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PHENOLOGY OF SAP PRODUCTION IN SUGAR MAPLE AND ITS VARIATION IN A CONTEXT OF CLIMATE CHANGE

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DEDICATION

Aos meus pais, Neide e Hideo Kurokawa, e à minha irmã Suzy
To my parents, Neide and Hideo Kurokawa, and sister Suzy
À mes parents, Neide et Hideo Kurokawa, et à ma sœur Suzy

FOREWORD

This thesis covers the results of my doctoral research under the supervision of Professor Sergio Rossi and Professor Sylvain Delagrange, prepared under the format of the doctoral program in biology. This doctoral thesis is presented in three chapters in the form of scientific articles, a general introductory and final concluding chapter. The introduction is a contextualization of the current knowledge in specific aspects of sugar maple production and environmental conditions addressed in this doctoral research. The three following chapters that are the core of the thesis are written as scientific articles and are published in scientific journals. The first chapter, describing the sap phenology of sugar maple in Quebec-Canada, was published in 2022 in the journal International Journal of Biometeorology. The second chapter, focusing on the new equipment to measure sap in a daily resolution was published in the journal iForest in 2024. The third chapter focuses on the responses to climate warming and other environmental conditions affecting the sap production was published in the journal Trees, Forests and People in 2025. The general conclusion summarizes the work of all the thesis in the form of concluding remarks and discusses the contributions of this doctoral work. I have participated as the lead in the conceptualization, sampling, methodology and formal analysis of most the samples used for this project as well as lead author in each of the manuscripts with the support of my supervisors. The articles included in this thesis and further details are listed below:

Chapter 1. Sap season at provincial scale and low resolution
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The version included in this thesis may differ partially from the published article in terms of formatting, style, and content.

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TABLE OF CONTENTS

ACKNOWLEDGMENTS II

DEDICATION IV

FOREWORD V

LIST OF FIGURES XI

LIST OF TABLES XIII

ABBREVIATIONS AND ACRONYMES XIV

RÉSUMÉ XV

ABSTRACT XVII

INTRODUCTION 1

0.1 Statement of the problem 1

0.2 Environmental and physical explanation for sap exudation 3

0.3 Methods of sap collection 6

0.4 Sap production timings and temperatures 7

0.5 The influence of climate change on the timing and yield of sap production 9

0.6 Objectives and hypotheses 11

0.7 Methodological approach and study sites 12

0.8 Structure of the thesis 15

CHAPITRE 1 SAP SEASON AT PROVICIAL SCALE AND LOW RESOLUTION 16

1.1 Abstract 17

1.2 Introduction 18

1.3 Materials and Methods 20

1.3.1 Study site 20

1.3.2 Data collection 21

1.3.3 Climate data 21

1.3.4 Data analysis and statistics 21

1.4 Results 22

1.4.1 Distribution of the timing of sap production 22

1.4.2 Daily change in the timing of sap production 22

1.4.3 Average daily temperature during sap production 24

1.5 Discussion 26

1.5.1 The physiological and physical explanations 26
1.5.2 Daily pattern of the onset and ending of sap production 27
1.5.3 Acknowledgements 29
1.5.4 Funding 30
1.5.5 Declarations 30

CHAPITRE 2 SAP SEASON AT REGIONAL SCALE AND INTERMEDIATE RESOLUTION 31

Measuring natural sap production in sugar maple at daily temporal resolution 31

2.1 Abstract 32

2.2 Introduction 33

2.3 Material and Methods 35

2.3.1 Testing the batteries of rain gauges 35
2.3.2 Monitoring sap production in the field 36
2.3.3 Data analysis and statistics 37

2.4 Results 38

2.4.1 State of charge under controlled conditions 38
2.4.2 Curve fitting of the state of charge 40
2.4.3 Comparing the coefficients of the models 41
2.4.4 Rain gauges in the field 41
2.4.5 Cumulative percentage of daily sap production 44

2.5 Discussion 45

2.5.1 Rain gauge as a tool for measuring sap production 46
2.5.2 Dynamics of sap exudation and sap yield 47
2.5.3 Daily distribution of sap exudation 49

2.6 Conclusions 51

2.6.1 Acknowledgements 52

2.7 Supplementary material 53

CHAPITRE 3 SAP SEASON AT LOCAL SCALE AND HIGH RESOLUTION 55

The divergent advancements of sap phenology in maple under warming conditions can shorten the sugar season 55

3.1 Abstract 56

3.2 Introduction 57

3.3 Material and methods 59

3.3.1 Study area 59
3.3.2 Tree selection and data collection 59
3.3.3 Climate data 60
3.3.4 Data analysis and statistics 61

3.4 Results 62
3.4.1 Sap phenology and total yield 62
3.4.2 Weather conditions 64
3.4.3 Relationships between temperature and sap phenology 67
3.4.4 Predicting the sap season under warming scenarios 68
3.5 Discussion 71
3.6 Sap dynamics and environmental conditions 71
3.6.1 Relationships between air temperatures and sap phenology 73
3.6.2 Sap phenology under greenhouse gas emission scenarios 74
3.7 CRediT authorship contribution statement 77
3.8 Declaration of competing interest 77
3.9 Acknowledgements 77
3.10 Funding 77
3.11 Data availability 77
3.12 Supplementary materials 78
CONCLUSION 81
REFERENCES 84

LIST OF FIGURES

Figure 0.1 Syrup yield variation per year and region in Quebec province.....2

Figure 0.2 Stages in the freeze–thaw cycle. Various stages in the freeze–thaw cycle is depicted within an adjacent fibre–vessel pair. Stages 1, 2, 3 depict the freezing process: when temperature drops, an ice layer grows on the inner wall of the gas-filled fibre as water is drawn via cryostatic suction through the porous cell wall. Stages 3, 4, 1 depict the reverse process as temperature rises. Note the reversed order of phase interfaces inside the fibre between stages 2 and 4. The blue arrows denote water transport either through the fibre–vessel wall or between roots and vessels (Graf et al., 2015). 5

Figure 0.3 Outline of the thesis chapters in terms of number of regions and data resolution ...12

Figure 0.4 The location of 19 sugar bushes included in chapter 1, and the provincial and local scale with * symbol included in chapter 2 and 3. 15

Figure 1.1 Location of the nineteen sugarbushes in Quebec, Canada. Sugarbushes colored in dark green are located at higher altitude. 20

Figure 1.2 Cumulative and frequency distribution of onset and ending of sap production recorded in 19 sugarbushes in Quebec, Canada. 22

Figure 1.3 Onset and ending of sap production during the springtime. Shaded areas represent the confidence interval. Studentized residuals vs Day of the year (predicted values), resulting from the mixed models performed on the timing of sap production in sugar maple. 24

Figure 1.4 Temperature recorded at the onset and ending of sap production. Line represents a regression. 25

Figure 2.1 Location of the four study sites in Quebec, Canada. 37

Figure 2.2 Variation in the state of charge in rain gauges exposed to different temperatures and set at two logging intervals. Data were fitted by nonlinear exponential decay models, whose standardized residuals (SR) are shown in the smaller panels. 40

Figure 2.3 Daily dynamics of natural sap production in sugar maple and the correlation coefficient of Spearman in each site. Note the different ranges of vertical axes. 43

Figure 2.4 Cumulative percentages of daily sap production. Diagonal line represents 1:1. 45

Figure S2.1 Air temperature before and during the sap season in 2022 in four sites in Quebec, Canada. 54

Sap exudation was discontinuous, with productive days followed by non-productive periods (Figure 3.1). The dynamics of sap production was synchronized between trees, as observed, for example, on the very productive DOY 115 in 2019, and the lack of sap exudation on

DOY 75 in 2021. The quadratic logistic regressions allowed the sap season to be estimated with a threshold of 10%. The performance of the classification model was evaluated using a confusion matrix, which assessed the predictive accuracy of the fitting. Predictions had 86.7 and 75.1% of values matching the productive and non-productive observations, respectively. In general, the sugar season varied from 40 to 53 days. The years 2019 and 2018 had the shortest and longest durations of sap season, respectively. 62

Figure 3.1 Daily sap production in four sugar maples during 2018-2022. The black bars represent the volume of sap production (l). The shaded areas represent the sap production season with the onset represented by a threshold of 10%. The quadratic logistic regressions (blue line) were fitted to represent the probability of occurrence of sap exudation (binary). The darker grey area is confidence interval with a 95% confidence level. 63

Figure 3.2 Mean and error bar comparing the onset and ending of sap production between years. Groups (i.e., onset or ending) with the same letters are not statistically different. 64

Figure 3.3 Maximum (red line) and minimum (blue line) air temperatures, snow depth (black line), soil water content (light grey line) and organic (brown line) and mineral (orange line) soil temperature. The shaded areas represent the estimated averaged extension of the sap season from 2018 to 2022.....66

Figure 3.4 Normal linear regressions between average monthly air temperature (i.e., minimum and maximum) and the onset (solid line) and ending (dashed line) between 2018 and 2022 (round symbol). The shaded area represents the 95% confidence interval. 68

Figure 3.5 Results of PLS (partial least squares) analysis showing model coefficients and variables of importance in the projections' (VIP) values for the onset and ending and phenological phases in sugar maple between 2018 and 2022 to monthly minimum, mean and maximum temperatures. 69

Figure 3.6 Actual and projections of the maximum (red lines), average (black lines) and minimum (blue lines) air temperatures from 2000 to 2100 of RCP 2.6 (lightest tones), RCP 4.5 (mid-tones) and RCP 8.5 (darkest tones) based on the Ouranos future climate scenarios at Simoncouche research station (48 °13'N, 71°15'W, 350 m a.s.l.).....70

Figure 3.7 The onset and ending of sap production according to February - April temperatures predicted from 2023 to 2100 by applying the selected PLS model. The dots represent the predicted onset and ending timings of sap production. 71

LIST OF TABLES

Table 1.1 Summary of linear mixed models (LMMs) for phases (i.e., onset and ending as phenological events), with treatments as fixed factors (DOY, phases) during spring 2018. The results include, for each effect, F statistic (F values) and probability (P). Symbol (*) indicates significant effects ($P \leq 0.05$) 23

Table 2.1 Location and climate of the four study sites in Quebec. 37

Table 2.2 Estimated coefficients and statistics of the nonlinear models describing the variation in the state of charge of rain gauges submitted to different temperatures and set up at different logging intervals. Values are reported as a mean ± standard error. 41

Table 2.3 Spearman's correlation coefficients (ρ) and relative probabilities of correlations in daily sap production during spring 2022 among the four study sites. NS=not significant. 44

Table S2.1 Tree characteristics at the four study sites during the sap season. 53

Table 3.1 Characteristics of the four sugar maple trees located at Simoncouche from 2018 to 2022. Diameter at breast height = DBH. 60

Table S3.1 PLS model summary: Q^2, determination coefficient for leave-one-out cross validation, PVE-X, percentage variation explained for cumulative X; PVE-Y, percentage variation explained for cumulative Y. 79

Table S3.2 Summary of linear regression model between monthly temperatures (i.e., maximum-Max and minimum-Min) and sap phenology (i.e., onset and ending timings) during spring 2018 to 2022. The results include, R^2 (Coefficient of determination) and probability (P). Symbol (*) indicates significant effects ($P \leq 0.05$) 80

ABBREVIATIONS AND ACRONYMES

° C	degree Celsius
a.s.l	Above see level
AIC	Akaike information criterion
AM	Ante meridien or Before noon
ASJ	L'Anse-Saint-Jean
BIC	Bayesian information criterion
CAD$	Canadian dollars
cm^3/cm^3	Cubic centimeter per cubic centimeter
CO_2	Carbon dioxide
DOY	Day of the year
ECMW F	European Centre for Medium-Range Weather Forecasts fifth generation Reanalysis
ERA5	Fifth generation ECMWF reanalysis
GEE	Google Earth Engine
h	Hour
km	Kilometer
kΩ	Kiloohm
LAT	Laterrière
LMM	Linear Mixed Model
m	Meters
M $	Million dollars
mA	Milliampere
MOR	Humus form
NC	North Carolina
NIPALS	Nonlinear Iterative Partial Least Squares
NIPALS	Nonlinear Iterative Partial Least Squares
p	p-value
PLS	Partial Least Squares Regressions
PLS	Partial Least Squares Regressions
PM	Post meridien or After noon
PMV	Parc National de Monts-Valin
R^2	R squared or coefficient of determination
RAP	Rivière-à-Pierre
RCP	Represented by the concentration pathway
SAS	Statistical Analysis System
V	Voltage
VIP	Variable importance in projection
VIP	Variable Importance in Projection
ρ	Correlation coefficient of Spearman

RÉSUMÉ

Les changements climatiques affectent la phénologie dans l'hémisphère Nord. Le réchauffement observé depuis les années 1970 a été le plus prononcé aux hautes latitudes, avec les plus fortes augmentations de température se produisant pendant les saisons d'hiver et de printemps. Ces changements entraînent des conséquences significatives pour la phénologie des érables à sucre et la production du sirop. La production de sirop d'érable, une activité traditionnelle et économique dans le nord-est de l'Amérique du Nord, est particulièrement vulnérable à ces changements climatiques. Le sirop est fabriqué en concentrant la sève extraite des érables, un processus qui dépend du cycle de gel-dégel typique au début du printemps. Cependant, le changement climatique modifie le calendrier et la durée de l'exsudation de la sève, avec des implications incertaines pour la production future. Par conséquent, étudier la production de sève et la phénologie des érables en réponse aux variations climatiques est crucial pour comprendre et atténuer les impacts du changement climatique sur ce produit économiquement et culturellement important. En raison du manque d'informations précises sur le calendrier et le rendement de la production de sève, des recherches supplémentaires dans ce domaine sont essentielles. Cette thèse vise à surveiller le calendrier et la dynamique de la production de sève à différentes échelles et résolutions, dans le contexte du changement climatique.

Cette étude a été menée au printemps, dans la province de Québec, au Canada, en recueillant les données horaires de production de sève à différentes échelles, des sites provinciaux aux sites locaux et de basse à haute résolution. Les sites s'étendaient des régions les plus productives de l'érable aux limites les plus septentrionales de la distribution de l'érable en Amérique du Nord. Initialement, les données ont été enregistrées par le biais d'enquêtes auprès des producteurs, qui ont été affinées par des mesures directes des horaires de production de sève à partir d'équipements installés sur des arbres individuels. Ces horaires ont ensuite été comparés aux données météorologiques, y compris la température de l'air, la profondeur de la neige, le contenu en eau du sol et la température du sol. La température de l'air, en tant que principal facteur environnemental de l'exsudation de la sève, a ensuite été utilisée dans les modèles de prédiction.

Les horaires d'exsudation de la sève ont montré une forte corrélation avec la température de l'air et un modèle cohérent observé entre et au sein des sites, malgré la co-occurrence d'autres facteurs météorologiques. De plus, la collecte de données à haute fréquence a montré les dynamiques détaillées du flux de sève dans l'érable à sucre, confirmant l'influence de la température et soulignant le rôle des cycles de gel-dégel. L'utilisation de pluviomètres comme outil automatique enregistrant des données de sève à haute fréquence a offert une avancée méthodologique significative pour mesurer le flux de sève. L'enregistrement des données avec les pluviomètres a démontré que la production de sève était discontinue, alternant les jours productifs et non productifs. Dans l'ensemble, 74 % de la sève a été exsudée pendant 20 % de la saison sucrière, ce qui correspondait aux proportions décrites par la loi de Pareto (c'est-à-dire la règle 80/20). Enfin, nous avons observé d'autres facteurs environnementaux co-occurrents avec l'exsudation de la sève. L'exsudation de la sève commence avec le début de la fonte des neiges, l'augmentation du contenu en eau du sol et la sève se termine lorsque la température du sol augmente. Pour les prédictions des horaires, une avancée divergente du début et de la fin de la production de sève sous les conditions de réchauffement est attendue, entraînant une durée

plus courte de la saison sucrière, avançant jusqu'à 20 jours pour le début et 26 jours pour la fin d'ici 2100 dans le scénario d'émissions le plus élevé. Les producteurs devraient commencer à préparer leurs érablières plus tôt que d'habitude pour s'aligner sur les horaires avancés attendus en raison du réchauffement climatique. Plus précisément, les horaires d'entaillement des arbres doivent être ajustés pour s'aligner avec le début de la saison de la sève. Tout retard pourrait entraîner des pertes de production importantes, en particulier pendant les saisons de sève plus courtes, comme prévu par les modèles.

En conclusion, des données horaires à haute résolution ont montré des modèles diurnes cohérents dans le flux de sève, fortement corrélés avec les fluctuations de température. Comme le début et la cessation du flux de sève étaient principalement déterminés par des seuils spécifiques de température de l'air, les autres facteurs météorologiques comme l'enneigement, le contenu en eau du sol et la température du sol jouaient un rôle secondaire. De plus, cette étude a montré un calendrier de production de sève cohérent dans la région étudiée, suggérant un modèle pour la production de sève d'érable dans la province de Québec. En adaptant les pluviomètres à seau basculant pour la mesure du flux de sève, des informations précises sur les variations quotidiennes et saisonnières ont été obtenues, améliorant ainsi la précision de la collecte de données. Cette étude innovante offre une avancée pour surveiller la production de sève et prédire les effets du changement climatique sur les horaires de sève, fournissant des connaissances précieuses pour la recherche et l'industrie du sirop d'érable. De plus, les résultats de cette étude ne font pas seulement progresser notre compréhension des impacts du changement climatique sur la phénologie de la sève d'érable, mais fournissent également une base pour développer une gestion adaptative, faire progresser les technologies de surveillance et soutenir la recherche continue pour assurer que l'industrie puisse continuer à croître et à perdurer à l'avenir

Mots clés : Exsudation de sève, collection de sève, température de l'air, *Acer saccharum* Marsh.

ABSTRACT

Alterations in climate are affecting the phenology in the northern hemisphere. The warming pattern observed since the 1970s has been most pronounced at higher latitudes, with the largest increases in temperature occurring during the winter and spring seasons. These changes cause significant consequences for the phenology of sugar maple trees and its syrup. Maple syrup production, a traditional and economic activity in northeastern North America, is particularly vulnerable to these climate shifts. The syrup is made by concentrating sap extracted from maple trees, a process that depends on the freeze-thaw cycle typical of early spring. However, climate change is altering the timing and duration of the sap exudation, with implications for the uncertain future production. Therefore, studying sap production and maple tree phenology in response to climate variations is crucial to understanding and mitigating the impacts of climate change on this culturally and economically important product. Due to the limited information on the precise timing and yield of sap production, further research in this area is essential. This thesis aims to monitor the timing and dynamics of sap production across various locations and resolutions, within the context of climate change.

This study was conducted during spring in the province of Quebec, Canada, collecting sap production timings at different scales, from provincial to local sites and from low to high resolution. Sites spanned the most productive maple regions to the northernmost limit of North American maple distribution. Initially, data were recorded through producer surveys, which were refined by direct measurements of sap production timings from equipment installed on individual trees. These timings were then compared with weather data, including air temperature, snow depth, soil water content, and soil temperature. The air temperature as the primary environmental driver of sap exudation was later used in the prediction models.

Sap exudation timings demonstrated a strong correlation with air temperature and a consistent pattern observed among and within sites, despite the co occurrence of other meteorological factors. Additionally, high-frequency data collection showed detailed dynamics of sap flow in sugar maple, confirming the influence of temperature and highlighting the role of freeze-thaw cycles. The use of rain gauges as an automatic tool recording high-frequency sap data offered a significant methodological advancement for measuring sap flow. The data recording with rain gauges demonstrated that sap production was discontinuous, alternating productive and non-productive days. Overall, 74% of the sap was exudated during 20% of the sugar season, which matched the proportions described by the Pareto law (i.e. 80/20 rule). Lastly, we observed other environmental factors co occurring with the sap exudation. Sap exudation begins with the onset of the snowmelt, the rising in soil water content and sap ends when the soil temperature increases. For the predictions of timings, a divergent advancement of the onset and ending of sap production under warming conditions are expected, resulting in a shorter duration of the sugar season, advancing of up to 20 days for the onset and 26 days for the ending by 2100 in the highest emission scenario. Producers should start preparing their sugarbushes earlier than usual to align with the advanced timings expected due to climate warming. Specifically, tapping schedules must be adjusted to align with the start of the sap season. Any delays could lead to substantial production losses, particularly during shorter sap seasons, as projected by the models.

In conclusion, a high-resolution hourly data showed consistent diurnal patterns in sap flow, strongly correlated with temperature fluctuations. As the onset and cessation of sap flow were primarily driven by specific air temperature thresholds, the other meteorological factors like snowpack, soil water content and soil temperatures played a secondary role. Additionally, this study showed a consistent sap production timing across the studied region, suggesting a pattern for maple sap production in the province of Quebec. By adapting tipping bucket rain gauges for sap flow measurement, detailed insights into daily and seasonal variations were obtained, thus improving the accuracy of the data collection. This innovative study offers an advancement for monitoring sap production and predict climate change effects in the sap timings, providing valuable knowledge for both research and the maple syrup industry. Furthermore, the findings of this study not only increase our understanding of the impacts of climate change on maple sap phenology, but also provide a foundation for developing adaptive management, advancing monitoring technologies, and supporting continued research to ensure the industry can continue to grow and endure in the future.

Keywords : Sap exudation, sap collection, air temperature, *Acer saccharum* Marsh.

INTRODUCTION

0.1 Statement of the problem

Maple syrup is one of the most important products to Canada, being also considered a 'liquid gold' since the eighteenth and nineteenth centuries (Thomas, 2005). In North America, only a few species of maple trees are native, and even fewer are suitable for tapping to collect sap for syrup production. The most commonly tapped species include the sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and, to a lesser extent, the box elder (*Acer negundo* L) and the silver maple (*Acer saccharinum* L.) (Farrell, 2013; Peters et al., 2020). These species are widely selected for their high sugar content sap and yield, which the sap is transformed into the maple syrup that is a staple of Canadian agriculture.

Quebec province is the heart of maple syrup industry, and production has seen a significant increase over the past decade. According to Statistical Overview of the Canadian Maple Industry, the production in 2002 was 32,490 million liters and in 2023 achieved 63,017 million liters (Government of Canada, 2024). This growth highlights the importance of maple syrup to the Canadian economy and the advancements in production techniques and industry practices. However, maple syrup is not constant, varying from one year to another, from one day to another, with a general increasing over time (Figure 0.1). This increase in maple syrup in the last years is related to the technological improvement and the better use of the sap, due to maximum use of the product like the buddy syrup. The problematic lies in understanding whether there will be an increase or decrease in sap water production between years or days, with the increasing in warming temperature.

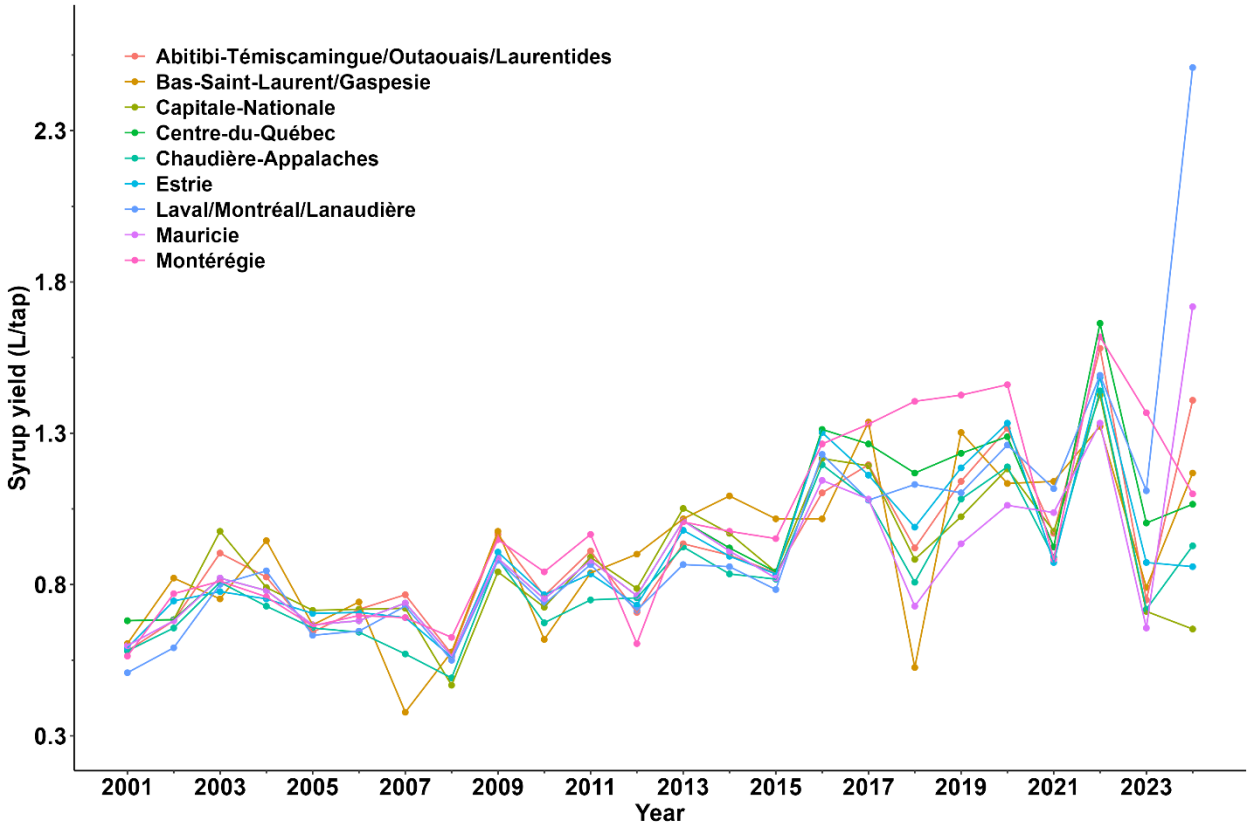

Figure 0.1 Syrup yield variation per year and region in Quebec province

Climate change is projected to significantly impact the phenology of sap production in sugar maple trees. Phenology can be defined as a recurring life cycle events and how these events are influenced by environmental drivers (Delpierre et al., 2019). In terms of sap phenology, we define as the timing of the onset, duration and ending of sap season and the climatic drivers influencing the sap exudation. Differential species responses to temperature and moisture variations may induce phenological mismatches between sap production onset and cessation. Studies showed a 4.3-day advancement in sap production for every 1°C increase in mean March temperature, with maximum sap volume achieved at a mean temperature of 1°C from January to May (Rapp et al., 2019). Other study reported similar findings, showing 4-day advancement in syrup production per degree Celsius increase, a relationship useful for predicting long-term changes in production onset under various annual temperature scenarios (Houle et al., 2015). While overall warming is expected, this increase is not uniform. Nighttime temperatures are projected to rise faster than daytime temperatures, a phenomenon known as asymmetric warming (Wen et al., 2018). This disproportionate warming, with nighttime temperatures

increasing at twice the rate of daytime temperatures, can create unfavorable conditions for maple sap production, especially in southern regions.

The consequences of climate change affect maple syrup production in complex ways, such as sap quality, quantity, management, and tree health. Warmer temperatures negatively impact sap quality by promoting bud formation, which leads to undesirable buddy syrup (Houle et al., 2015) and accelerate growth reactivation. Furthermore, climate change poses several other challenges: reduced sap quantity (Duchesne et al., 2009), increased risk of microbial contamination in collection tubing (Perkins et al., 2022), and compromised tree health due to elevated soil temperatures, which can favor pathogens and difficult nutrient uptake (Rademacher et al., 2023). These effects highlight the need for further research to ensure the dynamics and duration of maple syrup production in a changing climate.

0.2 Environmental and physical explanation for sap exudation

Maple sap production or sap exudation results from xylem sap flow driven by alternating sub-freezing and above-freezing temperatures (Ceseri & Stockie, 2013; Graf et al., 2015). This process occurs between the dormant leafless phase and the active transpiration phase, prior to growth reactivation. During this period, specific physiological processes trigger positive xylem pressure and convert stored starches into sugars, primarily sucrose (Pallardy, 2017). This sucrose is unloaded at low, non-freezing temperatures and partially released into the xylem vessels, enhancing the osmotic potential of the xylem sap in the beginning of the season (Graf et al., 2015). The resulting stem pressure cause sap exudation from holes or tapholes.

Positive xylem pressure during winter and spring can reverse frost-induced embolism in temperate woody plants (Améglio et al., 2002; Hacke & Sauter, 1996). In the absence of root pressure, an osmotic pressure difference between the apoplast and symplast contributes to sap flow (Yang & Tyree, 1992). Studies demonstrated that plants maintained at 1.5°C reached only 7% of their potential xylem sap osmotic pressure, generating pressures up to 40 kPa (Améglio et al., 2002). However, exposure to low, non-freezing temperatures followed by freeze-thaw cycles resulted in pressures of 210 kPa, or 39% of the theoretical osmotic pressure. While a simple osmotic model can explain the moderate positive pressures observed at low, non-freezing

temperatures, it does not account for the synergistic effects of freeze-thaw cycles (Améglio et al., 2001).

Several tree species, including maple, birch, walnut, and butternut, exhibit a unique mechanism for generating elevated stem pressure, leading to sap exudation in early spring. Specially maple trees exhibit higher stem pressures compared to other temperate species like grapes (*Vitis vinifera* L.) and birch (*Betula* spp.) due to the higher sugar concentration in their sap (Johnson et al., 1987). The underlying mechanism of this phenomenon has been the subject of studies from many decades. Some researchers propose that positive sap pressure originates in the stems rather than the roots (Schenk et al., 2021), driven solely by physical factors, including a combination of thermal and freeze-thaw effects (Milburn & O'Malley, 1984; Sauter, 1980). Previous research attributed the mechanism of sap exudation to an internal pressure develops between air-filled fiber and sap-filled vessels (Johnson, 1945; Wiegand, 1906). During freezing night temperatures, the gas within the fiber contracts, drawing water through the fiber walls (Figure 0.2). As temperatures rise during the day, the compressed gas expands, forcing the melting water out of the fibers and into the vessels (Milburn & O'Malley, 1984; Stevens & Eggert, 1945).

Alternatively, in the absence of an osmotic pressure difference, air bubbles could dissolve. In this condition, sap exudation would be driven by differences in sugar concentration, primarily sucrose, across semipermeable membranes separating xylem cells (Sperry et al., 1988; Tyree & Zimmermann, 2002). Sucrose, derived from starch catabolism, is actively transported from ray parenchyma cells into vessels via connecting membranes (Sauter, 1980). Studies using fluorescent dye to trace sucrose movement in the xylem have shown limited presence of the dye in parenchyma and vessels, with no presence in fibers. This observation is supported by more recent research demonstrating that fibers are essentially non-conductive due to the lack of end-to-end cell connections and the presence of mostly unpaired (blind) pits on their lateral walls, which are smaller and fewer in number compared to other xylem elements and tracheid (Cirelli et al., 2008; Sano et al., 2011). Despite these various theories, the precise mechanisms governing sap exudation remain incompletely understood.

Maple sap production under gravity is mainly driven by freeze-thaw cycles but other environmental factors such as soil moisture and snow cover can indirect affect sap exudation (Brown & DeGaetano, 2011; Skinner et al., 2010; Tyree, 1983). Soil moisture affects water availability for trees, impacting sap uptake. Higher soil moisture levels can improve the ability to produce sap during freeze-thaw cycles (Tyree, 1983). Additionally, the rate of sap uptake varies with the freezing rate, which is influenced by soil moisture conditions (Tyree, 1983). Indeed, snow cover and depth act as insulation, influencing soil temperature and water availability (Brown & DeGaetano, 2011; Tyree, 1983), which can help for initiating sap flow. Snow depth regulates soil temperatures, with researchers showing a modification occurring under approximately 0.4m snow depths (Zhang, 2005). Rapp et al. (2019) considered that sap flow is also site-specific factors beyond climate, including tree characteristics and soil conditions. More investigations are necessary to understand the relation between snow cover, soil conditions, and maple sap production.

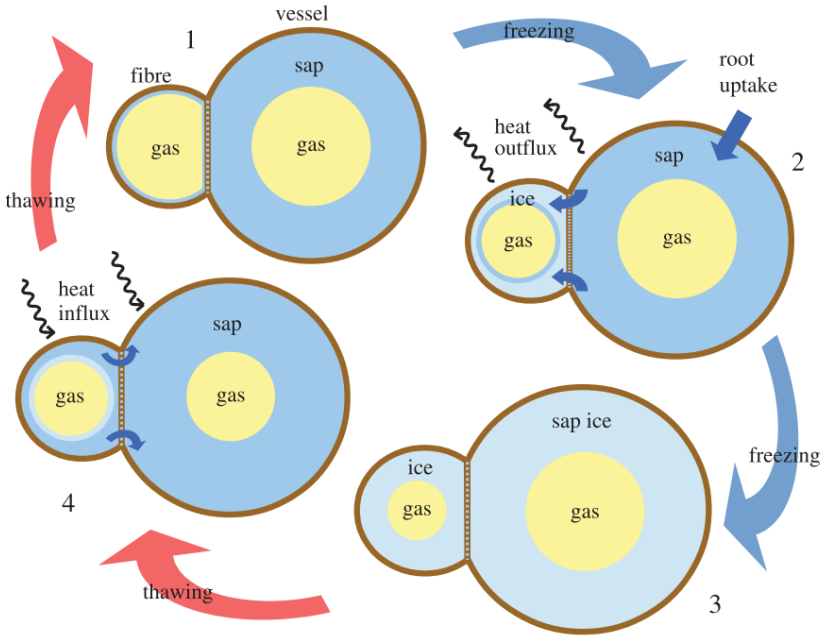

Figure 0.2 Stages in the freeze–thaw cycle. Various stages in the freeze–thaw cycle is depicted within an adjacent fibre–vessel pair. Stages 1, 2, 3 depict the freezing process: when temperature drops, an ice layer grows on the inner wall of the gas-filled fibre as water is drawn via cryostatic suction through the porous cell wall. Stages 3, 4, 1 depict the reverse process as temperature rises. Note the reversed order of phase interfaces inside the fibre between stages 2 and 4. The blue arrows denote water transport either through the fibre–vessel wall or between roots and vessels (Graf et al., 2015).

Increased sugar concentration in the ray parenchyma (sapwood), primarily in autumn, coincides with relatively low nighttime and high daytime temperatures (Gregory et al., 1986) and may be a result of the dehardening process. Soluble sugars act as osmoregulatory substances, protecting against freezing by lowering the freezing temperature in the stem and mitigating dehydration caused by ice formation. These sugars also contribute to cellular maintenance and respiration (Beauvieux et al., 2018; Charrier et al., 2013; Houle et al., 2015). Despite the prevailing theories implicating both freeze-thaw cycles and osmosis in sap production, the precise factors influencing this process remain unclear, highlighting the need for further studies.

0.3 Methods of sap collection

The sap collection system for maple trees has improved in recent years. Until 1960s, the use of buckets was the traditional and most used method, mainly because personal, low-energy alternative and small-scale use (Huyler, 1975). Collecting sap water using a traditional system leverages the natural flow of sap due to gravity while rely on the natural pressure generated by the sugar maple tree. This method is an alternative for its simplicity and lower energy requirements compared to vacuum systems. In physiology, the sap collection through gravity system allows researchers to assess the natural functioning of sugar maple and their physiological responses. This method minimizes external interference with the tree's internal processes. Consequently, sap collected via gravity systems often exhibits higher purity, as the natural flow mechanisms of the tree regulate sugar concentrations more effectively (Morrow, 1972). Additionally, this method mitigates risks by extracting sap in a way that allows for better recovery of tree resources (Isselhardt et al., 2016).

More recently, pipelines and tubing systems have become more widespread, allowing for more efficient sap collection on a larger scale and meeting the demands of the growing maple syrup industry. The decision to use a particular sap collection system, such as gravity or vacuum system, depends on different factors such as the size of the sugar maple stands or bush, the geographic distribution of the trees, and the available resources (Snyder et al., 2019).

After the sap collection, the sap is typically concentrated through the process of evaporation, which involves boiling off the excess water to obtain the concentrated sap or syrup. Evaporation

in large containers do not guarantee control of the quality, but reducing air access to the sap during the evaporation process can help producers better control the final product by limiting oxidation and other undesirable changes, such as the low quality syrup (Duchesne et al., 2009).

The vacuum systems have been widely adopted by maple syrup producers due to their ability to increase sap yields. Studies showed that the increase can reach up to 28% compared to traditional methods (Houle et al., 2015; Huyler, 1975). This method can compensate for the collection of sap in less favorable days and years, given the fluctuation in sap production from one day or year to the other. Moreover, vacuum system and reverse osmosis has been found to concentrate the sugars in the sap, resulting in a higher sugar content and improved syrup quality compared to traditional methods (Duchesne & Houle, 2014).

Other method for sap collection is conducted with surveys from maple producers across regions and years (Caughron et al., 2021; Legault et al., 2019; Snyder et al., 2019). This method consists in collecting detailed data from maple producers in different geographic areas and over multiple years on the timing of sap production, the volume of sap obtained, the quality characteristics of the sap and resulting maple syrup. Despite being the least accurate method, it still provides valuable insights into the regional and temporal patterns of sap production and how they may be changing over time. The importance also relies in creating a robust dataset to understand the long-term trends to predict the capacity for the producers to adapt to climate change and variability in sap production (Caughron et al., 2021).

0.4 Sap production timings and temperatures

February to May are the months when sap production typically occurs in sugar maple trees as a result of local weather conditions. The onset of sap production typically occurs between DOY 65 and DOY 83, with the peak in production often observed in April (Duchesne & Houle, 2014; Rapp et al., 2019). The ending normally occurs between DOY 100 and DOY 118 across 11 regions in Quebec, primarily in the Center of Quebec, Estrie, and Saint-Hyacinthe (Houle et al., 2015).

The peak production of metabolite-rich sap occurs during diurnal freeze-thaw cycles, characterized by daytime temperatures (6 AM–6 PM) above 0°C and nighttime temperatures (6

PM–6 AM) below 0°C (Cirelli et al., 2008; Johnson & Tyree, 1992; Tyree, 1983). While tapping season temperature is a stronger predictor of hourly sap collection timings than the optimal freeze-thaw period (Rapp et al., 2019), some researchers suggest that ideal conditions involve nighttime temperatures near 0°C and daytime temperatures exceeding 4°C (Pothier, 1995). Other studies emphasize the importance of maximum daily temperature, the diel temperature range, or the preceding months as determinants of sap production (Duchesne et al., 2009; Kim & Leech, 1985; Plamondon & Bernier, 1980). Continuous days with temperatures at 0°C cease production entirely within 24-36 hours, typically coinciding with bud burst (Wiegand, 1906). A study estimated an 80% probability of sap flow when the minimum temperature is below -1.1°C and the maximum temperature exceeds 2.2°C (Skinner et al., 2010). Other study observed reduced sap collection when minimum air temperatures fell below -8°C, and sap production continued even with minimum temperatures above 1.5°C and maximum temperatures exceeded 5°C (Rapp et al., 2019).

Sap timings variation can be attributed to different climatic factors, such as air temperature, and the timing of spring thaw (Duchesne & Houle, 2014; Houle et al., 2015). The high year-to-year variability in the timing of the sap production season has become a major concern for maple producers, who must constantly adapt their practices to the changing environmental conditions to ensure a successful harvest (Duchesne & Houle, 2014; Houle et al., 2015).

The same occurs with daily or hourly production in the field, one day is more productive than the other, and one hour is more productive than another. This variability underscores the importance of understanding the impacts of climate change, particularly given that Canada is warming at twice the global rate, with a greater impact during winter and spring (Bush & Lemmen, 2019). Maple syrup producers have expressed concerns about the increasing variability in the timing of the sap production season due to climate change (Houle et al., 2015). While annual time series data are mostly found (Houle et al., 2015; Rapp & Crone, 2014; Rapp et al., 2019), finer-scale such as hourly and daily scales are required for better understand sap timings.

0.5 The influence of climate change on the timing and yield of sap production

As sugar maple is increasingly exposed to the pressures of climate change, its ability to acclimate to warmer air temperatures will be critical; sap exudation could be substantially affected by environmental changes, leading to reduced yields and a shortened production period. Therefore, understanding the impacts of climate on sugar maple and developing strategies for adaptation and resilience are critical priorities.

Extended periods of warmer temperatures can significantly alter sap production dynamics, leading to reduced yields and earlier onsets of sap flow. Maintaining traditional collection schedules under these conditions may result in fewer sap flow days, further diminishing yields (Skinner et al., 2010). Yield reductions can also be caused from direct tree damage, altered physiological processes, or shifts in key phenological events such as bud break (Duchesne & Houle, 2014; Duchesne et al., 2005; Marvin et al., 1971). Warmer temperatures induce earlier bud break and leaf expansion, potentially disrupting the synchronization with the sap flow season. This premature cessation of sap flow shortens the production period, ultimately reducing total sap yield (Houle et al., 2015). Climate modeling of maple syrup yield in Quebec, Canada, demonstrates that over 80% of annual yield variation can be attributed to four monthly climate variables: temperature, precipitation, frost days, and snowfall (Duchesne et al., 2009).

Climate change projections indicate increased fluctuations in daily temperatures and soil water availability (rain or snow) across the sugar maple bush (Duchesne et al., 2009; Guilbert et al., 2014; Skinner et al., 2010). Projected temperature increases of 2.6°C and 3.9°C in April by 2050 and 2090, respectively, are associated with a predicted 15% to 22% decrease in sap production. These higher temperatures also contribute to earlier bud burst, marking the end of sap production and promoting a risk of microbial proliferation (Duchesne et al., 2009). The potential for earlier than usual sap flow onset requires advanced preparation among producers to avoid economic losses associated with missed sap collection days (Houle et al., 2015).

Even minor climatic variations, including temperature fluctuations and snowpack depth during severe winters, can influence sap production. Understanding the mechanisms governing sap production under changing climate conditions is therefore crucial. Short-term, extreme events

at daily or hourly scales can also significantly impact sap yields. Projected changes by the end of the century include temperature increases of 1.5°C to 7°C, winter precipitation increases of 5% to 20%, summer precipitation increases of 5%, and a 50% decrease in snowfall, coupled with a higher frequency of ice storms, hurricanes, extreme heat and cold events, and heavy rainfall (Zhang et al., 2010). Specifically, the Saguenay-Lac-Saint-Jean region is projected to experience a 2.8°C increase in average annual temperature and a 70 mm increase in total precipitation by 2050 (Cdaq, 2021). While sugar maples generally exhibit stability and resilience within a given environment, they are susceptible to the effects of climate change (Alvarez et al., 2010). Producer reports documented by NECSC (2018) indicated earlier sap seasons, shorter production durations, and impacts on sap quality. The economic implications of climate change on maple syrup production have garnered considerable attention from producers and researchers alike.

The relationship between total sap yield and optimal climate conditions has been a subject of debate. A study projected a more favorable environment 400 km north of the 43rd parallel, suggesting potential declines in syrup production in the northeastern United States and increased production in southeastern Canada in the coming decades (Rapp et al., 2019). Houle and Duchesne (2020) challenged the authors who created this model, arguing for uncommon stable production across a broad latitudinal and temperature gradient. Rapp et al. (2020) defended their model, emphasizing its reliance on in situ eco physiological data from individual trees across the species range, which they considered more accurate for identifying optimal climatic conditions for sap yield at different gradients. Houle and Duchesne debated again by arguing the use of aggregated industry data, including both natural and vacuum sap extraction methods, which they argued could mask true sap water movement and confound the influence of freeze-thaw cycles. Furthermore, Rapp et al. (2020) highlighted the regional limitations of the aggregated data, potentially obscuring the true extent of production across the species range. Further research is needed to clarify the concept of an optimal weather for syrup production and to determine whether such a weather or temperature scale exists, enabling producers to better adapt to the challenges of climate change according to their location.

0.6 Objectives and hypotheses

The general objective of my thesis is to monitor the timings at hourly, daily and annual scale, determine the duration and length of sap production and assess the environmental factors which affect or coincide with the sap exudation.

The specific objectives for three chapters are presented below:

Chapter 1. Sap production at provincial scale and low resolution

Quantifying the timings of onset and ending of sap water production at an hourly resolution and assess the temperatures occurring at the reactivation and cessation of sap water production. I also quantify the trends in daily onset and ending of sap production measured across the natural range of maple in Quebec, Canada. I raise the hypothesis that the duration of sap production lengthens during spring according to the gradual change in the timings of freeze and thaw before bud burst.

Chapter 2. Sap production at regional scale and intermediate resolution

Testing the use of the rain gauge as a tool for monitoring the timings and dynamics of sap production in sugar maple. Firstly, I test the performance of the batteries employed in the data logger in controlled conditions under a range of temperatures occurring during the spring. Subsequently, I test the rain gauge effectiveness in measuring sap volume in natural conditions during the sugar season and by assessing the correlation in sap production between and within sites along a latitudinal gradient in Quebec, Canada. I expect that a shorter logging interval or colder conditions would drain more battery than longer intervals or measurements realized under warmer thermal conditions.

Chapter 3 Sap production at local scale and high resolution

Assessing the daily timings of sap production in sugar maple (Acer saccharum Marsh.) between 2018 and 2022 to (1) evaluate the co-occurrence of several environmental factors (i.e., air and soil temperatures, soil water content and snow cover) on the sap season; and (2) predict the

timings of the sap season according to the greenhouse emission scenarios in Quebec, Canada. I test the hypothesis that warming conditions advance onset and ending of sap production in maple.

0.7 Methodological approach and study sites

This thesis project was separated by number of regions or sites and data resolution, from provincial to local scale and from low to high resolution data collection (Figure 0.3). The first chapter was collected data across Quebec province, the second chapter at 4 different sites located in different latitudes and the most northernmost stand of sugar maple in North America and the third chapter at Simoncouche research station. More detailed information of each location and data synthesis, are presented below:

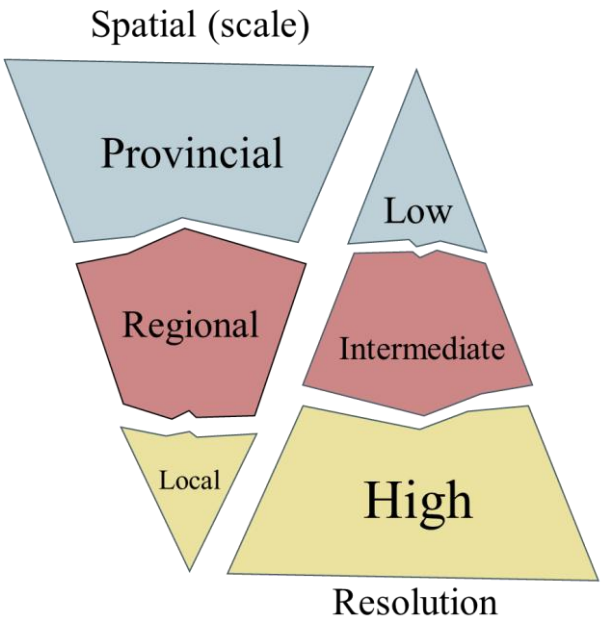

Figure 0.3 Outline of the thesis chapters in terms of number of regions and data resolution

- Rivière-à-Pierre (abbreviated as RAP), L'Anse-Saint-Jean (ASJ), Laterrière (LAT), and Parc National de MontsValin (PMV)

RAP (46°91'N,72°03'W) is in the hardwood forest subzone belonging to the sugar maple-basswood domain. The sugar maple-basswood domain extends further north and east compared to the sugar maple-bitternut hickory domain, showcasing a diverse array of plant life, although many species are found at the northernmost limits of their range. In more favorable areas, species such as basswood, American ash, hop-hornbeam, and butternut coexist with sugar maple, though their prevalence diminishes as one moves further north. This domain is divided into two subdomains, characterized by the abundance of red oak stands and their distinct precipitation patterns: the western subdomain, which experiences drier conditions, and the eastern subdomain, where precipitation is more plentiful (Saucier et al., 2003). The annual temperature is 3.9 °C and precipitation is 1325 mm. ASJ (48°19'N,70°22'W), LAT (48°28'N,71°14'W) and PMV (48°61'N,70°79'W) are located in the mixed forest subzone belonging to the balsam fir-yellow birch domain. PMV hosts the northernmost stand of sugar maple in North America. The balsam fir-yellow birch domain is located at an ecotone, acting as a transition zone between the northern temperate zone and the boreal zone. This domain extends westward into central Québec, situated between latitudes 47° and 48°, and includes regions such as the Gaspé Peninsula, the Appalachian hills east of Québec City, the Laurentian foothills north of the St. Lawrence River, and the lowlands of Lake Saint-Jean (Saucier et al., 2003). Notably, the sugar maple is found at the northernmost limit of its range in this area. The sites cover a range in annual temperature of between 1.3 °C and 3.5 °C and precipitation between 1160 and 1446 mm.

- Simoncouche (48°13'N,71°15'W, 350 m a.s.l.), Quebec, Canada.

The site is located at the boundary between two bioclimatic domains, the balsam fir–yellow birch domain and the balsam fir–white birch domain, where maple is close to the northernmost limit of its continental range. The climate of the area is continental, with long cold winters and short warm summers. According to the local weather station, the annual temperature between 2001 and 2022 was 2.5 °C, with an average maximum temperature of 17.5 °C occurring in July, and an average minimum temperature of -15.2 °C in January. The site receives a total precipitation of 915 mm, and snow depth reaches on average 85 cm. The mineral soil is podzol, with MOR-type humus and an organic horizon of 10-20 cm (Rossi et al., 2016).

- Data synthesis

In this study, we collected sap exudation data from different sources and resolutions, from hourly, daily to annual scale. The timings of sap exudation were monitored at each site at each tree or through surveys. The data collection happened during the sap season, from February to May between 2018 to 2022. The data collection was in traditional or a vacuum collection system. The information on the start and end of sap production was recorded hourly, when producers observed the first drop of sap arriving in the sap water collection reservoir. On the same day, the producers noted the time when they no longer saw sap exudation. The data were forwarded to MAPAQ in cooperation with the producers and then shared with our study group.

Data was collected at different methods and different years during the sap season. Data at the 19 sugarbushes was collected through survey in 2018, at the 4 sites was collected through rain gauges in 2022 and at Simoncouche research station was collected through rain gauges at different years from 2018 to 2022 (Figure 0.4). All the sap data at the 2 last chapters sites were collected using rain gauges from HOBO (HOBO Data Logging Rain Gauge RG3-M®, Bourne, MA, USA) and Campbell (5222-L, TE525MM-L, Campbell Scientific Corporation, Logan, UT) enterprise. More details of the sap collection and the analytical method are described in the material and methods of each chapter.

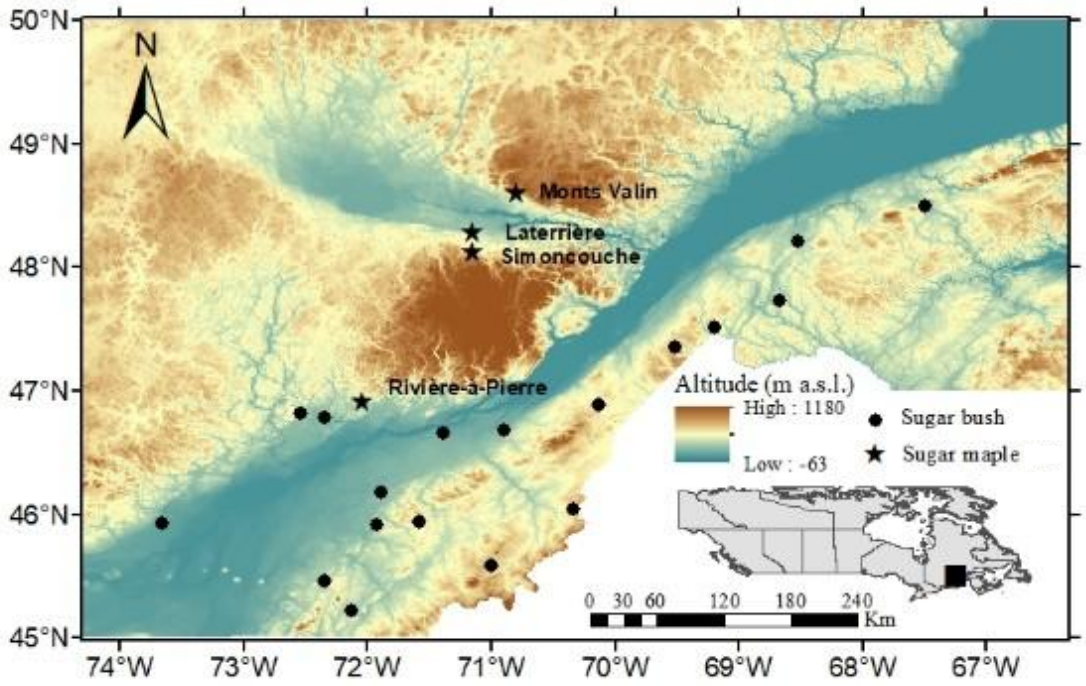

Figure 0.4 The location of 19 sugar bushes included in chapter 1, and the provincial and local scale with * symbol included in chapter 2 and 3.

0.8 Structure of the thesis

This thesis is formed by three chapters based on one of the objectives outlined earlier. Each chapter represents a scientific paper, which was either published or accepted to a peer-reviewed journal. The formatting of the texts has been standardized to enhance the document's readability. However, if published, a citation to the original manuscript is provided on the title page of each chapter.

CHAPITRE 1
SAP SEASON AT PROVICIAL SCALE AND LOW RESOLUTION

Daily timings of sap production in sugar maple in Quebec, Canada

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Keywords: phenology, hourly scale, sap exudation, *Acer saccharum* Marsh., temperature, maple syrup

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1.1 Abstract

Global warming is affecting plant phenology, with potential consequences on the dynamics of growth reactivation of sugar maple and the timings of maple syrup production. In this study, we assess the temperatures inducing the daily reactivation or cessation of sap production. We selected 19 sugarbushes across Quebec, Canada, using a tapping method associated with the tubing system, we recorded the daily timings of onset and ending of sap production during winter and spring 2018, and we associated the hourly temperatures at each site. Sap production occurred from mid-February to the end of April, starting on average between 10 and 11 AM, and ending from 6 to 8 PM. We observed a seasonal pattern in the onset and ending of sap production during spring, with the onset showing a greater change than the ending. Onset and ending of sap production occurred mostly under temperatures ranging between –2 and 2 °C. The production of sap in maple is closely related to circadian freeze–thaw cycles and occurs under nighttime and daytime temperatures fluctuating below and above 0 °C. The daily lengthening of the duration of sap production mirrors the changes in the timings of freeze and thaw events and can be explained by the physical properties of the water and the physiological processes occurring during growth reactivation. The ongoing warming will result in earlier and warmer springs, which may anticipate the cycles of freeze and thaw and advance sap production in sugar maple.

1.2 Introduction

As a product with a unique and striking flavor, maple syrup is consumed in more than 50 countries worldwide (Pires et al., 2021). Maple syrup originates from the Eastern North America, and Canada contributes up to 71% of the total syrup production. Compared to 2004, exports from Canada in 2020 have increased by 97%, reaching a total of 61 million liters of maple syrup, corresponding to 645 million CAD$. Maple syrup is obtained after boiling the sap water collected by tapping maples, principally sugar maple (Acer saccharum Marsh.) and red maple (Acer rubrum L.), in the period from late winter to early spring (Pallardy, 2017).

Sap production occurs during the physiological reactivation of sugar maple under thermal conditions. The end of winter and beginning of spring are characterized by circadian freeze–thaw cycles, with nighttime and daytime temperatures frequently fluctuating above and below 0 °C (Tyree, 1983; Tyree & Zimmermann, 2002). As these conditions vary over space and time, sap production is heterogeneous and changes at both hourly and daily scales, with some days being more productive than others (Duchesne & Houle, 2014). Such a heterogeneous production seems to be explained by the physiological mechanisms at the origin of sap production, which generate an anomalous positive pressure in the vessels when temperatures exceed 0 °C (Cirelli et al., 2008; Marvin & Erickson, 1956).

Marvin and Erickson (1956) found a close relationship between sap water movement and hourly twig temperatures. These relationships were also confirmed by Plamondon and Bernier (1980) who related the number of hours and degree hours above and below 0 °C with sap production. Greene and Marvin (1958) also found that a decrease in temperature induced a decrease in alcohol-extractable sap water in maple stems, a phenomena that increased vessel sap pressure and linked with maple sap water movement. More recent works also linked large daily fluctuations of air temperature to sap production (Skinner et al., 2010). It is expected that sap production stops when nighttime temperatures remain above 0 °C during 24–36 h, which generally corresponds with bud burst (Wiegand, 1906), but there is a lack of recent literature linking sap production with growth reactivation in maple.

Sugarbushes are equipped by a system of tubes for collecting the sap dripping from the taps into reservoirs or collection points. Under temperatures < 0 °C, the sap remaining within the tubes can freeze or increase its viscosity, resulting in a reduction or cessation of the flow along the tubes (Tyree & Zimmermann, 2002). The use of vacuum enhances sap production at the sugarbush but can also convey cold air into the tubes, increasing the rate of ice formation and speeding up freezing of the water.

As temperature is involved in the physical properties and physiological reactivation of maple (Kim & Leech, 1985), climate change may have a strong impact on sap production (Houle et al., 2015). Climatic events involving earlier and warmer springs are expected to occur more frequently under the current climate change, mainly at the northern latitudes (Wegge & Rolstad, 2017), potentially modifying the temporal dynamics (i.e., timing of sap production) or the amount of sap produced (Houle et al., 2015; Skinner et al., 2010). In Quebec, the Canadian Earth System Model predicts warmings of 3.9 °C and 8.5 °C under RCP 4.5 and 8.5, respectively, and an increase of precipitation of 10 and 7% for 2100 (Boulanger et al., 2021). Accordingly, the production period may advance by 2 to 3 weeks (Duchesne et al., 2009; Houle et al., 2015). A warmer temperature could also advance bud burst (Ren et al., 2020), possibly shortening the season of maple syrup production. Although data on annual sap production are widely available from producers' associations, information at higher resolution is still scarce or lacking (Marvin & Erickson, 1956; Plamondon & Bernier, 1980). Predictions of the potential changes in sap production require assessment of the temperatures involved in this process at finer time scales than the year. The literature provides analyses at annual or daily scale (Duchesne & Houle, 2014; Rapp et al., 2019), but data with an hourly precision are still little or not explored. High temporal resolution under a day could be better explored for explaining the timings of sap production. In this study, we quantify the timings of onset and ending of sap water production at an hourly resolution and assess the temperatures occurring at the reactivation and cessation of sap water production. We also quantify the trends in daily onset and ending of sap production measured across the natural range of maple in Quebec, Canada. We raise the hypothesis that the duration of sap production lengthens during spring according to the gradual change in the timings of freeze and thaw before bud burst.

1.3 Materials and Methods

1.3.1 Study site

Nineteen sugarbushes were selected across the main area of maple syrup production in Quebec, Canada (Figure 1.1). Sugarbushes are distributed in the northern part of maple distribution in North-Eastern America, where sugar maple (Acer saccharum Marsh.) is the dominant species. The topography is rolling, with hills reaching from 72 to 576 m a.s.l. The study area belongs to the sugar maple-yellow birch, sugar maple-basswood, and balsam fir-yellow birch domains. The climate is continental cold, with harsh winters and warm summers. The mean annual temperature at the sugarbushes is 4.7 °C, with absolute minimum and maximum temperatures reaching − 32.5 °C in January, and 33.5 °C in July, respectively. Annual precipitation is 1252 mm, 258 mm of which falls in the form of snow (Muñoz-Sabater et al., 2019). The growing season lasts from May to October, with later reactivations in northern sites, at higher altitudes, and close to the sea (Guo, Khare, et al., 2020; Rapp et al., 2019). The soil consists of podzol with a MOR-type humus (Chagnon et al., 2001), with some sugarbushes being located in gleysolic and brunisolic soils. Temperatures < 0 °C are recorded during 140 days, from October to April.

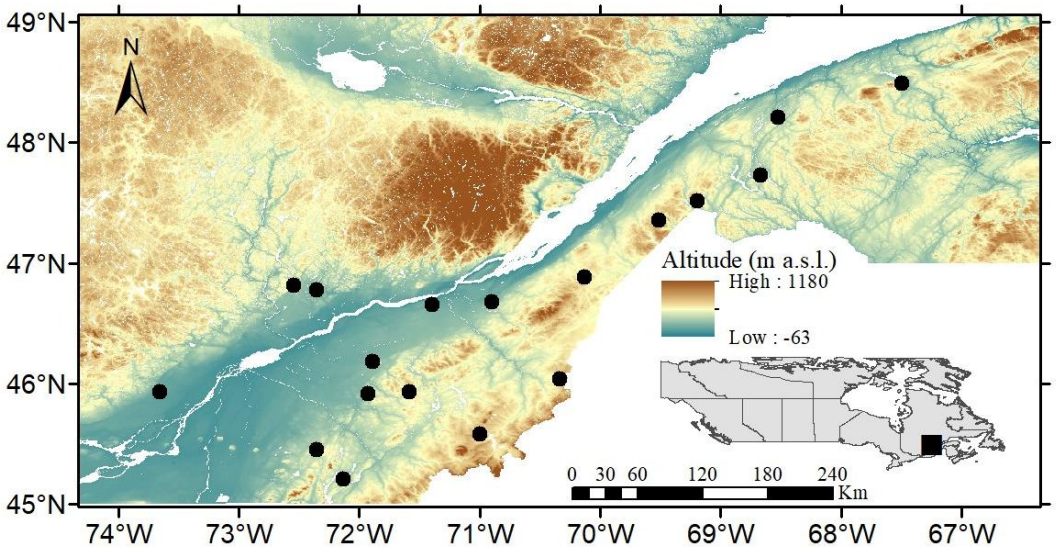

Figure 1.1 Location of the nineteen sugarbushes in Quebec, Canada. Sugarbushes colored in dark green are located at higher altitude.

1.3.2 Data collection

Sap from mature maple trees was collected at stand level using the tapping method associated with tubing connected to a vacuum system (Heiligmann et al., 2006). In spring 2018, the producer was asked to record the timings of onset and ending of sap water production at the sugarbush, where the sap is accumulated through the tubing system. The onset was defined as the time when the first drops passing through the pipe were observed to reach the reservoir at the sugarbush. The ending was defined as the time when the flow of sap water ran out. Data were collected from the same person in each sugarbush and reported to the nearest minute. Nighttime productions of sap water were occasionally recorded but were not included in the analyses because they were far from the topic of this study.

1.3.3 Climate data

Hourly temperatures occurring at each sugarbush were extracted from ERA5-Land database (ECMWF- European Centre for Medium-Range Weather Forecasts fifth generation Reanalysis) using the Google Earth Engine (GEE) platform. ERA5 provides the most recent climate data with a spatial resolution of 9 km (Muñoz-Sabater et al., 2019). The hours of onset and ending of sap production were associated with the hourly temperatures to analyze the thermal conditions for sap production.

1.3.4 Data analysis and statistics

Temporal changes in the timings of sap production were assessed by repeated measurements mixed models with autoregressive covariance structure using day of the year (DOY) and phenological events (onset and ending) as continuous and categorical variables, respectively. Preliminary analyses was unable to detect differences among the 19 sugarbushes. Thus, the model was applied to the dataset as a whole. The final regressions were validated by the fit statistics and visually comparing predictions and residuals with the observations. The relationships between temperature and DOY were analyzed with linear regressions. We tested for differences between temperatures at the onset and ending of sap production and 0 °C using parametric (Student t-test) or non-parametric tests (Wilcoxon signed rank test) after checking the distributions for normality. Data distributions were analyzed and tested for normality using

Kolmogorov–Smirnov statistics. All statistics were performed in SAS (SAS Institute Inc., Cary, NC).

1.4 Results

1.4.1 Distribution of the timing of sap production

Sap production in the studied area ranged from mid-February (DOY 50) to the end of April (DOY 118). Overall, sap production onset ranged from 4 AM to 2 PM, but more frequent values were observed between 10 and 11 AM (Figure 1.2). Seventy-seven percent of onset data occurred between 8 AM and 12 PM, and only 1% occurred after 1 PM. The ending of sap production ranged between 3 and 9 PM, with 33% being observed at 7 PM. Overall, 71% of the ending of sap production was concentrated between 6 and 8 PM. The onset of sap production had a larger variance than the ending. Onset and ending times of sap production exhibited a symmetrical and normally distributed distribution, as demonstrated by the Kolmogorov–Smirnov statistics, producing D of 0.05 ($p > 0.05$) and 0.04 ($p > 0.05$), respectively.

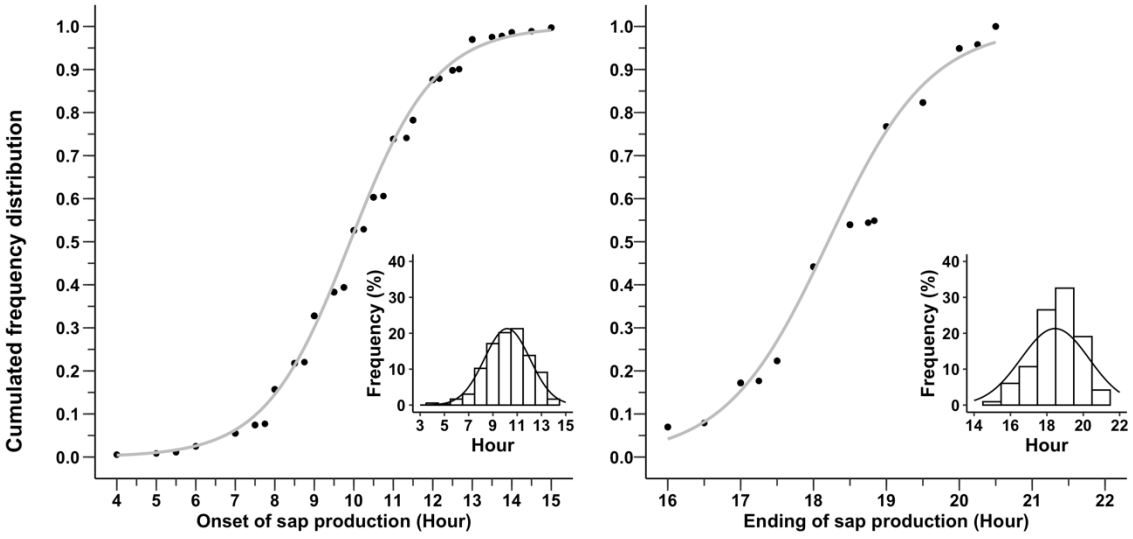

Figure 1.2 Cumulative and frequency distribution of onset and ending of sap production recorded in 19 sugarbushes in Quebec, Canada.

1.4.2 Daily change in the timing of sap production

Mixed model quickly met the convergence criteria after two iterations, producing an Akaike information criterion (AIC) and a Bayesian information criterion (BIC) of 2210.2 and 2212.1, respectively, which showed the goodness of fit. The two factors of the mixed model were

significant, the phenological events ($F = 31.05$, $P < 0.0001$) and their interaction with DOY ($F = 24.19$, $P < 0.0001$) (Table 1. 1). DOY was not significant ($F = 2.94$, $P > 0.05$). The mixed model demonstrated that the two phenological events had different timings and diverging patterns. The residuals were homoscedastic (Figure 1.3). No apparent trend was observed for the residuals, confirming that the model well represented the data and no additional pattern remained to be accounted for. The range between –2 and 2 included 77 and 90% of the Studentized residuals for onset and ending of sap production, respectively, suggesting that the model could be considered suitable for observing changes in the timing of sap production. The lower dispersion observed for the ending of sap production indicated that this phenological event was better estimated by the independent variables included in the model. The model described the daily changes in onset and ending of sap production during spring. The predicted onset of sap production ranged between 11.20 AM in mid-February (DOY 50) to 9.20 AM in mid-April (DOY 110), showing a gradual advancement during the day in spring. Sap production ended at 6 PM on DOY 50 and at 7 PM on DOY 110, with a gradual delay during spring. The daily length of sap production increased by 3 hours during spring, lasting 7 hours on DOY 50 to 10 hours in DOY 110 (Figure 1.3). The slope for onset was steeper than that for ending of sap production. Accordingly, the temporal variation in onset was higher, and the onset of sap production contributed more to the variation in duration of sap production. Accordingly, the temporal variation in onset was higher, and the onset of sap production contributed more to the variation in duration of sap production.

Table 1.1 Summary of linear mixed models (LMMs) for phases (i.e., onset and ending as phenological events), with treatments as fixed factors (DOY, phases) during spring 2018. The results include, for each effect, F statistic (F values) and probability (P). Symbol (*) indicates significant effects ($P \leqslant 0.05$)

Variable	F values	P
DOY	2.94	>0.05
phases	31.05	<0.0001*
DOY × phases	24.19	<0.0001*

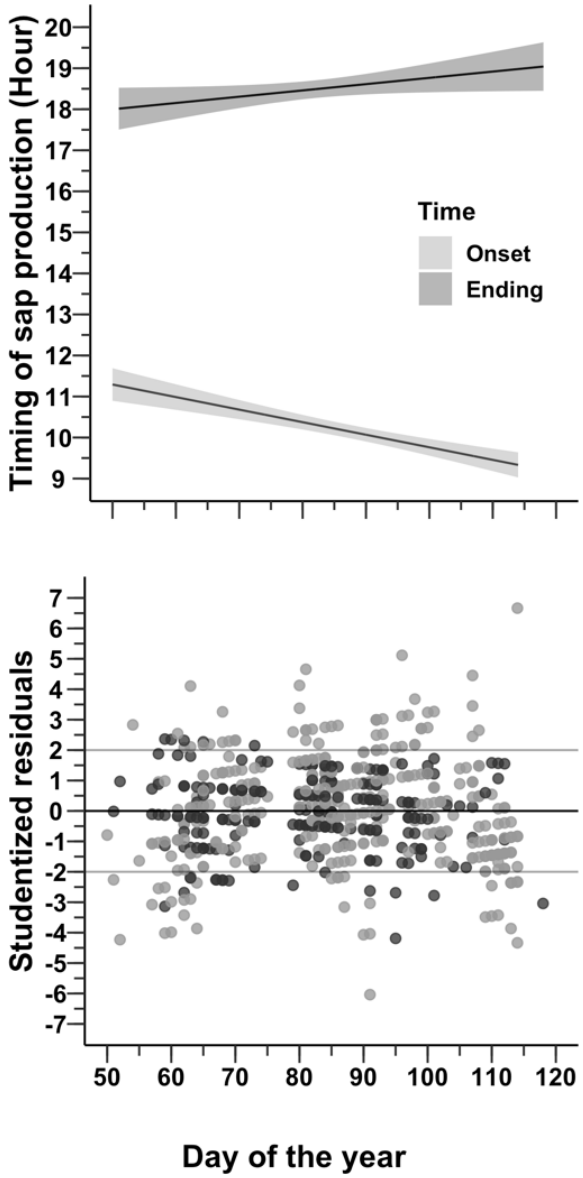

Figure 1.3 Onset and ending of sap production during the springtime. Shaded areas represent the confidence interval. Studentized residuals vs Day of the year (predicted values), resulting from the mixed models performed on the timing of sap production in sugar maple.

1.4.3 Average daily temperature during sap production

The temperature at the onset of sap production ranged between –10 and 13 ˚C (Figure 1.4). The more frequent temperatures observed at the onset of sap production ranged between –2 and 2 ˚C, including 60% of the values. The distribution was different from the normal curve (Kolmogorov–Smirnov statistics, $D = 0.08$, $p < 0.01$); thus, the analyses involved non-parametric tests. The Wilcoxon signed rank test indicated that temperatures were not different from 0 °C ($S = –10.90$, $p > 0.05$). No pattern in the temperature was observed during the study

period, as confirmed by the linear regression, whose slope was not different from 0 ($F = 0.00$, $p > 0.05$) (Figure 1.4). Overall, the temperature at the ending of sap production ranged between –6 and 7 ˚C, with 58% of temperatures occurring between –2 and 2 ˚C (Figure 1.4). Data followed the normal distribution (Kolmogorov–Smirnov statistics, $D = 0.08$, $p > 0.05$). The average was not different from 0 °C (Student t-test, $t = –1.53$, $p > 0.05$). No pattern in the temperatures at the ending of sap production was observed, as confirmed by the linear regression, which was not significant ($F = 0.25$, $p > 0.05$) (Figure 1.4).

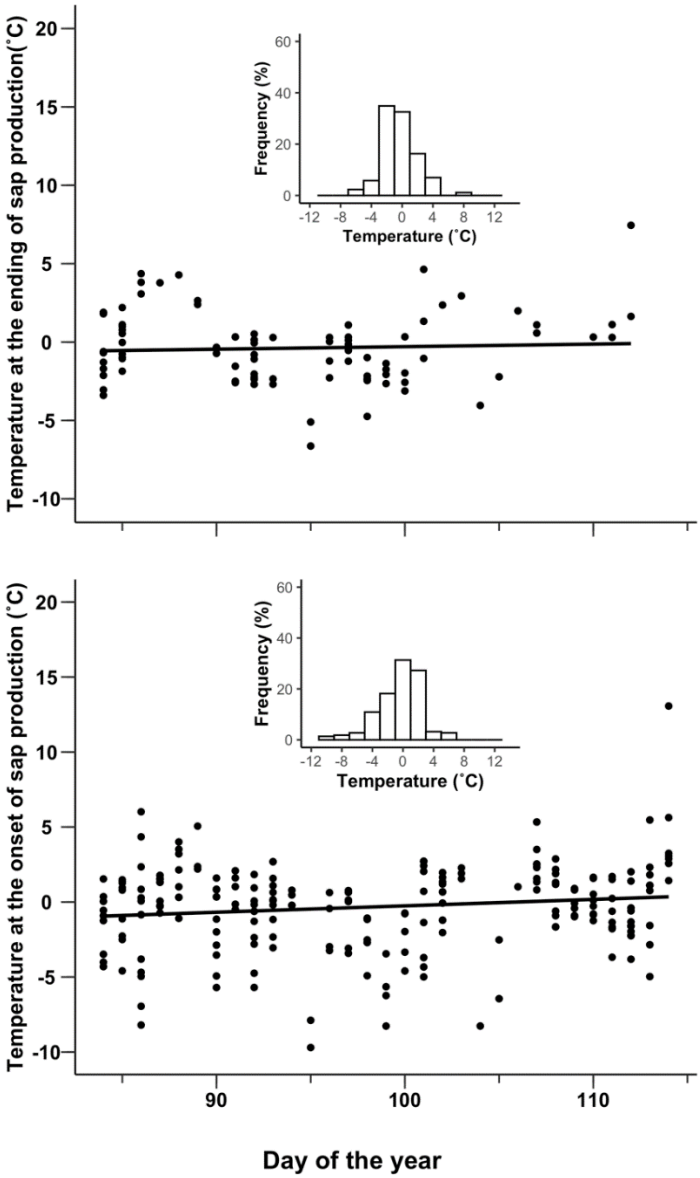

Figure 1.4 Temperature recorded at the onset and ending of sap production. Line represents a regression.

1.5 Discussion

In this paper, we analyzed the timings of sap production at an hourly resolution recorded on 19 sugarbushes located across the main area of maple syrup production in Quebec, Canada. Sap production started in the morning and ended in the afternoon. The daily duration of sap production increased during spring, according to the lengthening of the period when the temperature exceeded 0 ˚C. Our hypothesis that the duration of sap production lengthens during spring according to the timings of freeze and thaw events was accepted.

1.5.1 The physiological and physical explanations

Sap production is related to a series of sequential events closely connected with changes in temperature. At snowmelt in spring, the negative water potential of the roots replenishes the vessels with sap and the freeze–thaw cycles stimulate sap production (Matthews & Iverson, 2017). In the morning, the rising temperature expands the gases located in the xylem and creates a positive pressure (Schenk et al., 2021). Tapping the stems results in sap exudations. The circadian cycle of thermal conditions, i.e., nighttime temperatures < 0 °C and daytime temperatures > 0 °C, creates negative and positive pressures in the stem, respectively. This change in pressure allows the sap to flow from branches and stem and exudate through the tap, which explains the thermal threshold of 0 °C measured in this study (Graf et al., 2015). These results also confirm that the exudation of sap is mainly concentrated during the daytime (Heiligmann et al., 2006).

The literature provides several different hypotheses on the origin of the pressure for sap production in trees (Graf et al., 2015; Milburn & O'Malley, 1984; Tyree & Zimmermann, 2002). Our results support the hypothesis that the positive pressure of the sap originates from the stem rather than the roots (Pallardy, 2017). In this part of North-Eastern America, winter conditions and the thick snowpack maintain the soil at temperatures close to 0 °C from the end of autumn to the complete snowmelt in spring (Rossi et al., 2011). On the contrary, the stem is exposed daily to a wide variation in temperatures, that in our area range approximately from –20 to 20 °C during the studied period (Guo, Khare, et al., 2020). Unlike the constant conditions experienced by the roots, the daily changes in air temperature better explain the circadian pattern in sap production observed in maple. According to Schenk et al. (2021), the processes related to the

combination of freezing and thawing effects, and resulting in melting of frozen sap and thermal expansion in the fibers, should occur mainly on the main stem and branches, tissues coupled with the current air conditions. The physical properties of water may play a role in explaining our results. Maple sap collection takes advantage of a system of tubes connecting the taps to the sugarbush. The sap dripping from the stems flows along the tubes directly to a reservoir. Temperatures close to or lower than 0 °C increase the viscosity of the water or convert the water into ice, thus reducing or preventing the flow through the tubes. Warming conditions can stimulate the movement of sap water through the tubes because the water viscosity decreases by 2.4% per degree of temperature (Tyree & Zimmermann, 2002). Moreover, the vacuum systems can further reduce the temperature inside the tube and increase the rate of ice formation.

1.5.2 Daily pattern of the onset and ending of sap production

Our results showed that, during the study period from DOY 50 to 120, the onset advanced by 2 hours, while the ending was delayed by 1 hour. Accordingly, the onset of sap production exhibited a wider daily variation than its ending. During this period, daytime temperature warmed up faster than nighttime temperature (data not shown). The literature confirms that daytime temperature variation is typically greater than nighttime temperature variation (Easterling et al., 2000). Such a daily difference between thermal conditions may partially explain the diverging timings of sap production and may be a response to the thawing or freezing speed of the liquid stored in the outermost rays of the stem (Cirelli et al., 2008; Schenk et al., 2021), and allowing for the sap exudation. The increasing temperatures in the morning result in a thawing process, with the movement of water and sugars from the rays to vessels, via the radial transport developed by the rays, which may require more time under cold conditions for the transport of sap. The increasing temperatures due to a changing climate are affecting the timings and dynamics of forest growth worldwide, including the events occurring in late winter and early spring, when dormancy is broken and tree growth reactivates (Guo, Klisz, et al., 2020). The annual mean temperature across Canada has risen by 1.7 °C from 1948 to 2012 (Vincent et al., 2015), and further warming is expected during this century, with increases of up to 1.8 °C in the low CO2 emissions scenario (IPCC, 2021). The annual mean temperature over Eastern Canada is projected to increase by 0.4 °C in 2020s, 0.9 °C in 2050s, and then 0.5 °C in 2080s under RCP 2.6, suggesting an overall increase of 0.9 °C in < 100 years (Wang et al., 2022). In

our study, we observed that temperature is an important factor in maple, defining the boundary between the daily onset and ending of sap production. Under a warming climate, the threshold of 0 °C could be reached faster or earlier in winter, which may advance the metabolic processes involved in growth reactivation in trees (Boulouf Lugo et al., 2012; Prislan et al., 2019; Yang et al., 2017), and consequently sap production. A similar hypothesis was proposed by previous studies, which predicted advancements of 30 days up to 19 days in the period of sap production for 2100 under the current trend of climate warming (Houle et al., 2015; Rapp et al., 2019). In our study, sap production lasted 7 hours on DOY 50 and 10 hours on DOY 110. Such a daily change lengthens the working hours of producers and equipment in the sugarbush by 30%. Such a longer period of sap production at the end of the sap season increases the number of working hours per person, although the marginal effect of each additional hour on productivity declines, possibly resulting in reduced productivity (Delmez & Vandenberghe, 2018; Pencavel, 2014). However, the increase in daily working time due to the lengthening in sap production could not be related to the production volume. The relationship between the period of sap production and the amount of sap water collected remains to be investigated in more depth.

This study presents some limitations regarding the data collection of 2018. Maple syrup production is heterogeneous, with variations occurring across spatial scales as well as between years (Duchesne & Houle, 2014). According to Pothier (1995), more than 60% of the variation in both sap volume per tap and sap sugar concentration was related to year-to-year variations, while lowest intensities accounted for only a small portion of the variation. Collecting data from a single year prevents accurate comparisons or direct conclusions about interannual variability in sap production schedules and volume. Therefore, it is not possible to accurately infer how the patterns observed in 2018 would compare to other years. To deepen our understanding of the dynamics of sap production, a comparative approach with data from other years or the use of historical data would be essential to confirm the consistency of the identified patterns (Brown et al., 2015; Thapa et al., 2024).

The local sensors installed in our studies had some technical problems which limited the use of local weather data. The use of hourly temperature data from Google Earth Engine (GEE) is relevant for examining general trends in maple sap flow at a regional scale. The ERA5-Land database is a widely used global climate reanalysis recognized for its comprehensiveness and

quality (Mihalevich et al., 2022). For large-scale studies or to understand general temperature trends affecting different regions, these data can be considered robust (Muñoz-Sabater et al., 2019). However, future studies could benefit from comparing these data with measurements from local weather stations or sensors installed directly at the study sites (Hooker et al., 2018). Such an approach would allow for a better characterization of the microclimatic variations, particularly during freeze–thaw cycles. Conclusions

The timings of sap production in spring were collected at an hourly scale on 19 sugarbushes located in the northern part of maple distribution in North-Eastern America to compare the daily pattern of onset and ending of sap production with the changes in air temperature. The circadian cycle of freezing and thawing is a critical factor for the timings of sap production with potential effects on plant physiology, i.e., creating the positive pressures in the stem for sap exudation, or water properties, i.e., melting and freezing the sap in the tubes connecting the tap to the sugarbush. Understanding and predicting the period of the sap season allows producers to prepare the field activities and stem tapping sufficiently in advance in order to start the production on time. Mismatching tapping and sap production, i.e., tapping too early or too late, can result in a reduced volume of sap collected by the sugarbushes (MacIver et al., 2006). The ongoing changes in climate in North America will result in earlier and warmer springs, which may anticipate the cycles of freeze and thaw. Based on our results, such a warming scenario may advance sap production and affect the growth dynamics of sugar maple. More studies are required to verify whether changes in sap phenology can result in variations in the volume of sap production and how can be considered in the production strategies dealing with ongoing global warming.

1.5.3 Acknowledgements

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1.5.5 Declarations

Ethical standards The experiments comply with the current laws of the country in which they were performed.

Competing interests The authors declare no competing interests.

CHAPITRE 2
SAP SEASON AT REGIONAL SCALE AND INTERMEDIATE RESOLUTION

Measuring natural sap production in sugar maple at daily temporal resolution

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Keywords: *Acer saccharum* Marsh., state of charge, rain Gauge, sap exudation, sap yield, tipping bucket

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2.1 Abstract

Sap yield for maple syrup production is well studied at annual scale. However, the phenological timings of sap production have been less explored. Our study tested the use of rain gauges for monitoring timings and dynamics of sap production at daily temporal resolution. The batteries of the rain gauges were tested under controlled conditions at temperatures ranging from -20 to 5 °C and logging intervals of 15 and 30 minutes. In 2022, eight rain gauges were installed in the field on maples located in four sites along a latitudinal gradient in Quebec, Canada. The batteries performed well at all temperatures in both field and controlled conditions, showing a higher state of charge at logging intervals of 30 minutes with temperatures warmer than -15 °C. The dynamics of sap exudation were correlated among and within sites, demonstrating that trees respond to common environmental factors at regional scale. The natural sap production was discontinuous, alternating productive and non-productive days. Overall, 74% of the sap was exudated during 20% of the sugar season, which matched the proportions described by the Pareto law. Such a heterogeneous and unbalanced distribution in sap exudation exposes small producers to challenges for the use of equipment and makes maple syrup production sensitive to climate hazards in a context of climate change.

2.2 Introduction

Maple syrup is one of Canada's leading products for exportation and the Quebec region alone has 90% of the total sap yield, producing around 72.2 million litres in 2022, an increase of 59.1% from 2021 (Statistics-Canada, 2022). However, sap yield is exposed to huge variations. Sap yield in 2021 dropped by 24% compared to 2020. These interannual variations mainly come from the particular and specific set of meteorological conditions needed to collected sap from the sugar maple stems. Sap exudation depends on specific daily thermal ranges, from –10 °C to 13 °C for the onset and –6 °C to 7 °C for the end of the sap season, and drops sharply with minimum temperatures <–8 °C (Kurokawa et al., 2022; Rapp et al., 2019). Basically, the period time of these occurrences for these daily ranges and the number of their occurrences define respectively, the sugar season, and its yield. Although it is known that such a thermal variation is necessary for sap exudation, there is still a lack of information on the mechanisms occurring within the tree. While the total sap yield is known at annual scale (Rademacher et al., 2023; Rapp et al., 2019), the pattern of sap production at high temporal resolution has historically been less explored, due to the lack of suitable equipment. Information on daily and hourly production patterns could provide new insight into the eco-physiological processes acting at tree scale and have a great logistic interest for producers.

The sap yield reported in official records are obtained through annual surveys by consultants or from online platforms, using input coming directly from local producers (Caughron et al., 2021; Duchesne et al., 2009). Responses to the survey can include information about location, number of tapped trees, and the producers, but maple syrup production is provided exclusively in terms of total sap yield (Caughron et al., 2021; Duchesne et al., 2009). The volume of sap is collected in reservoirs and the seasonal estimate of the total volume is calculated. Total yield is determined by the ratio of annual production to the number of taps (Duchesne et al., 2009).

In a pioneer study performed in 1956, Marvin and Erickson (1956) measured the sap volume using a tipping bucket with a balance that held 15 ml at a time when it was completely full. When the bucket tilted to empty, an impulse was sent to a data logger, which recorded it on a graph at the same speed as the overturning and thus with low accuracy, due to the limitations of the technology at that time. Despite their work being focused on the effect of environmental

factors (i.e. temperature and its fluctuation) on sap production, contemporary equipment such as the modern rain gauge could represent a reliable tool to monitor sap production at tree scale, and daily temporal resolution.

A daily or hourly temporal resolution can be a solution to reach precise estimations of sap production. To obtain sap volume measurements at high temporal resolution, automatic tools precisely recording the hourly volumetric flow should be employed. As an example of automatic tool, the rain gauge is traditionally used to record rainfall intensity and duration of rain events (Stöhr & Lösch, 2004; Wu et al., 2018). Currently, it is widely used due to their adaptability to different data loggers, easy manipulation and because they provide precise measurements, allowing accurate records of local precipitation events to be obtained (Sypka, 2019). The data collected by rain gauges can be registered at specific intervals, such as minutes or hours. The measurement is done with rain gauges recording a minimum volume of 3.73 ml of water, which can be used to precisely assess rates, times and duration of a rainfall event (Onset®, 2018). Tipping bucket rain gauges could potentially represent an effective solution for monitoring sap production at high resolution temporal scale.

There is a need to quantify sap exudation during the sap season by means of specific or adapted measuring tools, e.g. using the tipping bucket rain gauge. To this end, we investigate the ability of rain gauge to operate under the harsh conditions typical of the spring of maple, where temperatures can drop below –20 °C, a possible primary constraint for the use of this equipment (Aris & Shabani, 2017). The data logger connected to the rain gauge is indeed supported by lithium ion (Li-ion) batteries, whose performance and lifespan can be reduced by temperatures above or below a certain recommended range (Kang & Rizzoni, 2014). Recently, studies have focused on the responses of a Li-ion battery to temperature, as this plays a crucial role in getting the batteries to run at maximum efficiency (Ahmed et al., 2015; Aris & Shabani, 2017; Ji & Wang, 2013). Most Li-ion batteries perform well between 15 and 35 °C, near room temperature (Khan et al., 2017). Batteries lose 1.5 to 2% of their capacity and 10% of their power capabilities when the temperature varies by 5 °C (Feng et al., 2018). Tipping bucket rain gauge could also be affected by the biochemical composition of maple sap. Recording the volume of an aqueous solution, such as maple sap, that contains low concentrations of reducing sugars, such as glucose,

fructose, and xylose (Lagacé et al., 2015) could be a challenge for the measurements by potentially sticking the pivot mechanism of the tipping buckets.

The aim of this study is to test the use of the rain gauge as a tool for monitoring the timings and dynamics of sap production in sugar maple. We firstly tested the performance of the batteries employed in the data logger in controlled conditions under a range of temperatures occurring during the spring. Subsequently, we tested the rain gauge effectiveness in measuring sap volume in natural conditions during the sugar season and by assessing the correlation in sap production between and within sites along a latitudinal gradient in Quebec, Canada. We expected that a shorter logging interval or colder conditions would drain more battery than longer intervals or measurements realized under warmer thermal conditions.

2.3 Material and Methods

2.3.1 Testing the batteries of rain gauges

Tipping bucket rain gauges (HOBO Data Logging Rain Gauge RG3-M, Bourne, MA, U.S.A.) were exposed to four constant temperatures (–20, –15, –10 and +5 °C) in controlled conditions (i.e. room fridge and freezer) recorded at 15 and 30 minutes. This range in temperature covered the thermal conditions experienced during the sugar season, from mid-February to the end of April, in Quebec, Canada (Kurokawa et al., 2022). Two rain gauges equipped with a new lithium battery (CR-2032 Lithium 3V, Sony, Japan) were installed at each thermal condition and set up to record data at a logging interval of 15 or 30 minutes. The state of charge was recorded every two days at the beginning of the experiment and weekly when it reached a stable level. State of charge was recorded using the Hobo software (Hoboware software, Bourne, MA) by connecting a data logger to a laptop through a coupler and collecting the measurements after 10 minutes. The rain gauges have a time accuracy of ± 1 minute per month at 25 °C, and collect data under a thermal interval ranging between –20 and 70 °C with an accuracy of ± 0.54 °C from 0 °C to 50 °C. The logger measured the state of charge with a resolution ranging between 3 and 7% (Onset®, 2018).

2.3.2 Monitoring sap production in the field

Four study sites, Rivière-à-Pierre (abbreviated as RAP), L'Anse-Saint-Jean (ASJ), Laterrière (LAT), and Parc National de Monts-Valin (PMV) were selected in Quebec, Canada, at the northern part of sugar maple distribution in northeastern North-America (Figure 2.1). RAP (46° 91′ N, 72° 03′ W) is located in the hardwood forest subzone belonging to the sugar maple-basswood domain. ASJ (48° 19′ N, 70° 22′ W), LAT (48° 28′ N, 71° 14′ W) and PMV (48° 61′ N, 70° 79′ W) are located in the mixed forest subzone belonging to the balsam fir-yellow birch domain. PMV hosts the northernmost stand of sugar maple in North America. The sites cover a range in annual temperature of between 1.3 °C and 3.9 °C (Table 2.1).

Eight rain gauges were used to assess timings and dynamics of natural sap production in tapped trees during spring 2022. We selected adult sugar maples, two per site equipped with rain gauges. We recorded tree characteristics as well as the daily air temperatures occurring during the sap season (See Table S2. and Figure S2.1 in Supplementary Material). A notch was made on the stem at 2 m from the ground using a drill following the last tapping procedures. A plastic spout was inserted into the notch and connected by tubing to the rain gauge. The rain gauge was covered and sealed to avoid rain, snow and debris from failing in or otherwise obstructing the measurement system. The data were recorded continuously by the data logger throughout the entire sugar season. The rain gauges were installed before the sugar season (from late February to late March) and removed at the end of it (from early May to early June) according to the weather conditions of the sites (Kurokawa et al., 2022).

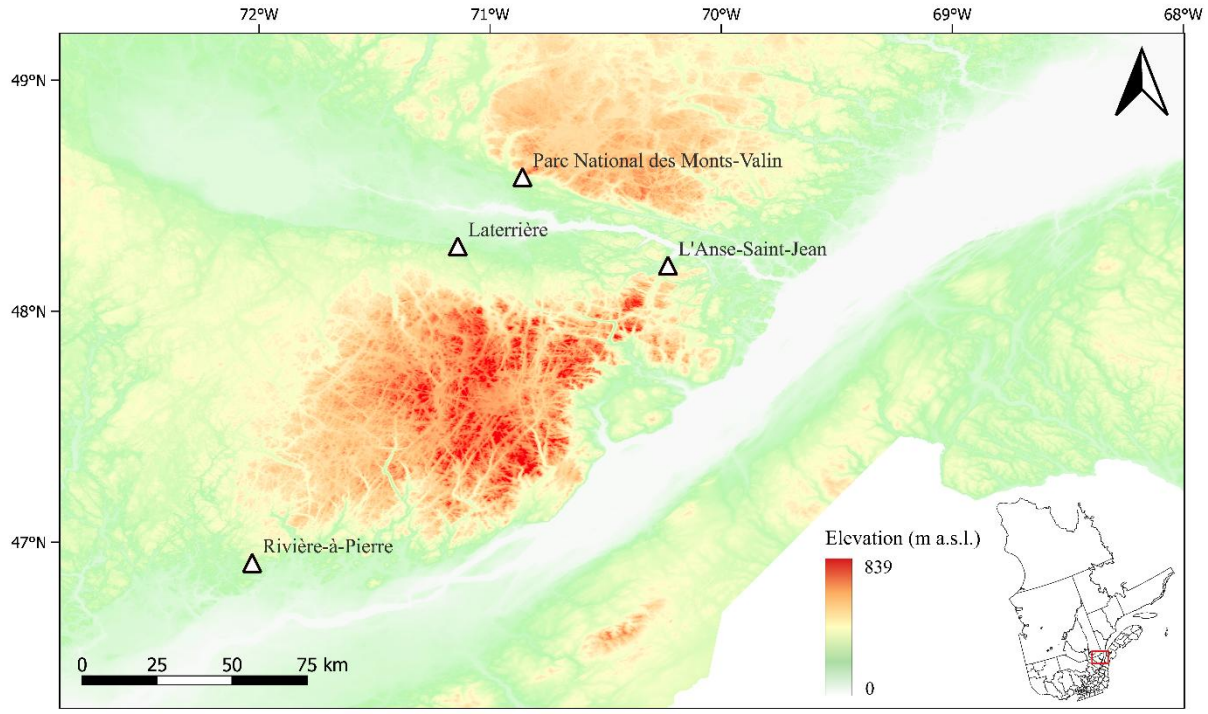

Figure 2.1 Location of the four study sites in Quebec, Canada.

Table 2.1 Location and climate of the four study sites in Quebec.

ID	Site	Elevation (m a.s.l.)	Annual Temp (°C)	Annual Rainfall (mm)	DBH (cm)	
					Tree 1	Tree 2
RAP	Rivière-à-Pierre	201	3.9	1325	34	34
ASJ	L`Anse-Saint-Jean	138	2	1221	28	33
LAT	Laterrière	200	3.5	1160	37	29
PMV	Monts-Valin	926	1.3	1446	22	16

2.3.3 Data analysis and statistics

The state of charge quantified in percentage from 0 % (uncharged) to 100% (fully charged), was fitted using a nonlinear least squares regression to describe the variation in time during the experiment. The exponential decay model was defined as follows (eqn. 2.1):

$$y = a+b.\exp\,(c\,x\,t) \tag{2.1}$$

where y represents the state of charge and t the day of experiment. The three coefficients represent the lower asymptote (a), the vertical amplitude of the curve (b) and rate of battery decay (c). The curve fitting was performed at each temperature and logging interval (*i.e.*, every 15 and 30 minutes) in the controlled conditions. Starting values were specified for each parameter and optimized using the Gauss-Newton algorithm by minimizing the sum of squares errors (Bates et al., 1992). Standardized residuals were checked for fitting the curve. The analysis was performed using the function "nls" implemented in the package "stats" in R version 4.2.1 (R Development Core Team, Vienna, Austria).

Volumes recorded by rain gauges were corrected using a conversion rate of 1.32 g ml-1 to consider the higher density of the sap (Duchesne et al., 2009). Indeed, each tipping bucket records 3.73 ml and it is equivalent to the sap volume of 2.83 ml, representing a reduction of 24% in the measurement compared to the density of water (1 g ml^{-1}). Sap production could be monitored precisely through the process of calibration and conversion to the appropriate density units.

Cumulative distribution functions were used for assessing the temporal variations in sap production. The cumulative percentage of the data organized in descending order of daily sap production measurements was calculated and plotted against the cumulative percentage of elapsed days. It allows a visual comparison of the amount of sap production along the season at a daily resolution and the frequency of productive days. The daily sums of sap production, expressed as day of the year (DOY), were calculated. Correlations using the non-parametric Spearman coefficient (ρ) were assessed within site (*i.e.*, between trees), and between sites (*i.e.*, between the averages of trees from each site). Correlations among trees or sites were calculated for the period of sap production. All statistics were performed using R version 4.2.1 (R Development Core Team, Vienna, Austria).

2.4 Results

2.4.1 State of charge under controlled conditions

The experiment of state of charge in batteries lasted 110 days. State of charge showed a negative exponential shape, with a drop occurring within the first days from the beginning of the

experiment (days 10 to 20), followed by stable values (Figure 2.2). Rain gauges showed starting state of charge at 100%, except those exposed to -10 °C, which started at 63%. Despite starting with lower state of charge, the batteries exposed to -10 °C reached the plateau after a similar number of days than the other batteries exposed to other temperatures. Logging intervals of 30 minutes showed the highest state of charge except at -20 °C comparing to the logging intervals of 15 minutes. The opposite pattern occurred for the temperature of -20 °C, which showed the lowest state of charge when recorded each 30 minutes. In general, the batteries exposed to warmer temperatures had a higher state of charge. The variation in the state of charge was similar between the two logging intervals. Accordingly, the two batteries exposed to the same temperature reached 50% of their charge during the same period but at different day of experiment.

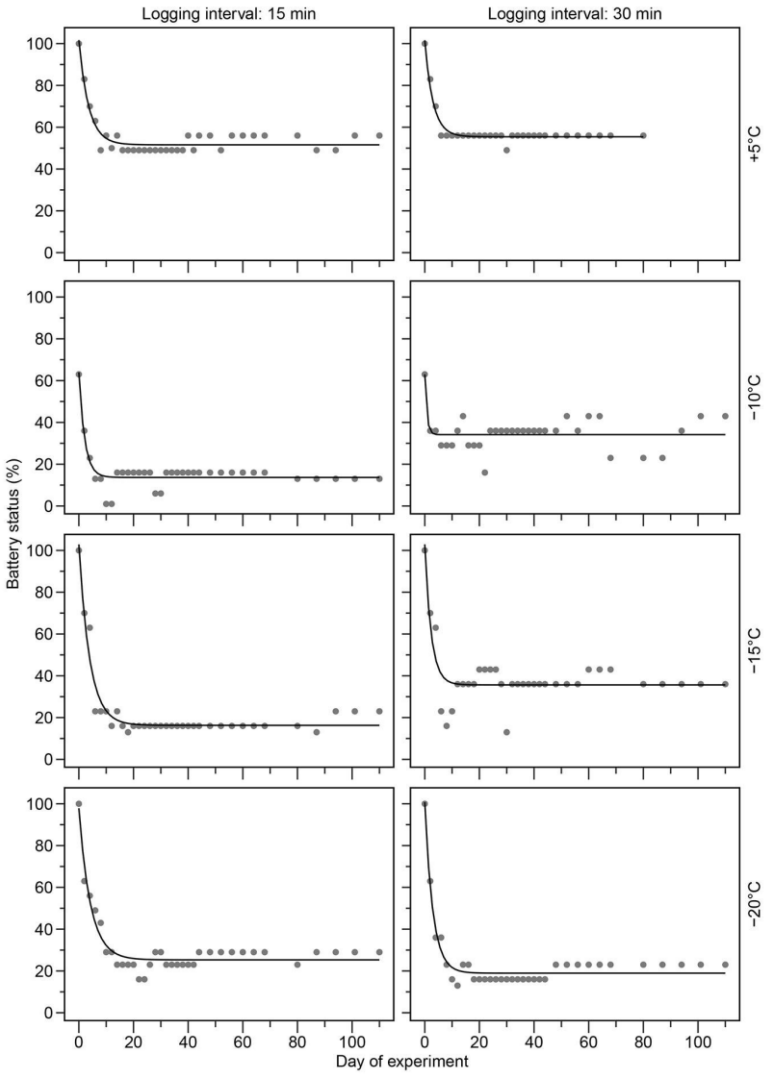

Figure 2.2 Variation in the state of charge in rain gauges exposed to different temperatures and set at two logging intervals. Data were fitted by nonlinear exponential decay models, whose standardized residuals (SR) are shown in the smaller panels.

2.4.2 Curve fitting of the state of charge

The quality of the fitting was confirmed by analysis of the residuals, which were uniformly distributed for all rain gauges. Most of the standardized residuals of these eight models converged from -2 to 2, confirming the model reliability (Figure 2.2). No apparent trend was observed for the residuals, confirming that the model well represented the data. The residuals exhibited a certain heteroscedasticity, with large residuals being concentrated during the first 20 days of the experiment. Overall, the results suggest that the model could be considered suitable for the observed changes in time of the state of charge.

2.4.3 Comparing the coefficients of the models

The nonlinear models produced coefficients varying within similar ranges (Table 2.2). The coefficient *a* represents the stability (*i.e.*, constant battery status) of the state of charge. The 30-minute logging interval showed higher values of state of charge than the 15-minute logging interval, except when exposed to a temperature of -20 °C where the order was reversed. The lowest value was observed at -15 °C and logging interval of 15 minutes. The highest value was calculated at +5 °C and logging interval of 30 minutes. The coefficient *b* represents the amplitude of the state of charge and showed the highest values with the logging interval of 30 minutes. The lowest value of the coefficient *b* was observed at -10 °C and logging interval of 30 minutes. The highest value was detected at -15 °C and logging interval of 15 minutes. The coefficient *c* indicated the speed to the battery drop or the rate of battery decline, and that the battery ran out faster at -10 °C and logging interval of 30 minutes. The lower value was observed at -15 and -20 °C (logging interval of 30 minutes Table 2.2).

Table 2.2 Estimated coefficients and statistics of the nonlinear models describing the variation in the state of charge of rain gauges submitted to different temperatures and set up at different logging intervals. Values are reported as a mean ± standard error.

Temperature (°C)	Logging interval(minutes)	a	b	c
5	15	51.58 ± 0.71	50.10 ± 3.49	–0.28 ± 0.04
5	30	55.44 ± 0.42	46.18 ± 1.98	–0.33 ± 0.03
–10	15	13.67 ± 0.81	50.27 ± 4.38	–0.47 ± 0.09
–10	30	34.15 ± 1.19	28.85 ± 6.79	–1.33 ± 1.68
–15	15	16.28 ± 0.88	86.59 ± 4.21	–0.25 ± 0.02
–15	30	35.64 ± 1.54	67.26 ± 8.28	–0.43 ± 0.11
–20	15	25.32 ± 0.89	72.53 ± 4.17	–0.24 ± 0.03
–20	30	18.95 ± 0.75	81.85 ± 3.85	–0.34 ± 0.03

2.4.4 Rain gauges in the field

We recorded the daily volume of sap production at the four sites between DOY 80 and 130. Sap production was discontinuous, as demonstrated during the period from DOY 104 to 112 at all

sites (Figure 2.3). We observed days with high production and days with low or no production. High productions occurred either on single days or during periods, as detected during DOY 88 and 96 at RAP. Low or no production was observed between DOY 108 and 110 at all sites.

The diameter at breast height of the trees varied from 16 to 37 cm, with a height of between 7.5 to 18 m. The maximum average temperatures varied between 2.8 and 3.6 °C, with the warmer site being RAP (Table S2. and Figure S2.1 in Supplementary material). The minimum average temperatures ranged from 2.2 to 2.9 °C, with the lowest minimum being recorded in ASJ (Table S2. and Figure S2.1 in Supplementary material). The highest correlation between trees was observed at ASJ (ρ = 0.88, p<0.001 Figure 2.3). One of the trees at RAP had a short season of sap production, from DOY 80 to DOY 115, which caused a low correlation between trees (ρ = 0.38, p>0.05). The earliest onsets of sap production were observed at PMV and RAP (DOY 80). The latest onset of sap production was detected at ASJ (DOY 95). The earliest ending of sap production was observed at RAP (DOY 115) and the latest ending at LAT (DOY 130). The total yield varied between trees and sites. The highest volume in one day occurred at PMV, with a total yield of 4.5 litres for tree 1.

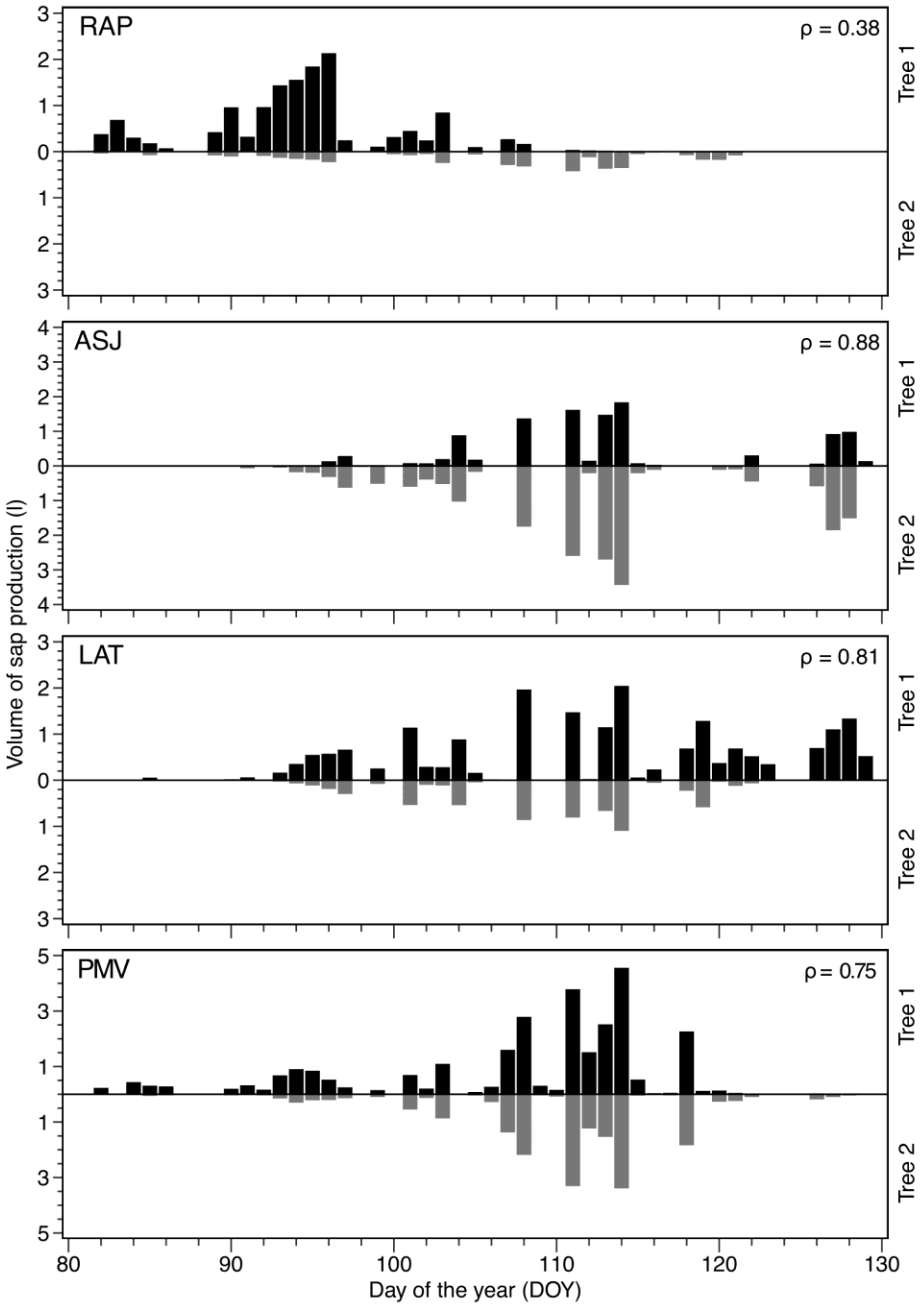

Figure 2.3 Daily dynamics of natural sap production in sugar maple and the correlation coefficient of Spearman in each site. Note the different ranges of vertical axes.

In general, sap production showed a spatial autocorrelation, where sites close to each other showed higher correlations. For example, ASJ and LAT showed a higher correlation (ρ =0.72, $p<0.001$) compared to RAP (Table 2.3). The correlation between RAP and ASJ, and between RAP and LAT were not significant (ρ ranging between 0.25 and 0.27, $p>0.05$). PMV was the

only site showing significant correlations with all studied sites (ρ ranging between 0.32 and 0.44, $p<0.05$).

Table 2.3 Spearman's correlation coefficients (ρ) and relative probabilities of correlations in daily sap production during spring 2022 among the four study sites. NS=not significant.

	RAP	**ASJ**	**LAT**	**PMV**
RAP		0.27	0.25	0.43
ASJ	NS		0.72	0.32
LAT	NS	p< 0.001		0.44
PMV	p< 0.01	p< 0.05	p< 0.01	

2.4.5 Cumulative percentage of daily sap production

The cumulative percentage of daily sap production showed an exponential decline. Such a pattern indicated that a substantial amount of sap production occurred within a few, very productive days. These productive days are located at the beginning of the curves shown in Figure 2.4 until the identity line (line 1:1). Most days of the sap season (in the middle and right part of the plots) had low or no sap production. The patterns are very similar between trees and sites despite the differences observed in the absolute amount of sap production, which indicates a common trend within and across regions. For example, the trees at RAP showed a different pattern of volume and period of sap production compared to other sites (Figure 2.3). Yet, the cumulative percentages were very similar to the other sites and trees (Figure 2.4).

The duration of sap production varied from 35 to 50 days. An average of 74% (from 62.2% to 84.6%) of the total sap production was exuded on eight very productive days (7 to 10 days), which corresponded to 20.1% (19.4% to 20.9%) of the sugar season. Most of the days (14 to 35 days) had low sap production, below 1 litre. No sap production was observed during 6 to 14 days, which corresponded to 23.7 % (16.6 to 40%) of the sugar season.

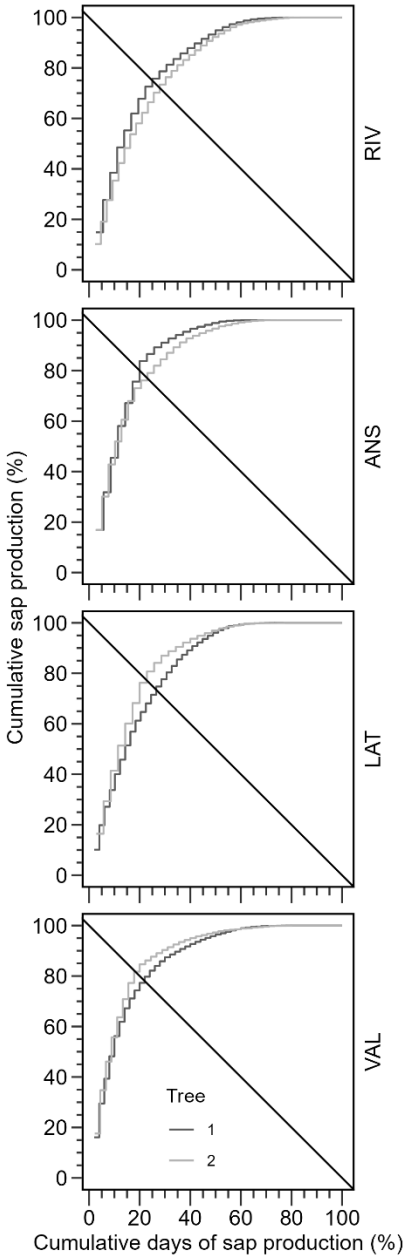

Figure 2.4 Cumulative percentages of daily sap production. Diagonal line represents 1:1.

2.5 Discussion

Our study utilized rain gauges to monitor sap production in maple at a daily temporal resolution. To confirm the use of rain gauges as an adequate tool to measure sap production, we conducted tests under controlled conditions and in the field. The rain gauges demonstrated the ability to record data across a wide range of temperatures in the field and continued to log data for over three months under controlled conditions, what is largely exceeding the duration of the sugar

season. Our results demonstrated that the rain gauges can remain active at temperatures of -20 °C despite sap exudation will not occur at that low temperature. Field measurements allowed the phenological timings of production to be compared among and within sites. Our findings showed the particular dynamics of sap exudation, which is concentrated in a few, and highly productive, days of the sugar season.

2.5.1 Rain gauge as a tool for measuring sap production

The performance of batteries is known to decline as the temperature falls below 0 °C. According to the coefficient *a* of our model, the batteries showed a higher stability at temperatures > 0 °C, and a lower stability at temperatures < -10 °C (Table 2.2). According to previous studies, batteries exposed to -10 °C exhibit a reduction in capacity by up to 95% compared to those exposed to ambient temperature (*i.e.*, 20 °C), which can explain such low battery status in the coefficient *a* values (Zhang et al., 2003). The coefficient *c* showed a faster battery decline. This is due to several factors, including slower chemical reactions, reduced rates of battery transfer kinetics, and decreased electrolyte conductivity, which limit the diffusivity of lithium ions in a negative electrode potential, making it easier to oxidize (Ji & Wang, 2013; Shiao et al., 2000; Zhang et al., 2002). At -20 °C, the extraction of energy is significantly limited and energy and power of the cells decrease, resulting in lower battery-transfer resistance (Zhang et al., 2003). These opposing forces can negatively impact the performance of the battery during its operation (Ji et al., 2013; Zhang et al., 2003).

The Lithium batteries were suitable for dataloggers running at low temperatures. The supply voltage of Li-Battery is 3V, and the input resistance of the datalogger is 100 kΩ, as mentioned in the datasheet of the datalogger (Onset®, 2018). Using Ohm's Law, the value of current is 3V/100 kΩ = 0.03 mA, ten times less than the rated current of the battery (0.3 mA for continuous drain according to the datasheet of Sony Li-Battery CR2032). Hence, a fairly low current is drawn from the battery by the datalogger. Even under a constant temperature of -20 °C, the rain gauge was able to record data for 110 days during the experiment. Except for very low temperatures, the time interval of 30 minutes was the best resolution to record data while maintaining a higher state of charge. However, a resolution of 15 minutes was more effective at -20 °C to ensure a long-lasting performance of the battery. Lithium batteries should undergo

pulse discharge when exposed to extreme temperatures, which can promote a better performance, even if lower temperatures result in minimal change compared to -10 °C.

Our experiment showed that the batteries performed better and had a higher battery level when they were used less frequently, *i.e.*, 30 minutes (Figure 2.2). Using the battery less frequently allowed voltage to rise and to maintain a higher battery level. However, at -20 °C, the results were reversed, with the battery performance being higher when the battery was used more often. When the temperature is below 0 °C, battery discharging warms up the cells due to an interaction between electrochemical and thermal processes (Jaguemont et al., 2014).The self-heating process contributes to maintain the state of charge stable over time (Jaguemont et al., 2014). At -20 °C, a shorter logging interval, *i.e.*, 15 minutes, warms up the battery more frequently, likely contributing to maintaining a higher state of charge than a longer logging interval, *i.e.*, 30 minutes. Nevertheless, a shorter logging interval, and consequently a more frequent heating of the cell system, can cause a quicker deterioration of cells, reducing the battery lifespan (Jaguemont et al., 2014; Martel et al., 2011).

The high input/output impedance (a low current flow in a circuit and potentially high voltage) of 100 kΩ of the data logger, combined with the short duration of current flow in a circuit of the battery, reduces the current requirement to maintain the battery functioning properly and significantly prolongs the battery life. In fact, our setup was able to use a CR-2032 3V lithium battery for the entire period of the experiment, exceeding the sap production season, which on average lasts 8 to 10 weeks (Kurokawa et al., 2022). As a result, the data logger can easily operate with the CR-2032 3V lithium battery for the entire sap production season without the need for battery replacements.

Overall, our experiment in controlled conditions demonstrates the rain gauge's ability to function under extreme temperatures for the whole sap season, making it a reliable tool for recording sap production in maple trees at high temporal resolution.

2.5.2 Dynamics of sap exudation and sap yield

The rain gauges were used in the field to assess sap exudation at high temporal resolution and validate the performance under natural conditions. The tool enabled accurate measurements and

comparisons of sap production throughout the entire sugar season. The phenological timings during the sap season (*i.e.*, the sap flow in late winter and early spring when temperatures fluctuate) were correlated between the study sites, which could be attributed to the similar climatic conditions that the maple population experienced across sites. Indeed, the period of syrup production as well as the annual yield are known to be strongly climate-driven (Rapp et al., 2019). In our study, we observed that the southernmost and warmest site (RAP) concentrated most sap production at the end of March (DOY 88) and beginning of April (DOY 98). The other sites, ASJ, LAT and PMV, showed the highest sap volume occurring in mid-April (DOY 108-112). This difference in timing between sites could be explained by the earlier warming occurring at the southern site (RAP), which experienced the ideal conditions for growth reactivation earlier than the northern sites, leading to an earlier onset of the sugar season. The later onset of sap production was observed at ASJ, possibly because of its cooler temperature compared to the other sites. Thermal thresholds, above and below 0 °C play a critical role in triggering sap exudation, and the specific conditions required to initiate the sugar season are well documented (Rapp et al., 2019; Skinner et al., 2010). In North America, this season typically occurs within a specific timeframe in late winter and early spring (Houle et al., 2015). The northern sites, located in the same climatic zone and experiencing similar weather, showed similar timings of sap exudation, with trees within the same site exhibiting comparable onset, ending and duration of the sugar season (Kurokawa et al., 2022). This result suggests that measurements collected in a few individuals could be sufficient to obtain a precise picture of the sugar season at site and regional scale. However, further investigations with a larger sample size are recommended to assess more accurately and extensively the variability in phenological timings among trees. The results suggest the need to evaluate carefully the minimum sample size for estimating the sap yield for the future experiments. Moreover, given the disparities in density between rainwater and sap, and the potential variations in sap density throughout the season (Perkins et al., 2022), it is advisable to conduct additional research to better relate sap volume to its density. Such a study would not only fulfil the practical necessity of accurately calibrating the rain gauge for fine-scale sap exudate measurement but could also yield insights into the underlying physiological processes contributing to sap density fluctuations during the sugar season.

Our results demonstrate clearly that sap production is discontinuous, showing either productive or non-productive days during the season. It is known that sap exudation occurs when trees experience freeze-thaw cycles, which are produced by the freezing nighttime temperatures followed by daytime warmings that induce alternating positive and negative pressures in the trunk and branches (Ceseri & Stockie, 2013; Graf et al., 2015; Kim & Leech, 1985; Tyree, 1983; Tyree & Zimmermann, 2002). The absence of sap production may be related to daytime temperatures < 0 °C or by low daily amplitudes in temperature (Wiegand, 1906). While the freeze-thaw cycle plays a major role in the sap exudation process, other factors can account for the variation in productivity (*i.e.*, more or less productive days), including environmental parameters such as maximum temperature during the day, water availability and solar radiation (Kim & Leech, 1985; Pothier, 1995; Robitaille et al., 1995; Watterston et al., 1963).

According to our results, trees from the same site show similar phenological timings and recurrence of productive and non-productive days, but very different daily and seasonal volumes of sap production. Some factors related to tree characteristics are known to be involved in sap yield. Trees with greater diameters (Grenier et al., 2007) and crown size (Tucker, 1990), or higher vitality can have higher sap yields (Rademacher et al., 2023). Reproduction effort of sugar maple has also been correlated to syrup production (Rapp & Crone, 2014).Moreover, anatomical differences (*e.g.*, the proportions of rays' cells) between trees may also explain part of the differences in sap yield (Gregory, 1977). Still, several sources of variability such as the tapping procedure or tapping location along the stem could affect the final production (Rademacher et al., 2023). Additional research is needed to better understand the dynamics of sap production at higher temporal resolutions (hourly or sub-hourly) and compare sap exudation with the production using a vacuum system.

2.5.3 Daily distribution of sap exudation

On average, 74% of the total sap yield was produced during 20% of the sugar season. Such a pattern matches the proportion described in economic studies, and referred to as the Pareto law, or 80/20 rule (Johnson, 1937). This principle, stating that 80% of consequences come from 20% of causes, is relevant to understand the processes involved in productive systems and their optimisation (Cravener et al., 1993). It also applies to sap production, with noteworthy

implications for producers and their strategic choices for the sugar farm. A possible explanation for this pattern may be related to either the weather conditions during or preceding the harvesting season (Duchesne et al., 2009; Marvin & Erickson, 1956). A prompt and reliable use of equipment and human resources is vital during these few, very productive days to ensure an optimal sap collection (Perkins et al., 2022). Equipment involves the correct functioning of the tubing system, which should avoid leakages, and losses of vacuum, which can negatively influence the sap flow and consequently the overall sap yield during the most productive days (Lagacé et al., 2019). A strategy is needed to plan for the peaks in production under the conditions of the 80/20 rule. Producers should ensure an adequate storage capacity for the large amount of sap that can be collected during the most productive days, and the necessary human resources to handle the increased volume of sap (Perkins et al., 2022). Statistics of sap production are commonly available at annual scale in Quebec, and there is a need of collecting and analysing sap production at higher resolution for exploring the eco-physiological processes involved in sap exudation driven by the weather (Ahmed et al., 2023; Rademacher et al., 2023).

The ongoing climate change raise concerns about the future of the maple syrup industry (Galford et al., 2014; Rapp et al., 2019). Warming winter and spring temperatures might anticipate the onset of sap exudation, forcing producers to modify the traditional tapping (Skinner et al., 2010). Changes in the frequency of freeze and thaw events (Rapp et al., 2019) could in turn affect the occurrence of the most productive days, with potential consequences on the daily sap yield. According to our results, given that up to 84.6% of the production is concentrated in 20% of the sugar season, changes in weather occurring during the most productive days and even more so the disappearance of the weather conditions creating the most productive days will result in a significant alteration of the seasonal sap yield. There is a need to increase knowledge on the timings, frequency, and intensity of weather events under climate change scenarios to better understand the consequences for sap production and the future of the maple syrup industry (Kurokawa et al., 2022; Marquis et al., 2022). Data collected at daily temporal resolution using rain gauges allow our understanding of the dynamics of sap exudation to be improved, thus contributing to optimizing the production practices based on the Pareto principle and ensure long-term sustainability of the maple syrup industry.

This study monitored the timing and dynamics of natural sap production in sugar maple trees at daily temporal resolution. The findings of this research included the use of equipment for generating high temporal resolution data and the discovery of sap production patterns that are scarce in the scientific literature. To better understand daily sap production, a more representative sample should be considered. Studies that examined interindividual variability with fewer than 15 individuals were inconclusive in determining whether sap yield corresponded to the tap hole orientation (Rademacher et al., 2023). This suggests that small samples size may not adequately capture the complexity of sap production dynamics across trees. While a limited number of tress may provide a reasonable initial estimate of the sugar season's timing, a larger sample size is recommended for a more comprehensive understanding of the heterogeneity among trees (Wright et al., 2005). As research projects progress and sample sizes increase throughout Quebec, it will be possible to have greater certainty the synchronization of trees and estimate the real timings of sap production. Future research should include more representative sampling, with a larger number of trees per site, to capture interindividual variability in sap flow patterns (Xiong Wei et al., 2008). A greater representation of individuals could also help clarify the discrepancies observed in the timings, including its spatial variations along latitudinal gradients (Duchesne & Houle, 2014). Furthermore, this study did not include sap volume per tree, which could further enrich the phenology of this species. These approaches would contribute to an understanding of sap flow dynamics for producers and improve sap exudation prediction models.

2.6 Conclusions

Our study has developed and tested the use of rain gauges for recording sap production in maple trees at a high temporal resolution. Our findings demonstrate that tipping bucket rain gauges can effectively perform under the harsh spring temperatures typical of the sugar season, including the extreme conditions of -20 °C. It has shown the ability to log data for extended periods, exceeding the typical duration of the sugar season. The results have demonstrated daily synchronisms in sap exudation among and within sites, showing the typical pattern described by the Pareto principle. The sugar season was discontinuous in all sites and exhibited both productive and non-productive days with most of the production being concentrated in 7-10

days. The synchronism in phenological timings among trees presents better than the different daily and seasonal volumes in sap yield.

Our results demonstrated that rain gauges are a reliable tool for monitoring sap exudation with high temporal resolution, offering a new method to deepen our quantitative understanding of the factors driving the sugar season and sap production. By associating the dynamics of sap production with weather data, new insights into the eco-physiological processes involved in sap exudation could be provided. These insights can directly impact the maple syrup industry by enabling producers to manage resources more efficiently and plan the collection of sap in order to better profit from the peak of production.

2.6.1 Acknowledgements

SK carried out the conceptualization, methodology, writing original draft preparation, writing-reviewing and editing. GB carried out the methodology, writing original draft preparation, writing-reviewing and editing. GS carried out the methodology, formal analysis, writing original draft preparation, writing-reviewing and editing. RS carried out the writing original draft preparation, writing-reviewing and editing. SD carried out writing-reviewing and editing. SR carried out the conceptualization, writing-reviewing, editing and supervision.

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2.7 Supplementary material

Table S2.1 Tree characteristics at the four study sites during the sap season.

Study site	Diameter of the stem (cm)	Tree height (m)
RAP	34	7.5-8
LAT	29-37	15
PMV	16-22	10-18
ASJ	28-33	9-10

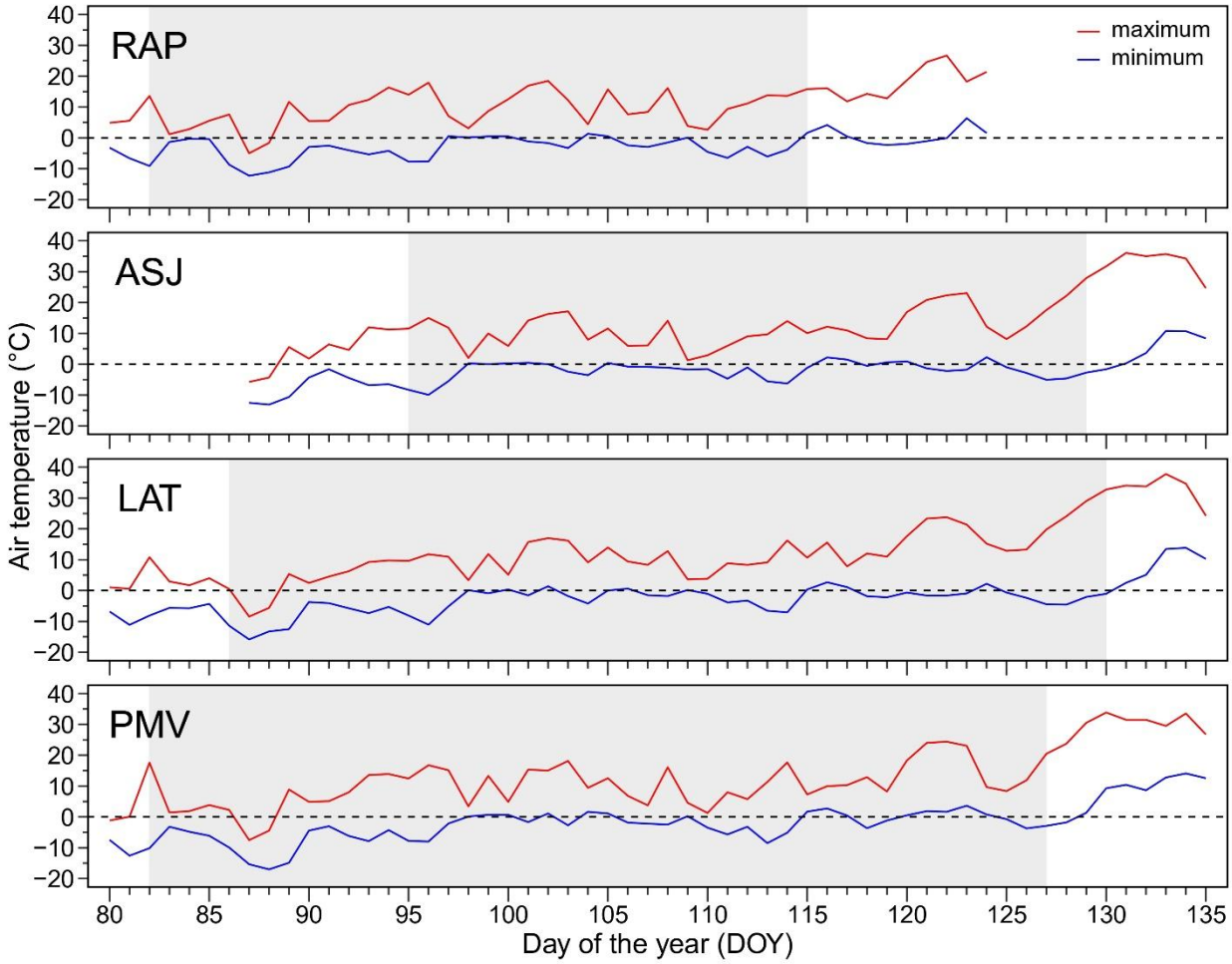

Figure S2.1 Air temperature before and during the sap season in 2022 in four sites in Quebec, Canada.

CHAPITRE 3
SAP SEASON AT LOCAL SCALE AND HIGH RESOLUTION

The divergent advancements of sap phenology in maple under warming conditions can shorten the sugar season

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Keywords: Acer saccharum, sap exudation, climate change, soil temperature, snow, soil water content, gravity sytem.

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3.1 Abstract

Climate change raises concerns for the maple syrup industry, mainly regarding the expected changes in the timings of the sugar season and the resulting uncertainty of sap yield. This study investigates the temporal relationships between the environmental factors and sap phenology (i.e., timings of the onset and ending of sap season) in sugar maple (Acer saccharum Marsh.) during 2018–2022 at the northern limit of the species in Quebec, Canada, and predicts the impact of warming under greenhouse gas emission scenarios (RCP 2.6, 4.5, and 8.5). March and April temperatures are correlated to the onset and ending of sap exudation, occurring on average on DOY (day of the year) 86 and 133, respectively. Sap exudation corresponds with the start of snowmelt and the consequent increase in soil water content. Complete snowmelt and the increase in soil temperature coincide with the ending of sap exudation. Our partial least squares regressions estimate an advancement of up to 20 days for the start and 26 days for the end of sap production by 2100 at RCP 8.5. The predictions suggest a divergent advancement of the onset and ending of sap production under warming, resulting in a shorter duration of the sugar season. The earlier sap season represents an important challenge for producers, who will need to adjust their activities in the sugarbushes to match the warmer conditions predicted for late winter and early spring. Any delay in tapping will increase the risk of substantial losses in production, especially in the context of a shorter sap season.

3.2 Introduction

As the largest producer in the world, Quebec stands at the epicentre of maple syrup production, with a sustained growth in the number of taps over the last decade (PPAQ, 2023). This rapid expansion has not only boosted the economy of the province, but also elevated maple syrup as a culturally-significant non-timber product in Canada (Snyder et al., 2019). The maple industry has grown into an international market, with maple syrup being consumed in more than 50 countries, generating a Canadian revenue of 616 M $ in 2022 (Government of Canada, 2024). Maple syrup production depends on the exudation of sap, a physiological process driven by weather and, specifically, by daily temperature oscillation (Cirelli et al., 2008; Tyree, 1983). As a result, the primary concern for producers is the impact of climate change, including the ongoing warming and shifts in the seasonal temperature (IPCC, 2023). These rapid changes exacerbate the wide variability in weather conditions and yield, which already represent a sustainability challenge for producers. In addition, projections in Quebec predict for the end of this century a warming in the annual mean temperature by 3.9 to 8.5 °C (Swart et al., 2019), raising further concerns for the long-term sustainability of the maple industry. In this large framework, the impact of climate change on the physiological processes of exudation and the consequences for sap yield still remain largely misunderstood.

Several studies have suggested that climate change can potentially impact maple syrup production (Ahmed et al., 2023; Houle et al., 2015; Kurokawa et al., 2022; Skinner et al., 2010), mainly on the timings of the sap season, and the resulting quality and amount of maple syrup (Caughron et al., 2021; Duchesne et al., 2009). The predictions suggest an earlier onset of the sugar season, with a potential advancement of up to two to three weeks (Houle et al., 2015). Such a change presents a significant challenge for producers, who must prepare their sugarbushes before the beginning of the sap exudation. One crucial task is the annual tapping of the maples (Ouimet et al., 2021). Tapping must be performed within a specific and narrow time window, as early tapping could dry up the tissues and affect the resulting sap flow (Perkins et al., 2022), while delaying it may result in missing the start of the sap season. Both early and late tapping can ultimately reduce the total sap yield. For this reason, a mismatch between tapping schedule and sugar season under warming could result in a potential reduction in sap yield ranging from 15% by 2050 to 22% by 2090 (Duchesne et al., 2009). Thus, it is imperative and

urgent to improve our ability to estimate the timings of the sap season as any mismatch between favourable weather conditions and tapping practices may result in substantial losses in the annual production of maple syrup.

The process of sap exudation is highly sensitive to air temperature (Rapp et al., 2019; Tyree, 1983). At night, when the temperature drops below the freezing point, the water within the xylem freezes. The gases dissolved in the sap form bubbles, which create negative pressure (also known as tension) within the vessels (Ceseri & Stockie, 2013; Cirelli et al., 2008). During the daytime, when temperatures rise above freezing point, the ice within the xylem starts to melt, and the gases that formed bubbles dissolve back into the liquid sap (Milburn & O'Malley, 1984). This phase increases pressure within the xylem, which forces sap upwards, or out of the tap hole produced by during tapping. These freezing and thawing cycles result in alternating negative and positive pressures, respectively, and allow sap to be collected from tapped trees under gravity (Tyree, 1983). The time window of sap exudation in maple represents the rehydration process of the tissues and indicates the imminent growth reactivation (Améglio et al., 2002). The ability to dissolve gases efficiently during the warming period allows the xylem to recover quickly from winter dormancy and maintain an efficient sap flow (Tyree & Yang, 1992). The alternating freeze-thaw cycle creates a pump-like mechanism that drives sap movement (Améglio et al., 2001), likely allowing the mobilization of resources stored in the parenchyma as a preparation for bud break and leaf-out (Schenk et al., 2021).

Sap production in maple could also be influenced by or correlated to a number of other environmental factors, such as water availability, soil temperature and snow melt (Graf et al., 2015; Robitaille et al., 1995; Skinner et al., 2010). Indeed, a freeze-thaw cycle can also be observed in correspondence to non-productive days (de Lima Santos et al., 2025). However, the effect of these factors on the sugar season and sap production remains largely uninvestigated. In this study, we assessed the daily timings of sap production in sugar maple (*Acer saccharum* Marsh.) between 2018 and 2022 to (1) evaluate the co-occurrence of environmental parameters (i.e., air and soil temperatures, soil water content and snow cover) on the sap season; and (2) predict the timings of the sap season according to the greenhouse emission scenarios in Quebec, Canada. We tested the hypothesis that warming conditions advance onset and ending of sap production in maple.

3.3 Material and methods

3.3.1 Study area

This study was conducted in a natural stand located at Simoncouche research station in the Laurentide Wildlife Reserve (48 °13'N, 71°15'W, 350 m a.s.l.), Quebec, Canada. The site was located at the boundary between two bioclimatic domains, the balsam fir (*Abies balsamea L.*)–yellow birch (*Betula alleghaniensis* Britton*)* domain and the balsam fir–white birch (*Betula papyrifera* Marshall*)* domain in the mixed forest, where maple is close to the northernmost limit of its continental range. The sugar maple trees are mature and even aged. The climate of the area is continental, with long cold winters and short warm summers. According to the local weather station, the annual temperature between 2001 and 2022 was 2.5 °C, with an average maximum temperature of 17.5 °C occurring in July, and an average minimum temperature of -15.2 °C in January. The site receives a total precipitation of 915 mm, and snow depth reaches on average 85 cm. The mineral soil is podzol, with MOR-type humus and an organic horizon of 10-20 cm (Rossi et al., 2016).

3.3.2 Tree selection and data collection

Four mature sugar maples (*Acer saccharum* Marsh.) were randomly selected for this study (Table 3.1). The trees had a diameter at breast height >20 cm, in accordance with the manual for minimum tree size required for tapping (Perkins et al., 2022). All trees were healthy, previously untapped and dominant. A rain gauge (5222-L, TE525MM-L, Campbell Scientific Corporation, Logan, UT) was installed on each tree to measure in continuous the sap exudated by gravity. A minimum volume of 4.73 ml of water is recorded each time the tip fills and the switch activate, enabling a precise and automatic assessment of sap flow rates, timing, and duration. The volumes recorded were corrected using a conversion rate of 1.32 g ml-1 to consider the higher density of the sap compared to water (Kurokawa et al., 2024). A notch was made on the stem at breast height at the beginning of February of each study year (2018-2022) using a drill. A plastic spout was then inserted into the notch and connected by tubing to the rain gauge. The equipment was sanitized before and after each sugar season to prevent microbial contamination. The top of the rain gauges was sealed to avoid any debris from falling in and obstructing the measurement system. At the end of the sap season, the spout was removed to avoid damages caused by the wounding. In 2018, two trees were initially tapped and equipped

with the rain gauges to assess their field performance for sap flow measurement. The sample size was subsequently increased in 2019. Data from two trees in 2022 were excluded from the analysis due to equipment malfunction resulting in large gaps of the sap chronologies.

Table 3.1 Characteristics of the four sugar maple trees located at Simoncouche from 2018 to 2022. Diameter at breast height = DBH.

Tree	DBH (cm)	Height (m)
1	34.5	16.9
2	20.5	9.4
3	25.5	14.8
4	33.0	16.7

3.3.3 Climate data

The weather conditions were recorded with a standard meteorological station installed in a forest gap at 1 km from the site. Sensors recorded air temperature (HMP45C212, Campbell Scientific, Logan, UT), soil temperature at the depth of 10 cm for organic layer and 20 cm for mineral layer (107- B, Campbell Scientific, Logan, UT) and snow depth (SR50A, Campbell Scientific, Logan, UT) with a resolution of 15-minute. The soil water content (CS616, Campbell Scientific, Logan, UT) was monitored at a depth between 12 and 20 cm. Data loggers CR1000 (Campbell Scientific Corporation, Logan, UT) stored the data in the form of hourly averages.

Temperature predictions for Simoncouche were obtained according to three greenhouse gas emission scenarios, represented by the concentration pathway (RCP 2.6, RCP 4.5 and RCP 8.5) extracted from the Ouranos database (ClimateData.ca, 2024). These scenarios are used to predict changes in temperature, precipitation, and other climatic variables over specific time intervals (Wang et al., 2022). The RCP 2.6 assumes a reduction in CO_2 concentrations in the atmosphere during the 21st century and projects the possibility to keep global mean temperature increase below 2°C (van Vuuren et al., 2011). RCP 4.5 is a middle scenario and would result in ongoing warming and higher overall precipitation levels for the duration of this century. The RCP 8.5 represents continuous high greenhouse gas emissions which would potentially cause substantial shifts in the precipitation seasonality and air temperature exceeding 4.5°C compared to the pre-industrial level (IPCC, 2021; Meinshausen et al., 2011).

3.3.4 Data analysis and statistics

Quadratic logistic regressions were used to estimate the daily probability of sap exudation, where the binary response represented the presence or absence of sap production. Day of the year (DOY) was the only predictor used for the model. A quadratic discriminant analysis was applied as an exploratory analysis to maximize the probability of correctly assigning the observations and predicted values. A final threshold of probability of 10% was chosen to define the onset and ending of sap production by avoiding excessive false negatives. A Tukey's HSD post-hoc test was used for multiple comparisons.

The relationships between sap phenology (response variable) and monthly air temperatures (explanatory variable) were assessed using normal linear regressions. We used Partial Least Squares Regressions (PLS) for building predictive models connecting sap phenology with monthly temperatures. Modelling included a Nonlinear Iterative Partial Least Squares (NIPALS) algorithm with leave-one-out cross-validation. This approach involved the iterative extraction of factors to reduce dimensionality and address multicollinearity. Initially, all independent variables (i.e., monthly maximum, average and minimum temperatures) were considered in model construction. To refine the model, the variables with a variable importance in projection (VIP) <0.08 were excluded (Cox & Gaudard, 2013; Prislan et al., 2019). Due to a phenological importance for the beginning of sap season, February was kept in the model, even if presenting VIP<0.08. Removing this month could affect the interpretation of the model and results (O'brien, 2007). The final predictors included monthly maximum, minimum and average temperatures from January to April. This step ensured that only the most influential variables were retained. A new model was then constructed based on the remaining temperature predictors, and its validation was performed by comparing observed and predicted data according to the estimated temperatures.

The final PLS model was applied to predict the timing of sap production under future climate conditions. The predictions were based on different emission scenarios (2.6, 4.5, and 8.5) incorporating projections until 2100 (Charron, 2016). Projections for 2100 indicate temperature increases of approximately 1.4°C, 2.4°C, and 4.9°C for RCP2.6, RCP4.5, and RCP8.5,

respectively (Charron, 2016). All analyses were performed in JMP version 13 (SAS Institute Inc., Cary, NC) and R version 4.2.2 (R Core Team 2022).

3.4 Results

3.4.1 Sap phenology and total yield

Sap exudation was discontinuous, with productive days followed by non-productive periods (Figure 3.1). The dynamics of sap production was synchronized between trees, as observed, for example, on the very productive DOY 115 in 2019, and the lack of sap exudation on DOY 75 in 2021. The quadratic logistic regressions allowed the sap season to be estimated with a threshold of 10%. The performance of the classification model was evaluated using a confusion matrix, which assessed the predictive accuracy of the fitting. Predictions had 86.7 and 75.1% of values matching the productive and non-productive observations, respectively. In general, the sugar season varied from 40 to 53 days. The years 2019 and 2018 had the shortest and longest durations of sap season, respectively.

On average, the onset of sap production occurred on DOY 86, with 2021 and 2019 showing the earliest (DOY 74) and latest (DOY 99) onset, respectively (Figure 3.3). The ending of sap production occurred on average on DOY 133, with 2021 and 2018 showing the earliest (DOY 120) and latest (DOY 146) ending, respectively. Each tree produced an average total yield of 12.3 l. The total yield varied among years, with a production ranging from 2.2 to 28.4 l. The year 2019 showed the greatest difference between the least and most productive tree. Sap production was discontinuous, and characterized by 24% of productive days over the sap season.

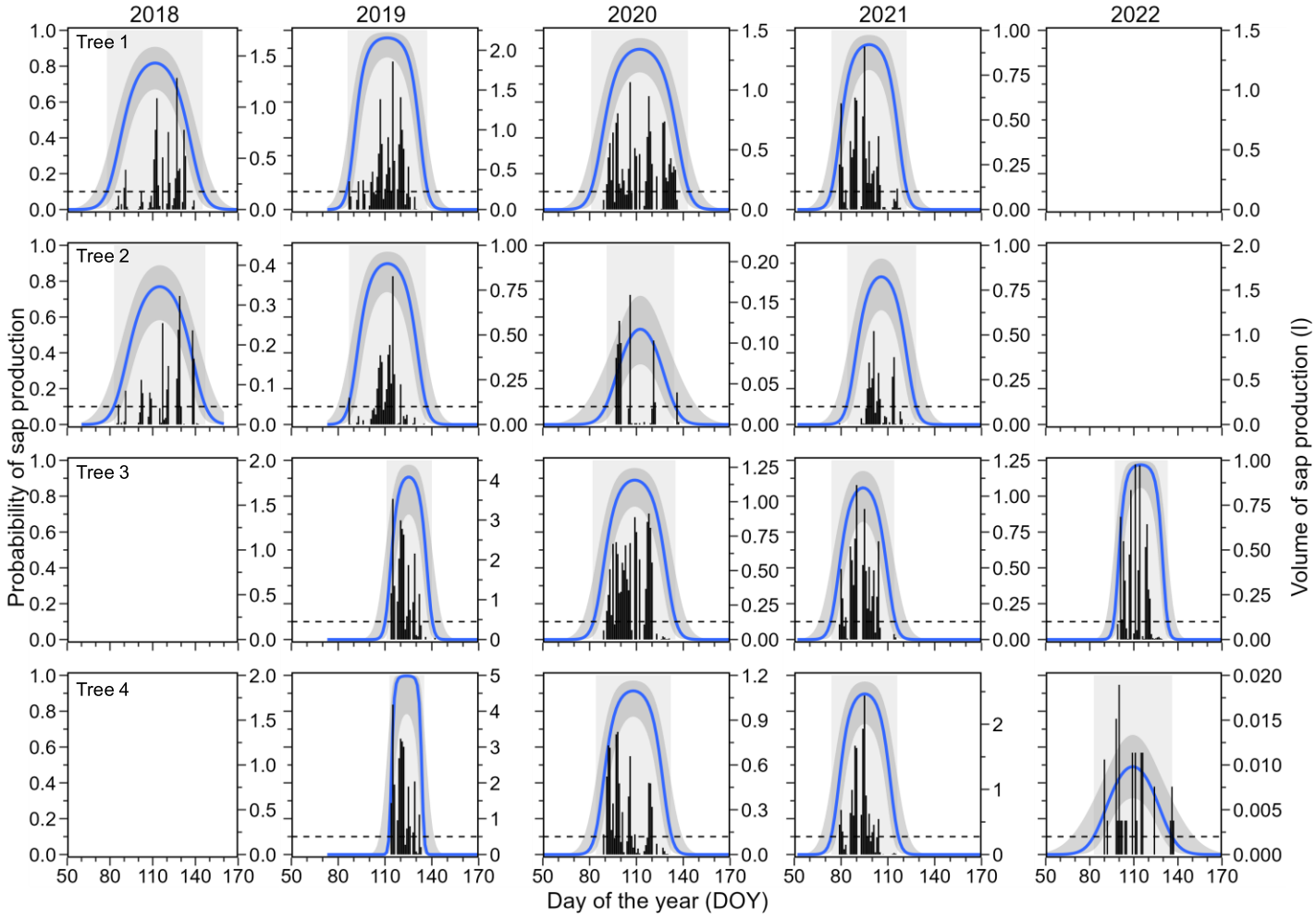

Figure 3.2 Daily sap production in four sugar maples during 2018-2022. The black bars represent the volume of sap production (l). The shaded areas represent the sap production season with the onset represented by a threshold of 10%. The quadratic logistic regressions (blue line) were fitted to represent the probability of occurrence of sap exudation (binary). The darker grey area is confidence interval with a 95% confidence level.

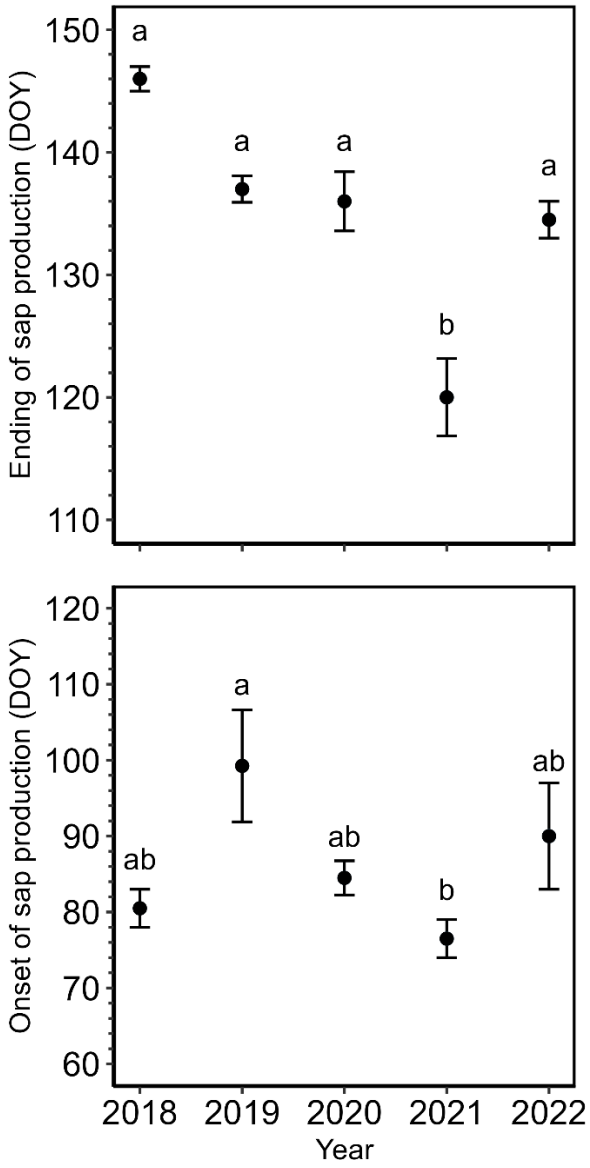

Figure 3.3 Mean and error bar comparing the onset and ending of sap production between years. Groups (i.e., onset or ending) with the same letters are not statistically different.

3.4.2 Weather conditions

The average maximum, mean and minimum temperatures during the sap season were 8.0 °C, 2.0 °C, and -4.1 °C, respectively (Figure 3.3). In this period, the temperatures had reached extreme values of up to 30 °C in the daytime, and -24.8 °C in the nighttime. The maximum snowpack was observed at the end of the winter, between the end of February (DOY 57) and end of March (DOY 75). The snowpack reached a peak of 1.17 m in 2022. The shallowest snow depth (0.47 m) was recorded in 2021. In winter, soil water content fluctuated between 0.2 and

0.3 cm^3/cm^3. Snowmelt started a few days before the onset of the sap season, with the snowpack thinning out gradually for the successive 30-50 days and contributing to abruptly increase the soil water content, which reached values of 0.55 cm^3/cm^3. Snow disappeared from the soil between the end of April (DOY 99) and beginning of May (DOY 128), before the ending of sap production. During winter, the temperature of the mineral layer remained close to 1.3 °C (FFigure 3.3). The organic layer had a colder temperature, but never reaching freezing point. In the last days of the sap season, when the snow had completely melted, the soil warmed up quickly, reaching temperatures of between 8 °C and 14 °C by DOY 180.

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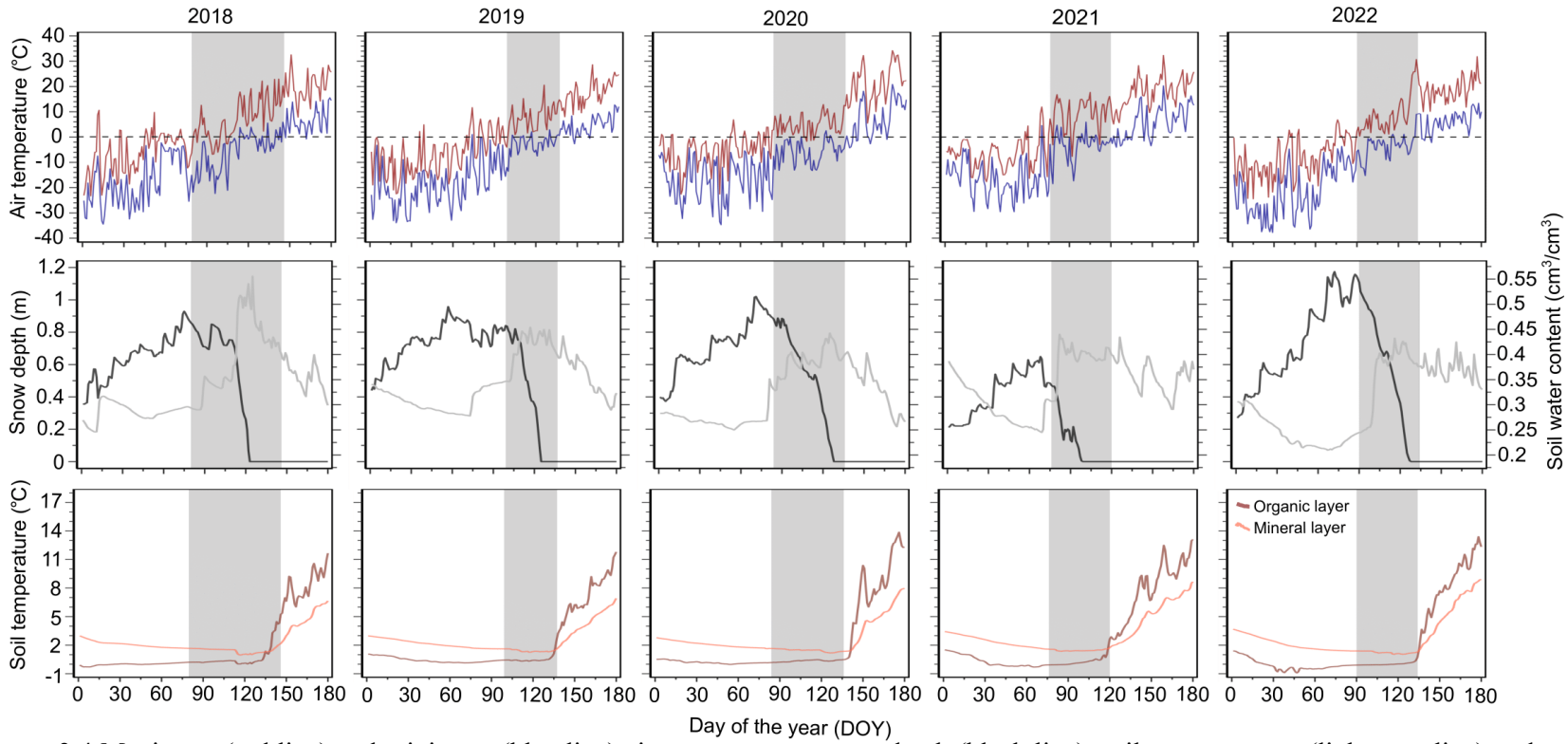

Figure 3.4 Maximum (red line) and minimum (blue line) air temperatures, snow depth (black line), soil water content (light grey line) and organic (brown line) and mineral (orange line) soil temperature. The shaded areas represent the estimated averaged extension of the sap season from 2018 to 2022.

3.4.3 Relationships between temperature and sap phenology

The variation in air temperature is expected to be the primary driver of sap exudation, which also influences the other environmental parameters. Specifically, rising air temperature reduces snowpack, leading to a subsequent increasing in soil temperature. The increase in soil water content due to the snowmelt confirms the influence of air temperature on this process.

The linear regressions between monthly temperatures and sap phenology indicated that higher temperatures in March and April were associated with an earlier timings of sap production. (Figure 4 and Table S2). Among the models, March minimum and maximum temperatures were significantly correlated with the onset of sap flow ($p < 0.05$; $R^2 = 0.83$ and 0.82, respectively). The beginning of sap production advanced by 5-6 days for each degree Celsius in March temperature (Figure 3.5). April minimum and maximum temperatures were correlated with the end of sap production ($p < 0.01$; $R^2 = 0.96$). The negative slopes indicated that higher temperatures corresponded with earlier ending of sap production. The slopes of the regressions between April temperature and the ending of sap production (-5.33 and -2.18) were steeper than those between March temperature and the onset of sap production (-2.05 and -2.33). This suggested a stronger response of the ending of sap production to temperature, and a reduction of the sap season under warming conditions (Figure 3.5).

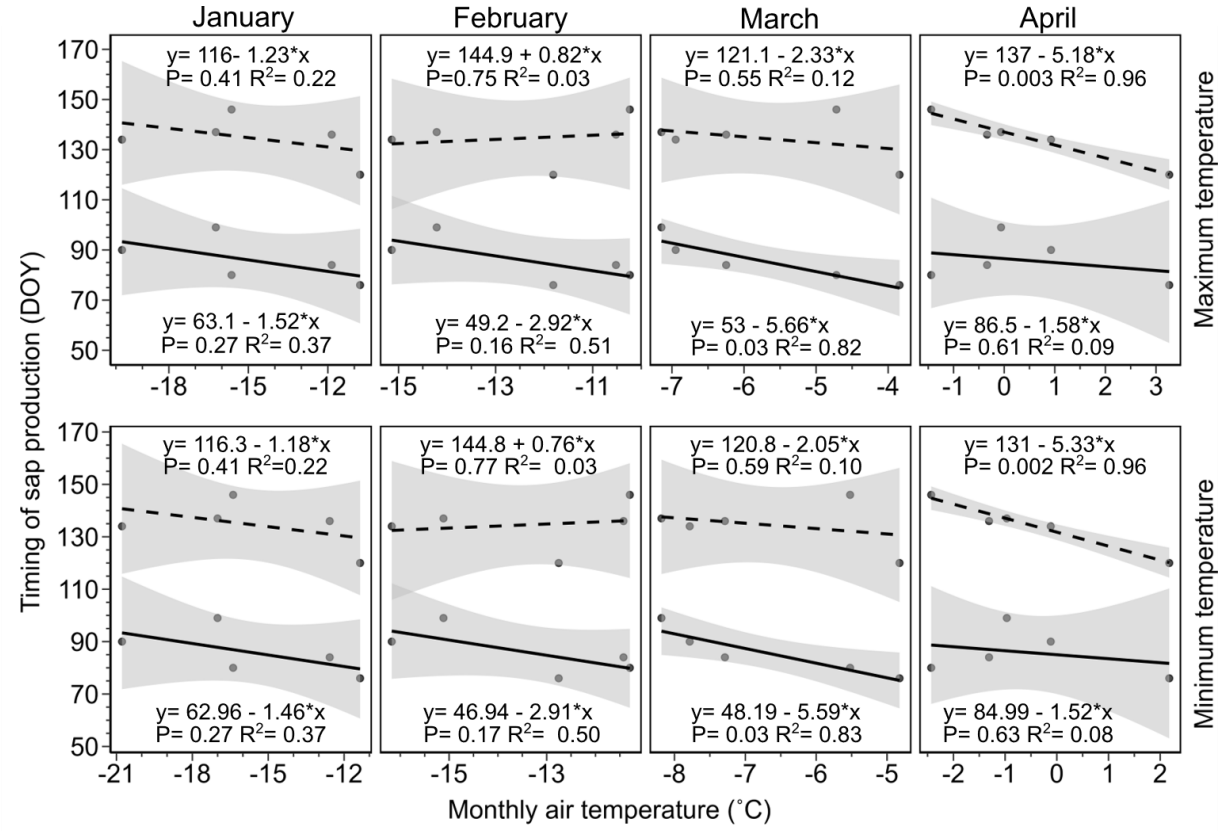

Figure 3.5 Normal linear regressions between average monthly air temperature (i.e., minimum and maximum) and the onset (solid line) and ending (dashed line) between 2018 and 2022 (round symbol). The shaded area represents the 95% confidence interval.

3.4.4 Predicting the sap season under warming scenarios

The initial model included monthly minimum, average and maximum temperatures from January to April, for a total of 12 predictors (i.e., the minimum, average and maximum temperatures from January to April). January was excluded due to its low VIP and correlation coefficients close to zero. As a result, the model was recalculated with two dependent variables (i.e., onset and ending of sap production) and 9 predictors (i.e., the minimum, average and maximum temperatures from February to April) (Figure 3.6and Table S3.1). In the revised model, March showed the strongest negative correlation with the onset of sap production, with a VIP >0.8. For the ending of sap production, April had the highest negative correlation coefficients, and a VIP >1.2. Although February was positively correlated with the ending of sap production, its VIP was <0.7 (Figure 3.6).

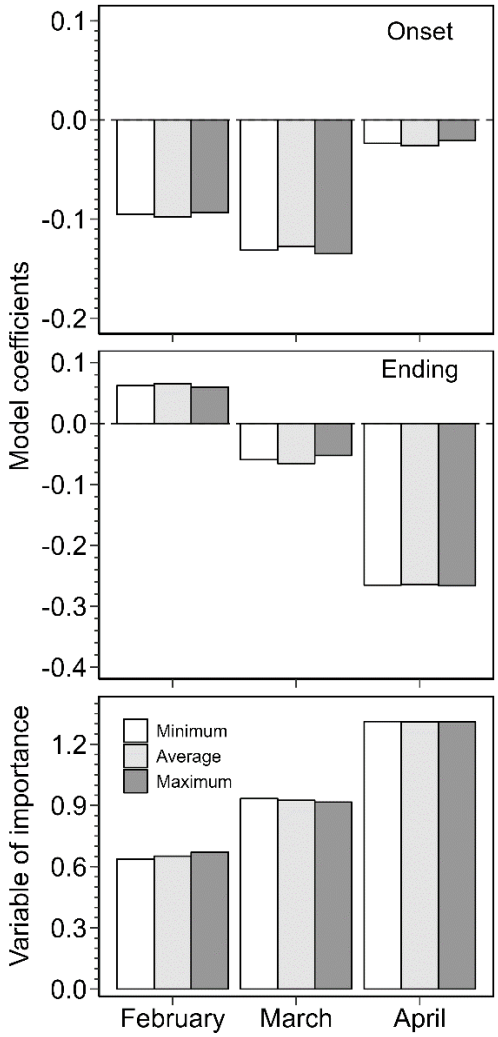

Figure 3.6 Results of PLS (partial least squares) analysis showing model coefficients and variables of importance in the projections' (VIP) values for the onset and ending and phenological phases in sugar maple between 2018 and 2022 to monthly minimum, mean and maximum temperatures.

When comparing the three greenhouse gas emissions scenarios (RCP 2.6, 4.5, and 8.5), the lower changes in temperature were observed at RCP 2.6, which is the scenario characterized by stringent mitigation efforts and high reductions of emissions (Figure 3.7). Despite inter-annual fluctuations, the warming quickly reached a plateau in 2030-2040. RCP 4.5, representing an intermediate scenario, indicated a moderate warming. In this scenario, maximum, average and minimum temperatures were projected to increase by 1.4 °C, 1.4 °C and 1.6 °C, respectively, in 2100. The higher emission pathway, RCP 8.5, showed the most pronounced increases in temperature. Temperatures were projected to rise significantly, with increases of up to 5.6 °C in 2100.

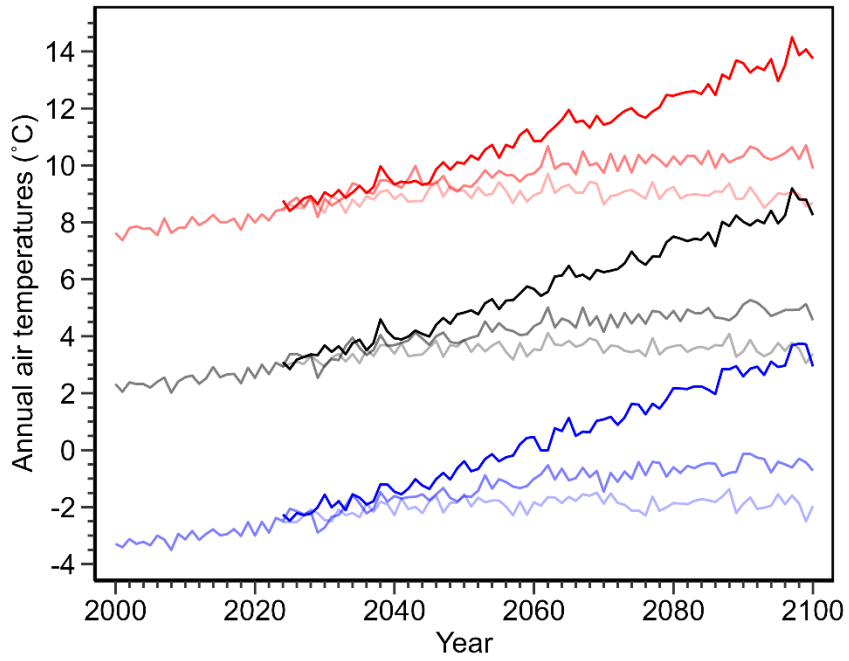

Figure 3.7 Actual and projections of the maximum (red lines), average (black lines) and minimum (blue lines) air temperatures from 2000 to 2100 of RCP 2.6 (lightest tones), RCP 4.5 (mid-tones) and RCP 8.5 (darkest tones) based on the Ouranos future climate scenarios at Simoncouche research station (48 °13'N, 71°15'W, 350 m a.s.l.).

The variation predicted in the onset and ending of sap production varied according to the RCP scenario (Figure 3.8). Across all scenarios, the end of the sap season showed greater variability and occurred earlier than the onset of sap production, consistent with the regression results. Specifically, at RCP 2.6, sap production was predicted to start 3 days earlier (DOY 83) and end 8 days earlier (DOY 126) in 2100 compared to the current conditions. At RCP 4.5, the model predicted advancements of 4 days for the onset (DOY 82) and 10 days for the ending (DOY 124) of sap production in 2100. The extreme scenario (RCP 8.5) advanced onset and ending of sap production by 20 (DOY 66) and 26 (DOY 108) days, respectively, compared to the current sap season (Figure 3.8).

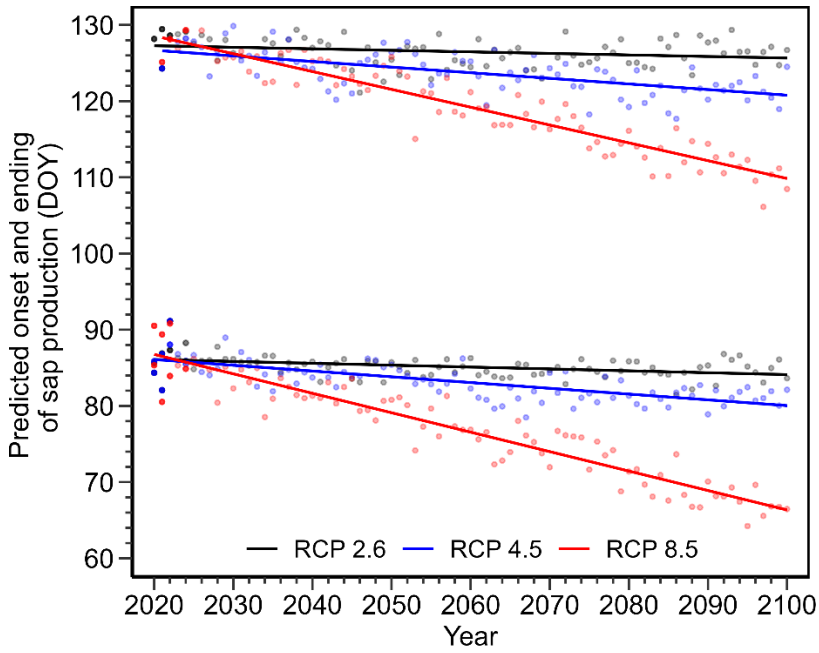

Figure 3.8 The onset and ending of sap production according to February - April temperatures predicted from 2023 to 2100 by applying the selected PLS model. The dots represent the predicted onset and ending timings of sap production.

3.5 Discussion

Climate change presents a significant threat to the maple syrup industry in a context of rising temperatures. In this study, we investigated the dynamics of sap phenology and weather conditions during the sap season to predict the timings of sap production under different climatic scenarios. Our model suggested that rising temperatures, particularly those occurring in March and April, can anticipate both the onset and ending of sap production. Compared to the current sap season, the phenological phases under extreme scenarios, i.e. RCP 8.5, could advance by 20 days for the start and 26 days for the end of sap production, including an important reduction in the duration of the sap season.

3.6 Sap dynamics and environmental conditions

The onset of sap exudation occurred in March, when temperatures started to exceed 0 °C, the snowpack reached its maximum, the soil temperature was close to 1.3 °C and soil water content was fluctuating between 0.2 and 0.3 cm^3/cm^3. The onset of sap exudation requires the occurrence of freeze-thaw cycles, which generate a positive pressure in the stem (Graf et al., 2015). Sap exudation began when the snowpack was still thick. During winter, the snow acts as an insulating layer, maintaining a stable soil temperature, thus protecting roots from the harsh

temperatures of winter and ensures water availability to resume sap exudation (Comerford et al., 2013). Given the abundant snow and cold temperature of the soil at the onset of sap exudation, the start of the sap season could be more likely influenced by daily weather conditions, particularly the warming observed at the end of winter, causing an earlier snowmelt. The increases in soil water content the beginning of sap exudation may suggest some involvement in the beginning of sap exudation, but this hypothesis needs deeper investigations to disentangle the effects of the other correlated factors.

Sap exudation was concentrated during the months of March-May, a time window in which temperatures fluctuated below and above 0 °C, snow was melting with a consequent release of abundant water, and soil temperature remained relatively constant and close to freezing point. The positive pressure of the xylem helps to rehydrate the tissues by refilling the living cells with water after winter dormancy (Schenk et al., 2021). The increased soil moisture supports the hydraulic conductivity within the tree, facilitating the movement of sap. An adequate soil moisture ensures that the roots can effectively uptake water, which is essential for maintaining the pressure gradient necessary for sap flow (Pilon et al., 1994). Several studies have linked soil water availability and soil moisture with sap flow and yield (Clark et al., 2016; Robitaille et al., 1995). Soil water availability is the source of water being transpired by the tree, which may explain some of the variability we observed among trees. Low soil moisture can lead to lower sap flow due to the loss of xylem conductivity resulting from soil water stress, leading to a reduction in water and nutrient transport.

Sap flow ceased between late April and May, when freeze-thaw cycles became rare, the snowmelt was complete, soil water content was high, and the soil started warming up. All these events correspond with the conditions required for growth reactivation in trees (Guo, Khare, et al., 2020; Rossi et al., 2011). In autumn, the trees lose water and accumulate sugars in the tissues to resist the frost conditions of winter. As temperatures rise in spring, the trees again absorb water and rehydrate the xylem. The sap, under pressure during the sugar season (Ewers et al., 2001; Melcher et al., 2003), is under tension when the water transport recovers, and no more exudation can occur (Wheeler et al., 2013). At that time, primary and secondary meristems are expected to start annual growth (Delpierre et al., 2019; Taylor & Dumbroff, 1975). According to our results, the end of sap exudation coincided with complete snowmelt and the subsequent

rise in soil temperature. These two environmental factors are well known for promoting the reactivation of root growth (Lupi et al., 2011; Radville et al., 2016), which could also affect the timing of the sap season by altering the pressure within the xylem. Overall, the end of sap production and onset of growth are probably closely linked, both being triggered by the transition from winter to spring conditions and associated to the environmental events occurring in spring. However, it remains unclear whether the growing period of the tree plays a role in the cessation of sap exudation as the physiological processes for tree growth dominated sap production mechanism by involving stored sugars, or if sap cessation is purely driven by environmental factors other than air temperature.

Sap exudation occurs during the transition period between the end of winter and beginning of spring, a time marked by significant environmental changes that trigger various physiological processes within the tree. Sap phenology is typically synchronous among trees within and across stands in the same area (Kurokawa et al., 2024). However, our study confirmed the huge variability in sap production among trees due to reasons that are not yet completely understood.

3.6.1 Relationships between air temperatures and sap phenology

Our results indicate that warming conditions, particularly if occurring in spring, can advance the timings of sap production by up to 6 days per degree Celsius in the monthly temperature. In our study site, the temperatures in March are linked to the onset of sap exudation, while the temperatures in April are correlated with the cessation of sap exudation. These results partially align with previous observations that correlate mean monthly temperatures from January to April with the timing of sap production (Duchesne et al., 2009). Moreover, maximum temperatures in February and March have been observed to influence the onset of sap flow (Duchesne et al., 2009; Houle et al., 2015), while higher temperatures in April are associated to the end of sap exudation (Duchesne et al., 2009). In comparison with the findings in the literature, our study shows that the temperatures in January and February had a marginal effect, either not significant in linear regressions or with low influence in the PLS model. This divergence is likely due to the location of our study site, which is near the northern limit of maple distribution, and with a later sugar season compared with the southern regions. At higher latitudes, cooler

temperatures tend to delay sap phenology and the successive processes involved in growth resumption, compared to observations at lower latitudes.

3.6.2 Sap phenology under greenhouse gas emission scenarios

In line with the observed relationship between sap phenology and monthly temperature, the results of PLS models confirmed the significant effect of warming on the timings of sap exudation, though the magnitude of this impact varies considerably depending on the RCP scenarios. As expected, RCP 8.5, which forecasts a substantial increase in annual mean temperature by 5.5 °C over the century, showed the most pronounced effects on the sap season. RCP 4.5 exhibited a moderate impact, while RCP 2.6 estimated minor changes in the sap season. These findings agree with previous predictions that suggested a temporal shift in sap production under climate warming (Ahmed et al., 2023; Matthews & Iverson, 2017; Skinner et al., 2010). The anticipated shift in the onset of sap exudation under all three scenarios presents a significant challenge for producers, who will need to progressively adjust their schedule of field activities to match an earlier sap flow and avoid losing part of their annual production. Our results show that the degree of change in sap phenology is highly dependent on the warming scenario.

Our model predicted that the milder winters expected under RCP 2.6 would trigger an earlier sap season with the onset and ending anticipated by 3 and 8 days, respectively. Due to the slight advancement of the sap season, the annual variability in temperature is likely to outweigh the overall warming effect predicted by the end of the century. This further highlights the need to monitor winter and spring weather conditions for more accurate short-term predictions of the conditions favorable to sap exudation (Kurokawa et al., 2022; Marquis et al., 2022). RCP 4.5 and RCP 8.5 point to a substantial advancement in both onset and ending of sap production, associated to an overall reduction of the sap season. Our model predicts advancements of 4 and 10 days for the onset and ending of sap exudation under RCP 4.5. These advancements increase to 20 and 26 days under RCP 8.5. Regardless of the future greenhouse gas emission scenario, our findings raise the need for improving short-term forecasting as a crucial step for helping producers to make adjustments and management decisions to the effects of weather on the dynamics of sap production. These practices could help producers to plan an efficient use of

equipment and human resources during these few but very productive days, which could ensure an optimal and timely collection of sap (Perkins et al., 2022).

The ending of sap production was more affected than the onset in all RCP scenarios, thus resulting in a shorter sap season. Previous studies have suggested that along with an earlier sap phenology due to climate change, sap yield could also decline due to a shorter sap season (Duchesne et al., 2009; Matthews & Iverson, 2017). Our measurements suggest that the shorter sugar season due to the advancement of sap phenology can reduce the number of productive days, thus affecting total sap yield, confirming the previous observations. In addition, warming conditions will advance the fluctuations of temperature around freezing point, leading to earlier (Ho & Gough, 2006; Skinner et al., 2010) and potentially fewer (Perkins et al., 2022) freeze-thaw cycles, which are closely connected with the best productive days (de Lima Santos et al. submitted). A reduction in freeze-thaw cycles may prevent the production of sufficient pressure in the xylem to sustain an abundant sap flow (Perkins et al., 2022).

Seventy four percent of the total sap extracted by gravity is obtained during a few productive days, representing approximately 20% of the sugar season (Kurokawa et al., 2024). Thus, a shorten sugar season could result in significant production losses, because a small reduction in the most productive days can affect the overall sap yield under gravity system. However, the relationship between sap season length and sap yield remains unclear and requires further investigation. While there is general agreement that climate change will advance the timing of sap production, its impact on overall yield is still debated. Indeed, some studies suggested that adjusting the tapping date and using technological advancements, such as the vacuum system, could mitigate the challenges posed by climate change and maintain sustained yields under less favorable conditions (Rapp et al., 2019; Skinner et al., 2010).

The findings of our study emphasize the need for producers to progressively prepare their sugarbushes earlier in a context of climate warming. In particular, the tapping schedule needs to be adjusted to match the beginning of the sap season. Any delays risk resulting in significant losses of production, mainly in the case of shorter sap seasons such as those predicted by our models. It remains unclear, however, whether the future climate scenarios will lead to an overall drop in sap yield. Technological advancements, such as improvements of the vacuum system,

could help to contrast the effects of a shorter season by maximizing the collection of sap collection during a shorter time window. Nonetheless, a major challenge in research will be enhancing our capacity to forecast the timings and productivity of sap flow before and during the sap season. Such an aim requires considerable efforts to deepen our understanding of the physiological mechanisms behind sap exudation under gravity and vacuum conditions and how these processes are influenced by a broader range of environmental factors beyond the simple thermal conditions. Moreover, a deeper monitoring of the environmental conditions of roots, especially snowmelt, soil moisture and soil temperature, will be crucial to understand the timings and dynamics of sap exudation in maple.

In this study, a four-year observation period was used to create the forecast model up to 2100, The need to increase the time dimension should be added to analyses using longer period of data collection. The integration of continuous long-term datasets with short-term forecasting capabilities enhances the capacity to capture trends, respond to variability, and guide both operational decisions and long-term adaptation strategies (Koziana et al., 2008).The strong relationship between freeze-thaw cycles and sap yield is a sensitive point to rapid climate variability in a short-term (Duchesne & Houle, 2014). A major research challenge will be improving the ability to predict sap flow timing and sap yield before and during the sap season.

Although we acknowledge the variability in sap production among trees due to reasons that are not yet fully understood, such a small number of individuals may limit the representativeness and generalizability of the results to the vast population of maple trees in Quebec or other maple syrup-producing regions. The results presented in this study apply specifically to the study site located at the northern limit of the sugar maple's distribution. Geographical limitations in the assessment of maple syrup production are often derived from specific regional datasets that may not adequately represent the broader range of production areas (Farrell, 2013). Furthermore, the relationship between sap season length and total sap yield remains uncertain and requires further investigation. The measurements suggest that a shorter sap season may reduce the number of productive days, affecting total yield under gravity systems, but the overall quantitative impact on yield is still debated and requires further elucidation (Duchesne & Houle, 2014). A deeper understanding of the physiological mechanisms underlying sap exudation under gravity and

vacuum conditions and how these processes are influenced by a wider range of environmental factors beyond simple thermal conditions should be considered in the future.

3.7 CRediT authorship contribution statement

Sara Yumi Sassamoto Kurokawa: Writing – review & editing, Writing – original draft, Visualization, Software, Investigation, Formal analysis, Data curation. **Roberto Silvestro**: Writing – review & editing, Writing – original draft. **Afsheen Khan**: Writing – review & editing. **Gian de Lima Santos**: Visualization, Validation, Software. **Sylvain Delagrange**: Writing – review & editing. **Sergio Rossi**: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

3.8 Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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3.11 Data availability

Once accepted for publication, the data that support the findings of this study will be available in Borealis, the Canadian Dataverse.

3.12 Supplementary materials

PLS model equations:
Predicted Onset = 60.31-0.33* Feb.Avg -0.69* Mar.Avg -0.10* Apr.Avg - 0.34 * Feb.Max - 0.67 *Mar.Max -0.11 *Apr.Max -0.32 *Feb.Min -0.70 * Mar.Min -0.09 *Apr.Min

Predicted Ending = 138.32 + 0.21 * Feb.Avg -0.31 * Mar.Avg -1.14* Apr.Avg + 0.22 * Feb.Max - 0.34 * Mar.Max -1.12 *Apr.Max + 0.20 * Feb.Min -0.27 * Mar.Min -1.16 * Apr.Min

Where:

Feb.Avg = Average temperature of February
Mar.Avg = Average temperature of March
Apr.Avg = Average temperature of April
Feb.Max = Maximum temperature of February
Mar.Max = Maximum temperature of March
Apr.Max = Maximum temperature of April
Feb.Min = Minimum temperature of February
Mar.Min = Minimum temperature of March
Apr.Min = Minimum temperature of April

Table S3.1 PLS model summary: Q^2, determination coefficient for leave-one-out cross validation, PVE-X, percentage variation explained for cumulative X; PVE-Y, percentage variation explained for cumulative Y.

Model summary	
Number of responses	9
Number of factors	2
Root Mean PRESS	3.08
Q^2	8.57
PVE-X	96.3
PVE-Y	73.5

Table S3.2 Summary of linear regression model between monthly temperatures (i.e., maximum- Max and minimum-Min) and sap phenology (i.e., onset and ending timings) during spring 2018 to 2022. The results include, R^2 (Coefficient of determination) and probability (P). Symbol (*) indicates significant effects ($P \leq 0.05$)

Timings	Temperature variable	R^2	P
Onset	Max-January	0.37	0.27
	Max-February	0.51	0.16
	Max-March	0.82	0.03*
	Max-April	0.09	0.61
	Min-January	0.37	0.27
	Min-February	0.5	0.17
	Min-March	0.83	0.03*
	Min-April	0.08	0.63
Ending	Max-January	0.22	0.41
	Max-February	0.03	0.75
	Max-March	0.12	0.55
	Max-April	0.96	0.003*
	Min-January	0.22	0.41
	Min-February	0.03	0.77
	Min-March	0.1	0.59
	Min-April	0.96	0.002*

CONCLUSION

The big question is what will happen to maple syrup production with climate change. Sugar maple is a prominent tree species in North America, known for its valuable sap that is used in the production of maple syrup. However, the phenology of sap production in sugar maple, and how it may be affected by climate change, is not completely well understood. Understanding the patterns and drivers of sap production is crucial for predicting the impacts of climate change on maple syrup production. This doctoral project offered valuable insights into the timing and dynamics of maple sap production, focusing on measurements at yearly, daily, and hourly resolutions. It also examined the influence of environmental factors across different locations, investigating scales from provincial to local levels and comparing various environmental variables.

This thesis explored the dynamics of sap production in sugar maple stands in Quebec, Canada, emphasizing the influence of environmental factors and methodological advancements in monitoring sap flow. By examining the influence between temperature fluctuations, sap flow patterns, and the impacts of warming conditions, this study enhances our understanding of the eco physiological processes affecting sap production. The findings of these studies confirmed the critical role of air temperature fluctuations above and below zero degrees Celsius as the primary driver of sap flow. Temperature variations consistently estimate the initiation and cessation of sap production, providing a reliable pattern for predictive models. The use of rain gauges as a novel method for continuous, high-resolution monitoring of sap flow confirmed the efficiency in collecting daily sap production. This equipment can be safely used to show detailed traditional gravity methods, enabling a more precise daily sap dynamics and data collection. By integrating innovative monitoring techniques with a detailed examination of environmental and physiological factors, this research provides an understanding of sap production dynamics and adapting to future challenges.

This study underscores the significant impact of climate change on the physiological processes driving maple sap production. The divergent advancements in sap phenology, characterized by earlier onsets and cessations of sap flow, are closely tied to changes in temperatures, with projections indicating an advancement of up to 20 days for the onset and 26 days for the end of

sap production by 2100 under the RCP 8.5 scenario. These shifts are projected to reduce the duration of the sap season, posing potential risks to maple syrup production, as producers may struggle to adapt their tapping schedules to these changes.

Moreover, the onset of sap exudation closely follows the beginning of snowmelt and the subsequent increase in soil water content, while the end corresponds to complete snowmelt and a rise in soil temperatures. This relationship highlights the interplay between snowmelt dynamics and soil moisture, which occur during the sugar season. As warming conditions continue, these environmental changes are expected to exacerbate the challenges faced by maple syrup producers, necessitating the development of adaptive strategies to address the shortening sugar season and mitigate potential losses in maple syrup yields during these few productive days. Future studies should incorporate a wider range of climate data, including snowpack dynamics, soil moisture, air pressure, and precipitation, to develop more robust predictive models of sap production. This comprehensive approach will be important in the context of climate change, as it can elucidate other climate factors affecting sap flow and the phenology of plants. Under a warming climate, the threshold of 0 °C could be reached faster, potentially advancing the metabolic processes involved in growth reactivation in trees and leading to the consequent cessation of sap.

Some methodological limitations should be acknowledged. First, although high-temporal resolution data (hourly and daily) provided valuable insights into sap production dynamics, the analyses were often constrained by short time frames or limited sampling. In particular, the reliance on data from a single year in 2018 restricted the possibility of assessing interannual variability in sap yield and timing, which is known to be heterogeneous across years and sites. The small sample size in chapter 2 and chapter 3 limited the representativeness of interindividual variability and prevented robust conclusions about spatial or latitudinal differences. In addition, sap volume per tree was not measured, which could have provided a more complete understanding of the phenology of sap production. Another limitation is related to only four years of observations—insufficient to capture long-term variability and limiting the robustness of projections to 2100. This limitation is related to the duration of the thesis project, which should be completed in 4 years. Moreover, uncertainties remain regarding the relationship between sap season length and total sap yield, as well as the physiological mechanisms driving

sap exudation under gravity and vacuum systems. These limitations highlight the need for future studies to expand temporal coverage, increase the representativeness of sampling across sites and individuals, and integrate complementary physiological and climatic data. Such efforts will be essential to strengthen predictions of sap production dynamics and to provide more reliable guidance for producers adapting to the challenges posed by climate change.

This thesis showed significant advancements in our understanding of maple sap production, but several avenues for future research remain, such the total sap yield. Sap yield and timings were not presented in this study, since a long duration of sap is not related to a greater sap yield. Due to this non-synchronism, sap yield should be carried out with a greater number of samples and for a longer experimental time to accurately observe sap production. Future research should explore the relationship between daily sap flow patterns and overall yield, considering factors such as tree size, genetics, and stand characteristics. This information is crucial for optimizing tapping practices, maximizing syrup production and better compare with sap timings.

The potential impacts of climate change on maple syrup production signalise the vulnerable regions and the possible strategies to mitigate the negative effects of climate change. Producers must not only adapt to environmental changes but also adopt strategies to maximize sap yield and maintain the economic viability of their operations. These strategies include the advancements in tapping methods, such as more precise tap sizes or vacuum systems, to optimize sap collection while minimizing tree stress. Regularly evaluating and updating tapping practices can ensure sustainable extraction without damaging the trees. Producers can also adopt high-efficiency tubing systems with improved vacuum technologies which can enhance sap yield and reduce losses. Modern systems designed for consistent sap collection, even under variable weather conditions, can contribute with the less favorable days during the sap season. Beyond syrup, producers can explore other secondary products, such as buddy syrup in beers, cosmetics and exclusive maple syrup recipes. Collaboration between academia and industry will be crucial in addressing emerging challenges, fostering innovation, and developing a comprehensive understanding of maple sap production dynamics. This partnership not only secures a vital cultural and economic resource but also enriches the knowledge that only research can provide.

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