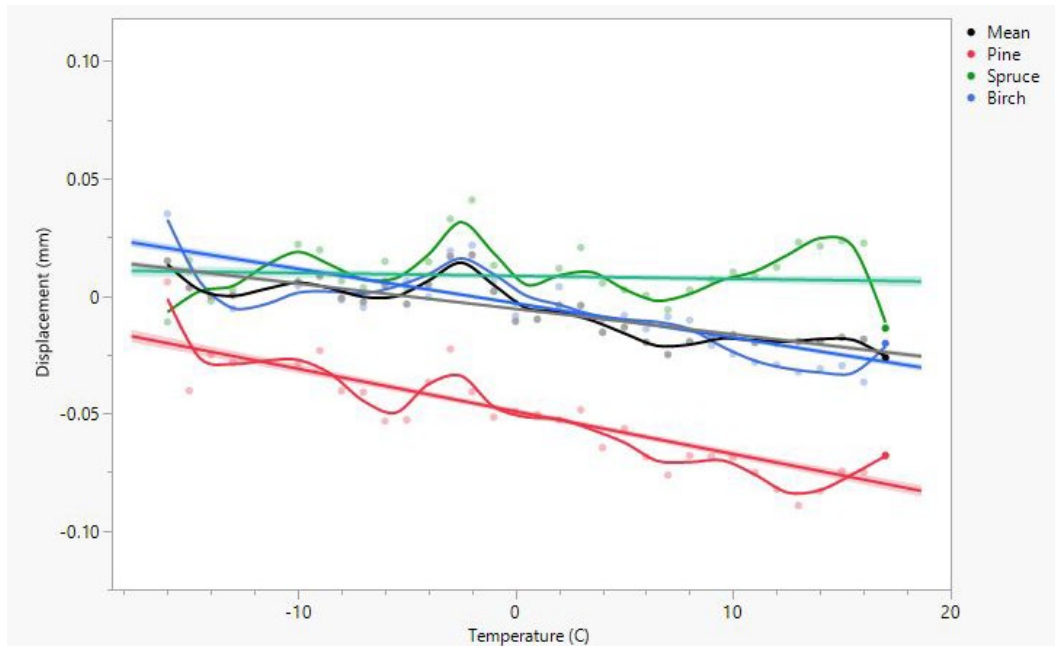
Figure 14. Stem diameter change (mm) by species mean with temperature during freeze-thaw cycles.

around the initial freezing (0°C to -2°C) and one around (-8°C to -10°C). The most pronounced relationship, indicated by the slope of the line of fit (Figure 14) between temperature change and stem expansion occurred in Scots pine logs, while the highest overall fluctuations with temperature appeared in Norway spruce. Silver birch logs showed a lower variation in radial fluctuations than Norway spruce or Scots pine, possibly due to differences in bark and wood structure of hardwood species. Mean stem expansion below freezing for all species, shown as percent of mean annual growth for boreal trees at the Svartberget forest, was around 6% (± 1.8) (Table 2).

Table 2. Stem expansion measured by point dendrometers as percent mean annual growth at the Svartberget forest (2mm/yr, ICOS Sweden unpublished data).

Log	Expansion Max %	Shrinkage Min %	Total Range %
All Spp. Mean	5.99 ± 1.8	-7.96 ± 2.7	13.95 ± 3.3
Pine Mean	8.60 ± 0.04	-5.62 ± 0.9	14.22 ± 0.8
Spruce Mean	8.46 ± 1.1	-6.49 ± 3.5E-15	14.95 ± 1.1
Birch Mean	3.20 ± 0.9	-7.96 ± 5.6	11.16 ± 6.5
Tree 1	8.60	-6.56	15.16
Tree 2	8.34	-3.74	12.08
Tree 3	5.00	-1.66	6.66
Tree 4	8.66	-5.34	14.00
Tree 5	9.86	-3.74	13.60
Tree 6	6.26	-9.56	15.82

4. Discussion

4.1 Stem water content

Water stored inside living tree stems is an important component of whole-tree water use. Stem water is one of the most important sources of water for transpiration (Matheny et al., 2015; Steppe, Sterck, et al., 2015), particularly when soil water is insufficient or unavailable, such as early spring when the soil is still frozen (Harpold et al., 2015; Sevanto et al., 2006; Zweifel et al., 2001). It has been demonstrated that stem water storage is critical to transpiration at the start of spring, as rehydration from snowmelt occurs after transpiration onset (Nehemy et al., 2022). Rapid temperature fluctuations, typical during the winter-spring transition, can drive changes in stem water content (Améglio et al., 2001), which makes reliable measurements of water content during these conditions an important aspect of understanding whole-tree water use and its relationship to the onset of transpiration in spring.

This study demonstrated that the TEROS sensors have a temperature-dependent limit, below which the sensors become unreliable for measuring water content (Figure 5). Above this limit, at around 5°C, measurements of water content can be considered reliable. Sensor measurements are reliable for a shorter temperature range during thawing, compared to freezing (Figure 6). The hysteresis between temperature and volumetric water content shown in Figure 6 indicates that the TEROS sensors are more reliable during freezing, and can maintain readings for a few degrees below zero, but do not estimate water content at the same temperature during thawing. During the freezing process, the sensors become unreliable close to -4°C, and remain unreliable during the thawing process until reaching 5°C. Sap movement has been observed in trees at temperatures below the freezing (Gutierrez Lopez et al., 2021; Moore et al., In Review), and as such these measurements can be considered reliable in the freezing direction. The manufacturer specifications for the TEROS sensor claim functionality and accuracy down to -40°C, and so the high temperature limit observed in this study could be attributed to the rapid changes in temperature occurring during freeze-thaw cycles which the sensor is unable to calibrate at the temporal resolution used in this study. This may also be due to

conditions inside the wood which may disrupt sensor measurements, such as bi-directional flow from freeze-thaw cycles, or the time it takes for water inside the wood to freeze and thaw (Lopez et al., 2021).

Water content from heat pulse sap flow sensors also showed a comparable temperature-dependent limit around -5°C (Figure 7). The temperature limit observed in this study is similar to the findings of Lopez et al., (2021), which reported heat pulse sensors fail to measure sap flow at temperatures below -5°C. These sensors also appear to be more reliable during the freezing process than during thawing. However, as previous studies have found that most sap flow occurs during the thawing process, at temperatures slightly below freezing between -1.2ºC to -0.2ºC (Lopez et al., 2021), this indicates that further research is needed for proper measurements of sap flow during freeze-thaw conditions. The water content from the sap flow sensors correlate well with those from the TEROS readings (Figure 8), indicating that at temperatures above the observed threshold, and in the absence of sap flow, these sensors are able to reliably estimate water content. The notable offset in values between the heat pulse and FDR TEROS methods suggests that parameterization is needed to improve the water content readings from the sap flow sensors, but that overall heat pulse methods are able to relate thermal properties to water content to produce estimates of water content.

Fast temperature changes resulted in false readings, but the sensors appeared to function during the period when logs were left outside and temperatures fluctuated around the freezing point (Figure 7). This may be attributed to the freeze-thaw cycles during this period featuring a smaller, and more gradual change in temperature than those produced by the freezer. Sensor depth did not appear to have an influence on results, as patterns were consistent for both the sap flow and the TEROS sensors, despite differences in sensor length. However, previous studies have shown that sap flow direction can vary with sapwood depth, particularly as changes in temperature around the freezing point can cause irregularities in the water potential gradient inside stems (Lopez et al., 2021), and measurements at different depths should still be taken into account for estimating whole-tree water use. This indicates that the temperature-dependent limit to measurements of water content is likely driven by other factors, such as the total temperature differential or rate of change.

4.2   Stem water content and thermal properties

Changes in temperature are generally not accounted for in heat pulse method calculations, but can be a significant source errors in sap flow estimations (Vandegehuchte et al., 2015). Previous studies have found that positive temperature changes lead to underestimation in HRM, which was reduced when the averaging period for temperature readings was taken closer to the start of the heat pulse (Lopez

et al., 2021; Vandegehuchte et al., 2015). However, under conditions of very fast temperature changes, averaging periods closer to the start of the heat pulse may still be a source of error (Burgess et al., 2001; Lopez et al., 2021; Vandegehuchte & Steppe, 2012). This would suggest that corrections can be applied to heat pulse measurements based on the temperature change occurring during the measurement period, but the rate of temperature change needs to be taken into account to improve the accuracy of heat pulse sap flow methods for conditions of fast temperature fluctuations in spring. Negative temperature changes have been shown to produce more errors and imaginary readings (Vandegehuchte et al., 2015), which Clearwater et al., (2009) suggested correcting for by subtracting the rate of change from the measured temperature. These errors are also dependent on wood thermal properties (Vandegehuchte et al., 2015), which indicates that establishing the relationship for wood thermal properties has potential use for developing models to correct these measurements.

Water content in living stems can vary greatly with seasonality and environmental conditions (Vandegehuchte et al., 2012). Since measurements of thermal properties are dependent on water content (Green et al., 2003), this effects sap flow measurements, for example, the maximum temperature difference used to estimate flow velocity increases when stem water content declines (Vergeynst et al., 2014). This results in more errors produced by generalized values of thermal diffusivity used in calculations of sap flow at low water content (Vandegehuchte et al., 2012), and suggests that corrections based on the relationship between thermal properties and water content are needed to produce reliable estimations of whole-tree water use during spring, when stem water content can change as a result of environmental conditions. Further studies on this topic which validate the water content estimated by sap flow sensors with gravimetric measurements would be useful in order to produce such corrections.

The thermal properties ρc and K measured in this study, by both the sap flow sensors and the TEMPOS thermal properties sensor across the temperature range of the freeze-thaw cycles, reflect the established relationship between thermal properties and temperature across the freezing threshold (Figure 11 and Figure 12). The spike in readings at the freezing point can be attributed to the changes in thermal properties associated with phase change at the freezing point, which affect both FDR and thermometric measurements. Below freezing, ρc in the stems appears to stabilize and decreases more gradually and at a linear rate, but at values below those of the ρc at temperatures above 0°C (Figure 11 and Figure 12). This suggests that the sensors are able to produce reasonable measurements of thermal properties in the wood at temperatures below freezing, and potentially correction functions can be developed to compensate for the irregularities that occur at the freezing threshold.

The relationship of ρc and temperature measured by the heat pulse sensors maintains linearity for the entire temperature range -5°C to 25°C (Figure 9), but showed a strong temperature-dependent threshold of around 19°C for relating water content to values of K. Based on the calculation method used to produce these values, this suggests that the function may be using generalized values of K to calculate ρc for temperatures below this threshold, where measurements of K became unreliable, to compensate for lack of actual values. This would be an explanation for why the data maintains strong linearity for ρc but not for K (Figure 9). However, the sensors were able to relate water content to K for temperatures above the threshold, which indicates that heat pulse based methods are able to estimate water content under conditions of warmer temperatures and no sap movement, and there is a possibility that correction functions can be developed for these sensors to adjust for changes in thermal properties below the freezing threshold, enabling heat pulse sap flow sensors to reliably estimate stem water content at low temperatures. This would improve measurements of transpiration at seasonal transition periods, and make estimating stem water content more efficient and cost-effective.

Most studies on sap flow measurements have been conducted on temperate and tropical trees, and it has been suggested that species-specific calibrations of wood thermal properties could improve sap flow sensor accuracy (Green et al., 2003). Consequently, there is a need for studies which test these sensors on boreal trees, as it has been shown that high wood density is associated with higher thermal diffusivity and lower water content, and that narrow growth rings in boreal trees cause low permeability, which reduces the hydraulic conductivity of sapwood compared to temperate trees (Baldocchi et al., 2000; Vergeynst et al., 2014). This further supports the importance of validating the relationship between water content and thermal properties used in calculations of sap flow and transpiration of boreal trees.

4.3 Radial stem expansion

The results of this study show evidence of stem diameter reduction with loss of stem water content over time (Figure 13), as the magnitude of radial displacement decreased in correlation with the decrease in volumetric water content of the logs. This is supported by other studies on stem diameter changes, which assert that bark and other elastic tissues should shrink with drying during freeze-thaw cycles (Améglio et al., 2001; Vergeynst et al., 2014). Additionally, diameter expansions below freezing were also accompanied by shrinkage at warmer temperatures (Figure 14). The shrinkage is primarily attributed to stem water loss through drying, as the trees in this cut-log experiment were not sealed at the ends, connected to soil water, or transpiring. However, this water loss may introduce error to trends of stem

expansion with temperature, as it is an additional factor which influences stem diameter. The Scots pine logs in this study showed the largest fluctuations as well as the largest reduction in stem diameter over time, which appears to stabilize towards the end of the study period. This may indicate that the pine logs were approaching a threshold of moisture content by the end of the freeze-thaw cycles, beyond which freezing and thawing have little effect on diameter expansion. Norway spruce logs displayed the least stem diameter variation among the three species (Figure 13), highlighting the importance of species-specific measurements. The lack of diameter change in Norway spruce could be due to ambient moisture in the location where logs were set out to thaw, or differences in bark structure, which is a highly dynamic component of stem water storage that varies with individual and species physiology, and is considered the major contributor to short-term radial fluctuations (Améglio et al., 2001; Zweifel et al., 2001). Although the bark was removed for placement of the point dendrometers, the Norway spruce logs had visibly thicker bark than the other species in this experiment, and there is the possibility of some bark remaining which would affect these results. Additionally, error can be introduced to these measurements by the reference point selected for calculating displacement from the point diameters, if the sensor had not fully settled at the time selected to be the first stable measurement, the magnitude of displacement observed would be affected.

The increase in stem diameter below freezing temperatures observed can be attributed to expansion in wood tissue due to ice formation, as there was no transpiration occurring during this study. This contrasts with the pattern of temperature driven radial expansion cycles shown by some previous studies in live forest trees (Nehemy et al., 2023; Zweifel & Häsler, 2000), and agrees with other studies that have recorded stem expansion from ice formation in winter of up to 10% (Améglio et al., 2001; Lintunen et al., 2017; Moore et al., In Review). The results of this study on non-transpiring stems support the framework that radial displacement due to temperature and log water content changes can occur independent of diurnal cycles and turgor pressure associated with transpiration. As freezing in tree stems does not occur at once, and the process can vary with several factors, it can be difficult to determine the time of freezing through direct measurements, and as such, understanding the freezing point of sap is a topic of ongoing study.

Diameter fluctuations with temperature in this study showed two small peaks below freezing temperatures at approximately -4 and -10°C, supporting the idea that freezing of wood tissue inside stems occurs in phases (Figure 14). This finding was also reported by Améglio et al., (2001), who suggested this may occur from extracellular ice freezing first before intercellular water due to differences in solute concentration. Additionally, time lag effects from thermal diffusivity in the wood may also be a contributing factor (Vasheghani Farahani et al., 2020). Previous

studies have suggested that freezing of water in trees mainly occurs from the outer parts of the tree inward, as most natural freezing fronts occur in the radial direction (Graf et al., 2015).

Winter and springtime diameter fluctuation in transpiring trees is typically attributed to diurnal cycles driven by temperature (King et al., 2013; Matheny et al., 2015; Nehemy et al., 2023; Zweifel et al., 2001). In absence of all ET and xylem pressure from the non-transpiring logs, the expansion observed in this study can be attributed to the freeze-thaw cycles, and used to adjust measurements of stem dehydration in autumn and rehydration in spring. The radial displacement from freezing observed in this study can be up to 10% of annual growth rates (Table 2), and supports the findings of previous studies (Améglio et al., 2001; Zweifel et al., 2016), which also recorded that variation in stem diameters can be a substantial percentage of annual growth.

The shift to transpiration-driven diurnal cycles of radial expansion is often used to demarcate the start of the growing season (Nehemy et al., 2022, 2023; Zweifel et al., 2016). However, it has also been observed that there is a lag time between transpiration onset where stem water storage is depleted first, before the start of diurnal cycles which rely on soil water from spring snowmelt for nighttime recharge (Hao et al., 2013; Nehemy et al., 2022). Additionally, the period of spring recharge is not always clearly demarcated due to variations in climate conditions between years (King et al., 2013). This reinforces the role of expansion from ice formation that should be taken into consideration when using stem diameter growth for determining the onset of transpiration-driven cycles at the start of spring.

4.4   The ecological context of water content in green stems

Few studies have focused on ET at high latitudes, and there is still little known about tree water use in ecosystems with winter dormancy (Kozii et al., 2020; Nehemy et al., 2022). In boreal systems, conifer-dominated forests without a phenological demarcation of the transition between dormancy and active transpiration can experience highly variable timing for the onset of the growing season (Barnard et al., 2018). There are still uncertainties in understanding the timing and drivers of transpiration onset in spring, and as winter climate conditions become more unstable, it is increasingly important to understand ET and tree water use during the winter and spring transition (Kjellström, 2004; Pierrat et al., 2021).

It has been shown that photosynthesis can occur during warm conditions in the winter (Bowling et al., 2018; Sevanto et al., 2006), and carbon uptake outside the growing season can contribute substantially to annual ecosystem productivity (Barnard et al., 2018). There is strong seasonable variation in the relative importance of ET in boreal forests, (Gutierrez Lopez et al., 2021; Kozii et al., 2020). Air temperature is the primary driver of spring onset of photosynthesis in boreal

systems, and can occur before soil thawing (Barnard et al., 2018; Pierrat et al., 2021). Stem water storage is the primary source of water during active transpiration, and an important buffer from cavitation in conditions where soil recharge is insufficient, such as warm winter days and during early spring before soil thawing (Harpold et al., 2015; Matheny et al., 2015; Sevanto et al., 2006; Zweifel et al., 2001). This indicates the critical role of water storage in the stem for transpiration in early spring.

Changing climate conditions are accelerated in boreal regions, and have begun to alter the timing and relationship of important components of the water balance of boreal forests (Gutierrez Lopez et al., 2021). The growing season in northern Sweden has already recorded earlier onset and a significant increase in duration (Hasper et al., 2016; Pierrat et al., 2021). Warming in the boreal region is expected to have the most notable impact on winter temperatures (Kjellström, 2004), which will likely disrupt the timing and duration of spring snowmelt, with substantial impacts on the ecosystem functioning of boreal forests (Chan & Bowling, 2017; X. Chen et al., 2015; Kropp et al., 2022). This is relevant to forest ecosystem functioning as productivity of boreal forests during the growing season is largely determined by conditions in early spring (Gutierrez Lopez et al., 2021; Knowles et al., 2018; Nehemy et al., 2022).

Changes in winter conditions leading to shifts in the timing, duration, and quantity of snowpack in boreal forests can negatively impact forest water availability and limit productivity (Gutierrez Lopez & Laudon, 2023; Harpold et al., 2015; Knowles et al., 2018). Reductions in forest water availability during the growing season as a result of reduced snowpack and warmer winter temperatures could potentially lead to water-limitation (Gutierrez Lopez & Laudon, 2023; Hasper et al., 2016). Changes in precipitation timing and snowpack with climate change could additionally lead to positive feedbacks on regional warming from changes in albedo, resulting in cascading effects such as permafrost melting, and increased frequency and severity of disturbance such as fire (Bradshaw & Warkentin, 2015; Kropp et al., 2022; Moen et al., 2014). Boreal forest habitats in Sweden host a disproportionate amount of endangered species in Europe (Bradshaw et al., 2009), and changing climate conditions which impact ecosystem health and functioning could have wide reaching implications.

4.5   Limitations of this study

This study focused on validating measurements stem water content in boreal trees, using thermal properties which many current sensor methods are based on. The sensors used in this study were subjected to conditions outside of the established range for reliable measurements, and sources of error may include the effects of repeated freezing and thawing on sensor accuracy and calibration. The

number of logs used in this study was limited, and results may be influenced by variations or irregularities in individual tree anatomy. The ends of the logs used in this experiment were not sealed, which may also have an effect on the rate of water loss observed during thawing periods. Additionally, cracks began to form in the wood of certain logs with advanced stages of drying, particularly Log 6, which developed a noticeable crack which nearly reached the sensor location by the end of the study period, and could potentially lead to underestimations of water content. Freezing action can be inferred by the temperature spikes produced from endothermic phase change, but as stems do not freeze at once and are affected by heat and cold fronts, the 15-minute frequency of measurement used in this study may not be able to entirely capture the pattern that occurs.

5. Conclusion

The purpose of this study is to validate methods for measuring stem water content in trees using thermal properties which many current sensor methods are based on. The aim of this work is to improve measurements of transpiration during shifting winter and spring conditions, which are experiencing the most severe disruption from global climate change in the boreal regions.

In this study, I tested four hypotheses: (1) It is possible to establish a relationship between water content and volumetric heat capacity to reliably estimate water content at below freezing temperatures (2) Volumetric heat capacity increases as stem water crosses below the freezing point. (3) Heat pulse sap flow sensors can reliably estimate thermal properties and stem water content, as long as there is no sap flow occurring. (4) Expansion from ice formation will result in increased diameter at decreasing temperatures, and higher stem water content will be correlated with higher diameter fluctuations.

The results of this experiment showed:

RA1. The TEROS FDR sensors used in this study were unable to reliably estimate water content below the freezing threshold, therefore it can be concluded that this method is not ideal for measuring stem water content during winter and spring conditions for boreal forests. Heat pulse sap flow sensors were able to reliably relate stem water content and volumetric heat capacity at temperatures above freezing, but became unreliable with rapid temperature change approaching the freezing threshold and phase change. This suggests that heat pulse sap flow sensors have potential use for measuring water content in trees, and there is a need for further research into methods to account for rapid temperature fluctuations and the phase change point in measurements across the entire temperature range.

RA2. Volumetric heat capacity measured by the sap flow sensors and TEMPOS did increase as stem water crossed the freezing point. However, as temperatures continued below freezing ρc decreased and began to stabilize at a value below what was observed at temperatures above freezing.

RA3. Sap flow sensors were able to reliably measure thermal properties and stem water content at temperatures above freezing. However, they were not able to reliably measure water content at the freezing threshold or during rapid temperature changes occurring in the freeze-thaw cycles, and were not able to relate thermal properties to water content below freezing, which suggests that further research is

necessary to understand if correction functions can be developed and applied to readings to expand the range of sap flow measurements. This would enable estimations of transpiration to extend into the winter and spring seasons, and improve annual estimates of ET for boreal forests.

RA4. Stem diameters showed expansion at decreasing temperatures below freezing, which can be attributed to ice formation, and diameter fluctuations decreased with decreasing stem water content.

This study provided a foundation for measurements of stem water content during the freezing and thawing cycles characteristic of winter and spring conditions in boreal forests. Based on these findings, current sap flow sensor methods can potentially be corrected to produce reliable estimates of water content and thermal properties across the freezing threshold and during rapid changes in temperature, to enable more accurate calculations of transpiration and water use at the onset of spring, and further our understanding of the impacts of shifting seasonal timing for boreal forests.

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Popular science summary

Global warming is causing warmer springs and an earlier start of the season when plants are active in northern Scandinavia. Usually in spring, warm days and cold nights create a pattern of freezing and melting that makes measuring plant activity difficult. One way to measure this activity in trees is by measuring the water inside their stems using sensors called sap flow sensors. But because these sensors use the thermal properties of wood, they make mistakes when the temperature changes quickly, and need to be tested to make them more reliable. This study tests how sap flow sensors can measure the water inside tree stems temperatures between range -15 and 25ºC. This sudy also tests if trees expand when ice is formed during the freezing and melting that happens in spring. The results showed that the sensors we currently use can reliably measure the water in trees at warm temperatures, and need adjusting near freezing temperatures. The results also showed that trees do expand during freezing. This study helps us understand how trees use water and how we can measure their activity at the start of spring, which is important for measuring the effect of climate change on northern forests.

Acknowledgements

Appendix 1

Supplemental 1. Log equipped with point dendrometer, heat pulse sensor, TEROS water content sensor, and TEMPOS thermal properties sensor (left). Log weighed on scale with point dendrometer attached for measuring gravimetric water loss (right)

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