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To flow or to grow? Impacts of tapping on sugar maple

par Hannah McNulty

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Québec, Canada

RÉSUMÉ

L'érablière est une industrie en pleine expansion en Amérique du Nord, avec plus de 60 millions d'entailles en 2022. Chaque saison, les arbres sont entaillés à des endroits différents, subissant ainsi des blessures répétées et un épuisement des ressources dû à la collecte de l'eau de sève. L'augmentation du nombre d'entailles souligne l'urgence de comprendre l'impact potentiel de la collecte de la sève sur les arbres pour assurer la santé des érablières et la longévité de l'industrie. Cette étude vise à comprendre les effets de l'entaillage et de l'exsudation de la sève sur la croissance radiale annuelle du bois et sur les caractéristiques anatomiques et fonctionnelles de l'érable à sucre (*Acer saccharum* Marsh.). Huit arbres matures situés à la limite nord de la distribution de l'érable à sucre, ont été suivis sur une période de quatre ans (2018-2021). Quatre arbres ont été entaillés pour la collecte de la sève, tandis que quatre arbres non entaillés ont servi de contrôle. Les carottes de chaque arbre ont été analysées pour déterminer la largeur des cernes, l'anatomie du bois a été évaluée pour les caractéristiques des vaisseaux et des cernes, et la conductivité hydraulique a été calculée. En 2018, la première année d'entaillage, la largeur moyenne des cernes de tous les arbres était de 2,24 mm. Les années suivantes, la largeur moyenne des cernes des arbres entaillés a varié entre 1,54 et 1,62 mm. Par rapport au témoin, les arbres entaillés présentaient des cernes plus petits dans les années suivant l'entaillage. La densité des vaisseaux a montré une croissance régulière dans les arbres non entaillés, passant de 525 vaisseaux mm^{-2} en 2018 à 767 vaisseaux mm^{-2} en 2021, tandis que la densité des vaisseaux dans les arbres entaillés est restée plus constante, passant de 431 vaisseaux mm^{-2} en 2018 à 514 vaisseaux mm^{-2} en 2021. La réduction de la densité des vaisseaux a contribué à la diminution de la conductivité hydraulique potentielle au cours des années d'étude, avec une moyenne de 0,06 et 0,11 Kg m^{-1} MPa^{-1} s^{-1} dans les arbres entaillés et non entaillés, respectivement. Aucune différence significative n'a été constatée entre les arbres entaillés et les arbres non entaillés en ce qui concerne la surface du lumen des vaisseaux. Malgré l'absence de variations significatives de la surface des vaisseaux, le diamètre hydraulique des vaisseaux des arbres entaillés (12,55 μm) était inférieur à celui des arbres témoins (13,88 μm). Les variations des caractéristiques anatomiques du xylème peuvent représenter une solution adaptative pour équilibrer l'efficacité hydraulique et le soutien structurel. Nous avons démontré l'existence d'un compromis entre l'extraction de la sève, l'épuisement des ressources et la réduction de la croissance des arbres. L'épuisement répété des ressources par l'entaillage peut avoir un effet néfaste sur la croissance de l'arbre, même si l'effet sur la fonction hydraulique reste marginal. Ces observations soulignent la nécessité d'adopter des pratiques d'entaillage durables qui tiennent compte de la santé et de la productivité à long terme des érables à sucre.

Mots-clés: Acer saccharum; extraction de sève; largeur des cernes; anatomie du bois; xylème

ABSTRACT

Maple sugaring is a rapidly growing industry in North America, with more than 60 million taps in 2022. Each season, trees are tapped in different spots, thus experiencing repeated wounding and resource depletion due to sap water collection. The rising number of taps underscores the urgency to understand the potential impact of sap collection on trees for ensuring the health of maple stands and the longevity of the industry. This study aims to understand the effects of tapping and sap exudation on annual radial wood growth and anatomical and functional traits in sugar maple (*Acer saccharum* Marsh.). Eight mature trees located at the northern limit of sugar maple distribution, were monitored over a four-year period (2018-2021). Four trees were tapped for sap collection, while four untapped trees served as a control. Tree cores from each tree were analyzed for tree-ring width, wood anatomy was assessed for vessel and ring traits, and hydraulic conductivity was calculated. In 2018, the initial tapping year, the average tree ring width from all trees was 2.24 mm. In the subsequent years, the average tree-ring width ranged between 1.54 and 1.62 mm. Compared with the control, tapped trees exhibited smaller rings in the years following tapping. Vessel density showed steady growth in untapped trees from 525 vessels mm^{-2} in 2018 to 767 vessels mm^{-2} in 2021, while the vessel density in tapped trees remained more constant ranging from 431 vessels mm^{-2} in 2018 to 514 vessels mm^{-2} in 2021. The reduction in vessel density contributed to the decrease in potential hydraulic conductivity over the study years, averaging 0.06 and 0.11 Kg m^{-1} MPa^{-1} s^{-1} in tapped and untapped trees, respectively. No significant difference in vessel lumen area between tapped and untapped trees was shown. Despite the lack of significant variations in vessel area, the hydraulic vessel diameter in tapped trees (12.55 μm) was lower than that of the control (13.88 μm). Variations in the anatomical characteristics of xylem may represent an adaptive solution to balance hydraulic efficiency with structural support. We showed evidence of a trade-off between sap extraction, resource depletion, and reduced tree growth. The repeated depletion of resources through tapping can have a detrimental effect on tree growth, even if the effect on the hydraulic function remains marginal. These insights underscore the need for sustainable tapping practices that consider the long-term health and productivity of sugar maple trees.

Keywords: *Acer saccharum*; sap extraction; tree-ring width; wood anatomy; xylem

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CHAPTER I

GENERAL INTRODUCTION

Throughout southeastern Canada and the northeastern United States, the sugar maple (*Acer saccharum* Marsh.) are found and easily recognized by their characteristic five-lobed leaves, and their colorful foliage in the autumn months (Copenheaver *et al.* 2014). Coordinating with the shortening of the summer days, the foliage ranges from yellow to red for weeks before colder temperatures and defoliation. The species growth range is restricted to cool, moist climates. Sugar maple trees are commonly found in mixed forests where they dominate other broadleaf species (Boakye *et al.* 2023). The seasonal defoliation provides biomass to forest soils, and tree litter provides wood for heating and food for wildlife (Boakye *et al.* 2023). The sugar maple creates a distinct ecosystem full of valuable resources.

Sweet sap is a key characteristic of the maple species, although the ability to maintain a heavy sap flow is limited to regions where nightly temperatures drop below 0°C and daily temperatures rise above 0°C (Copenheaver *et al.* 2014). When these conditions are met, sap flows within the xylem of the sapwood are heavy enough for potential syrup production. Sugar maple is one of the most utilized maple species for syrup production because of the large concentrations of sugars found within the xylem sap (Ouimet *et al.* 2021). During the active photosynthetic period, from leaves unfolding in spring, to leaves senescence during fall, atmospheric carbon undergoes a set of chemical reactions that lead to the formation of carbon compounds, especially in the form of carbohydrates (Muhr *et al.* 2016). These sugars play an essential role in tree functioning, as a part of them are immediately used to support plant growth and sustain metabolic processes, another fraction remains stored during tree dormancy.

In the phenological cycle of the sugar maple, tapping occurs first in the spring, followed by bud break and photosynthesis, then growth, and finally dormancy at the end of fall through the winter months. When the tree is tapped in the spring, the starch that is mobilized and removed comes from the dormancy storage, preserving the long-term carbon storage, which can refoliate the entire canopy at least one time (Muhr *et al.* 2016). After photosynthesis, the newly assimilated carbon is allocated towards repair and growth, with the extra carbon added to the long-term storage. In the second year of tapping, the tree must access long-term carbon mobilization and sap exudation storage. Consequently, later in the cycle, when the tree photosynthesizes and needs to grow, the depleted storage forces the tree to prioritize storage above growth, reducing tree ring width after the second successive year of tapping.

Maple production operations are found exclusively in North America, 77% being produced in Quebec, Canada. The maple industry has historically been successful, and continues to rapidly grow. In 1988 there was estimated to be 17.5 million sugar maple taps, whereas in 2022 there is now more than 60 million sugar maple taps (Government of Canada 2023). Sugar maple trees are not a plastic species, but they do exhibit phenotypic plasticity to some degree when certain conditions are not met (Fonti *et al.* 2010). While past research has heavily emphasized the role of climate in determining tree characteristics (Rapp et Crone 2015), another disturbance that should be considered is extraction of important resources through sap collection. Recently, evidence has been found to challenge the assumption that sap collection is sustainable. When comparing the ratio of twig length prior to and following sap extraction, a negative trend was found. This trend was further exacerbated by increasing levels of sap extraction (Isselhardt *et al.* 2016). However, much is still unknown about how the plant adjust the anatomy of the xylem tissues to meet different needs (Zanne *et al.* 2010), such as to account for sap extraction.

This study is conducted at the northern limit of the ecological niche for sugar maple trees in Quebec, Canada. The aim is to understand if tree formation is influenced by a disturbance such as tapping. I observe and record wood formation in undisturbed and disturbed maple trees, and determine if alterations in wood anatomy are present. This research seeks to determine if there are long-term impacts of tapping on sugar maple trees, potentially informing sustainable practices in the maple industry.

CHAPTER II

TO FLOW OR TO GROW? IMPACTS OF TAPPING ON SUGAR MAPLE

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2.1 Abstract

Maple sugaring is a rapidly growing industry in North America. Maples are tapped annually, thus undergoing repeated wounding and resource reduction for sap water collection. We aim to understand the effects of tapping and sap exudation on annual radial wood growth and xylem traits in sugar maple (*Acer saccharum* Marsh.), utilizing eight mature trees monitored during 2018-2021 in Simoncouche, Canada. Compared against the first year of tapping, trees exhibited a 49.7% drop in tree-ring width. Vessel density, potential hydraulic conductivity and hydraulic vessel diameter decreased, but not lumen area. We showed evidence of a trade-off between sap extraction, resource depletion, and reduced tree growth. The repeated depletion of resources through tapping can have a detrimental effect on tree growth, even if the effect on the hydraulic function remains marginal. These insights underscore the need for sustainable tapping practices that consider the long-term health and productivity of sugar maple trees.

Keywords: *Acer saccharum*; sap extraction; tree-ring width; wood anatomy; xylem

2.2 Introduction

In Canada, maple syrup production holds a symbolic place and plays a significant economic and cultural role. Indigenous peoples introduced maple sap to the European explorers who were colonizing the Americas (Koelling *et al.* 1996). This traditional knowledge has been passed down through the generations and has become an integral part of Canadian heritage. Since its introduction, the maple syrup industry has persevered through time and recently, experienced remarkable growth supporting local economies through job creation, and contributing to the economic stability and development of several regions (Whitney et Upmeyer 2004; Duchesne *et al.* 2009). Today, the maple industry is an international market, with maple syrup consumed in more than 50 countries worldwide (Pires *et al.* 2021) with exports of maple products earning 616 million dollars for Canada (Government of Canada 2023). Quebec is the world's top producing area, accounting for about 77% of all maple syrup production in North America (Government of Canada 2023). A near-constant increasing number of tapped trees is being driven by a combination of increasing demand for exportation and technological advancements in tapping (Rademacher *et al.* 2023). Although these innovations have significantly boosted production and efficiency, the impact of intensive tapping on the overall health and longevity of sugar maple trees remains uncertain, potentially jeopardizing the long-term vitality of the industry.

Traditional sap collection involved attaching a bucket to the tree trunk to gather sap exuded from freshly drilled holes in the xylem (Cirelli *et al.* 2008; Lagacé *et al.* 2019; Rademacher *et al.* 2023). Sap exudation mainly occurs due to the positive stem pressures generated by freeze-thaw cycles (Copenheaver *et al.* 2014). In the 1960s, plastic tubing systems were implemented, and vacuum pumps started to be used to manipulate the pressure differential outside the tree artificially, intensifying sap flow and yield (Lagacé *et al.* 2019; Ouimet *et al.* 2021). Nowadays, vacuum levels of up to 95 kPa make the amount of sap collected per tree on average 2-3 times greater than the historical gravity-based methods (Isselhardt *et al.* 2016; Ouimet *et al.* 2021). When tapping a tree for sap extraction, the tap hole constitutes an injury that allows air and micro-organisms to enter, potentially creating a pathway into the sapwood where bacteria could be fostered and harm the sapwood (Rademacher *et al.* 2023). To limit the risk of propagating foreign agents, the tree compartmentalizes the wound (Gibbs et Smith 1973; Perkins *et al.* 2015; van den Berg *et al.* 2016; Guillemette *et al.* 2023). The wound eventually becomes a non-conductive part of the xylem, affecting water transport and future sap production (Perkins *et al.* 2015; van den Berg *et al.* 2016). For this reason, each season, the tree is tapped in a different spot, submitting the tree to repeated wounding (Chantuma *et al.* 2009). These repeated wounds are considered defects in lumber production, which diminish the manufacturing value of maple boards (Guillemette *et al.* 2023). Furthermore, the period of sap collection coincides with the time when maples rely on the natural mobilization of stored sugars in early spring (Dietze *et al.* 2014; Muhr *et al.* 2016; Lagacé *et al.* 2019; Ouimet *et al.* 2021), thus reducing the resources for the trees.

To date, questions remain as to whether, and how much, tapping and the consequent resource depletion from sap collection affect the growth process in maple. Investigations on tree ring width addressing the issue have shown contrasting results. Some studies reported a negative correlation between tapping and growth (Copenheaver *et al.* 2014; Isselhardt *et al.* 2016), while others remained inconclusive (Ouimet *et al.* 2021). These diverging results may depend on several factors such as the frequency and intensity of tapping, tree age and environmental conditions (Ouimet *et al.* 2021; Boakye *et al.* 2023), suggesting that maples in different geographical regions and environmental stressors may respond differently to tapping.

The response of wood anatomical traits in tapped trees is a relevant issue, as it may provide important information on changes in resource allocation and the hydraulic functioning of tapped trees. Current understanding of wood anatomical traits is largely dominated by studies in conifers (Chen *et al.* 2022), while broadleaves, and especially maple, remain partially neglected. For example, anatomy of red maple in the northeastern United States demonstrates a high plasticity in relation with the length of the growing season, but seems to be unrelated to climate (Chen *et al.* 2022). Similarly, the hydraulic architecture of sycamore maple in the Mediterranean basin did not show any adjustment for efficiency or safety under climate variation, although a slight positive relationship between average vessel size and vessel density was found with precipitation (Rita 2015). Although a solid relationship between the wood traits of maple and climate stressors still remain to be demonstrated, sap exudation may result in a different outcome because it is a constant stressor that could possibly induce resource reduction to a point in which growth is negatively impacted. Therefore, a detailed assessment of tapping effects on growth performance and wood characteristics is needed to guide sustainable practices and ensure the long-term viability of the maple syrup industry.

This study takes place at the northern limit of maple, at the boarder of its ecological niche, where the individuals are most sensitive to disturbances. Such sites could provide valuable insights into carbon allocation dynamics and plant growth. We aim to understand the impact of tapping and sap collection through a gravity system on radial stem growth. We evaluate whether tapping alters xylem anatomical and functional traits, including vessel size and density, average lumen area and hydraulic conductivity, as these traits, to our knowledge remain partially unknown in the scientific literature. Accordingly, we test the hypotheses that (1) maple tapping leads to a reduced wood growth performance; and (2) tapping results in changes in xylem anatomical and functional traits, specifically leading to reduced xylem hydraulic conductivity to increase hydraulic safety.

2.3 Materials and methods

2.3.1 Study area

The study was conducted in a sugar maple (*Acer saccharum* Marsh.) stand at the Research forest of Simoncouche (48°15'N, 71°15'W), Quebec, Canada. The stand is located in a mixed forest including yellow and white birch (*Betula alleghaniensis* Britt. and *Betula papyrifera* Marsh.) and coniferous species, such as balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss.). Climatic conditions are typically boreal, characterized by cold winters with absolute minimum temperatures of -34 °C and short cool summers, with absolute maximum temperatures occasionally reaching 33 °C. The mean annual temperature is 2.2 °C. Total precipitation is 1382 mm, of which 131 mm falls as snow from November to April (Rossi *et al.* 2011). The site is situated on well-drained podzolic soil with an organic layer of 10 cm in thickness.

2.3.2 Experimental design and tapping

The study was conducted on eight co-dominant, healthy, mature sugar maples that had not been previously tapped. In spring 2018, four trees were selected for tapping, and four were used as an untapped control. The trees were tapped annually for the duration of the sugar seasons until 2021, for a total of four years. Tapped trees were >20cm in diameter at breast height (avg. 26 cm, DBH, Table S1), and only one taphole was used per year following best practices for maple syrup production (van den Berg *et al.* 2016) and Quebec government regulations (Gouvernement du Québec 2018). Control and tapped trees have an average diameter of 23.6 cm and 28.4 cm, respectively (DBH, Table S1). The tap holes, 0.8

cm (5/16 inch) in diameter and 3.5-3.8 cm in depth, were equipped with a traditional tubing spout used for the gravity sap collection system (Kurokawa *et al.* 2024).

2.3.3 Wood cores and data collection

In October 2023, after radial growth cessation, we collected four wood cores at breast height from each tree using a 5 mm increment borer (Haglöf, Sweden). The cores were collected vertically at least 12 cm apart from the tap holes to avoid interference with non-conductive wood columns associated with prior tapholes. The cores were airdried, glued into wooden blocks, and prepared for ring-width analysis by sanding, polishing, and applying chalk to enhance visibility. All samples contained the previous 8-10 tree rings, which were used to date the growth years accurately. This study only focused on years the 2018-2021.The tree-ring widths were measured using a LINTAB 6 (Rinntech, Victoria, Canada).

2.3.4 Anatomical measurements

After the tree-ring width measurements, the cores were boiled in water and sectioned using a rotary microtome into transverse sections 13-15 μm in thickness, stained with safranin for 5 minutes, rinsed in ethanol, and mounted using Eukitt Quick-hardening mounting medium. We collected anatomical images of each tree ring at ×5 magnification and measured the anatomical traits using WinCELL V.2019e (Regent Instruments Inc., Quebec, Canada)(Fig. 1). Measurements included vessel density, number of vessels, cross-sectional vessel lumen area, and area of the tree ring per each complete tree ring segment with a uniform tangential dimension. We also measured the relative horizontal and vertical positions of each vessel within the tree ring to describe the variation in vessel lumen area trend across the tree ring.

Vessel density utilized a standardized area excluding the late-wood formation portion of the ring. A loess function was applied to obtain continuous values across the tracheidogram.

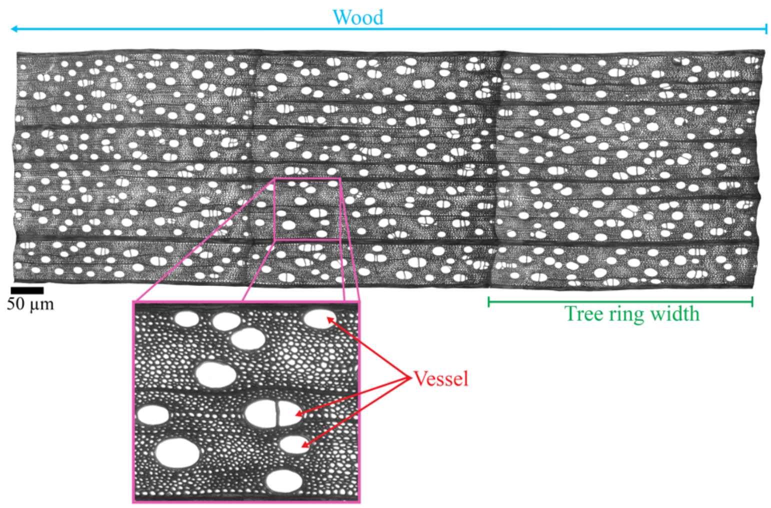

Figure 1. Cross sectional view of a tree core of a studied sugar maple tree compiled from images taken at ×5 magnification. The inset shows an actual tree ring segment where vessel measurements were taken. Ring length is uniform in the radial direction for all tree cores. Scale bar = 50 µm

Vessel diameter was calculated from the lumen area, assuming a perfect circular shape. Two different measurements of hydraulic performance were computed, the hydraulic vessel diameter (D_h, µm), i.e., the average diameter of vessels contributing most to water movement, and the potential hydraulic conductivity (K_p, Kg m^{-1} MPa^{-1} s^{-1}), i.e., the ability with which a plant can move water through the stem. The hydraulic vessel diameter within the ring was calculated by the following formula (Sperry *et al.* 1994; Buttó *et al.* 2021):

$$\boldsymbol{D_h = \frac{\Sigma_{i=1}^{n} d^5}{\Sigma_{i=1}^{n} d^4}}\,. \qquad (1)$$

Where *d* is the vessel diameter and *n* is the number of vessels in the tree ring portion. The theoretical conductivity, K_h (m^{-3} s^{-1}), of the tree ring portion was calculated by first adding up the conductance of all vessels from Hagen-Poiseuille's equation:

$$\boldsymbol{K_h = \frac{\pi \times \rho \times \Sigma D^4}{128 \times \eta}}\,. \quad (2)$$

Where ρ is the density of water (998.2 kg m^{-3}), and η is the viscosity of water (1.002 10^{-9} MPa s), both at 20 °C (Cruiziat *et al.* 2002). Then, potential conductivity, K_p, was calculated by the following formula (Zimmermann *et al.* 2021):

$$\boldsymbol{K_p = \frac{K_h}{A}}\,. \qquad (3)$$

Where K_h is the calculated theoretical hydraulic conductivity, and *A* is the area of the analyzed tree ring from the corresponding wood segment.

2.3.5 Statistical analyses

The effects of tapping on tree ring width and anatomical traits were assessed by mixed models, with the year and tapped status being included as fixed effects. The cores nested within the trees were considered as a random effect. We analyzed the effect of tapping, year, and their interaction on tree-ring width and anatomical traits using a Tukey's HSD test for multiple comparisons. We also used a Principal Component Analysis (PCA) to verify the association between growth, and anatomical and functional traits. All statistics were performed in R version 4.1.2 (R Core Team 2021) and JMP Pro 17 (JMP Statistical Discovery LLC 2022).

2.4 Results

2.4.1 Tree-ring width

In 2018, the initial year of experimentation and the first year of tapping, our analysis revealed no significant difference in tree-ring widths between treatments (tapped and untapped trees) (Fig. 2, Fig S5). In 2019, tree cores from untapped trees had a total average tree-ring width of 2.01 mm, while the tree-ring width in tapped trees reached 1.21 mm, showing a 54.4% decrease compared to the previous year (Fig. 2, Fig. S5). In the next two years (i.e., 2020 and 2021), tree-ring width in both untapped and tapped trees remained consistent with the measurements in 2019 (Fig. 2, Table S1, Fig. S5). Overall, after the first year of tapping in 2018, tapped trees exhibited a 49.7% drop in tree-ring width (Table S1, Fig. 2, Fig. S5).

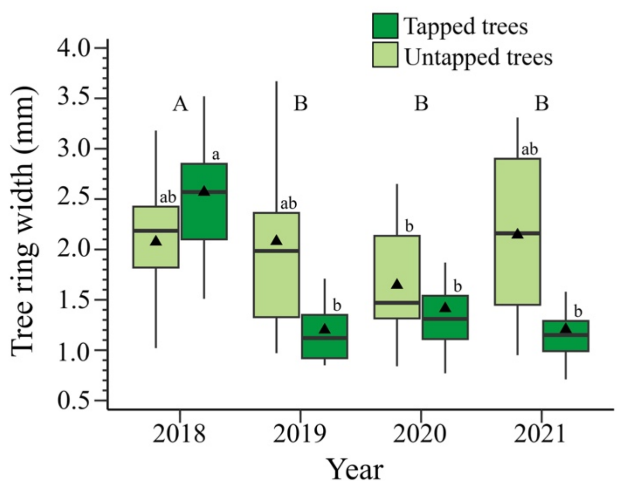

Figure 2. Tree ring width in tapped and untapped sugar maples during the four study years in Simoncouche, Quebec, Canada. The boxplots represent upper and lower quartiles, with the whiskers indicating the 10th and 90th percentiles. The horizontal black line represents the median, the black triangles represent the average. According to post-hoc analysis, tapping

treatment was significant, the lowercase letters indicate differences in the interaction between year and treatment, and the capital letters indicate differences among years.

2.4.2 Vessel lumen area

On average, no differences in vessel lumen area were observed between years, treatment, or their interaction (p>0.05, Table S2, Fig. 3a). We observed a larger variation in the size of vessels in tapped trees. Specifically, tapped trees showed an average lumen area ranging from 53.2 to 148.7 μm^2, while the lumen area of untapped trees ranged from 84.9 to 128.8 μm^2 (Fig. 3a). The vessel size throughout the tree rings showed similar trends between tapped and untapped trees, although with the average lumen area slightly higher in untapped trees (Fig. 3b).

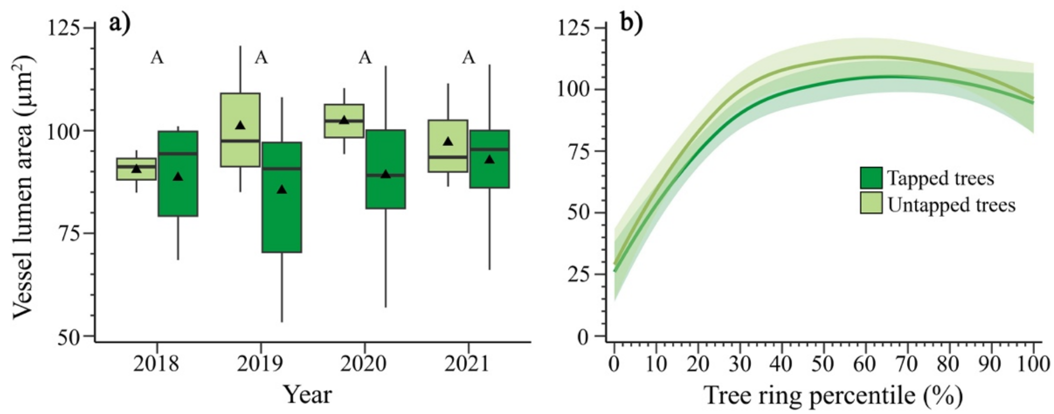

Figure 3. a) Vessel lumen area in tapped and untapped maples in Simoncouche, Quebec, Canada. The boxplots represent upper and lower quartiles, with the whiskers indicating the 10th and 90th percentiles. The horizontal black line represents the median, the black triangles represent the average. The capital letters indicate differences among years, tapping treatment and year were not significant according to post-hoc analysis. b) Trend of average vessel lumen area across tree rings in tapped and untapped maples in Simoncouche, Quebec, Canada. The trend lines result from a loess function (span 1.2), with the respective color backgrounds representing 95% confidence intervals of the loess.

2.4.3 Hydraulic conductivity

Tapping affected vessel density in the stem across years, and post-hoc tests showed significant variations in the interaction of year and treatment ($p<0.05$, Table S3, Fig. 4). In untapped trees, vessel density showed steady incremental increases over the years, starting from a density of 525 vessels mm^{-2} in 2018 to 767 vessels mm^{-2} in 2021 (Fig. 4). In tapped trees, the density remained more constant, ranging from 431 vessels mm^{-2} in 2018 to 514 vessels mm^{-2} in 2021 (Fig. 4).

Hydraulic vessel diameter showed significant variation for the interaction tapping $\times$ year. ($p<0.05$, Table S6). In 2018, the first year of tapping, no significant variations between tapped and untapped trees were observed, with hydraulic vessel diameters of 12.6 μm and 13.3 μm, respectively (Fig. 4). In 2019, the average hydraulic vessel diameter of tapped trees was statistically lower than that of untapped trees, including the significant interaction year $\times$ tapped status ($p<0.05$, Table S6, Fig. 4). The results of our model exhibited a significant effect of tapping on potential hydraulic conductivity ($p<0.05$, Table S5, Fig. 4). The potential hydraulic conductivity was 0.06 and 0.11 Kg m^{-1} MPa^{-1} s^{-1} in tapped and untapped trees in 2018, respectively. We observed a gradual increase of 0.01 Kg m^{-1} MPa^{-1} s^{-1} per year in the potential hydraulic conductivity in tapped trees over the study period, starting from 0.06 Kg m^{-1} MPa^{-1} s^{-1} in 2018 to 0.09 Kg m^{-1} MPa^{-1} s^{-1} in 2021 (Fig. 4).

Notably, there was a large amount of variation after the first year of tapping with the widest range detected in 2019 from 0.008 to 0.213 Kg m^{-1} MPa^{-1} s^{-1} (Fig. 4).

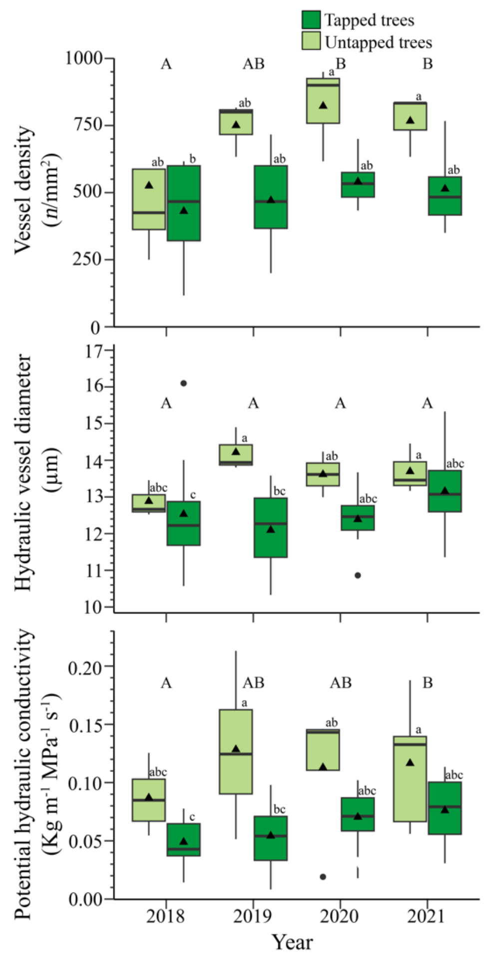

Figure 4. Hydraulic conductivity within the stem in tapped and untapped maples in Simoncouche, Quebec, Canada. The boxplots represent upper and lower quartiles, with the whiskers indicating the 10th and 90th percentiles. The horizontal black line represents the median, the black triangles represent the average. According to post-hoc analysis, tapping treatment was significant for potential hydraulic conductivity, the lowercase letters indicate differences in the interaction between year and treatment, and the capital letters indicate differences among years.

2.4.4 Principal component analysis

The relationships between anatomical and hydraulic traits were analyzed in detail by performing a PCA (Fig. S6). The two components explained 80.8% of the variance in the studied variables. The first principal component (PC1) explained 61.6% of the overall variance and was positively associated with vessel density, potential hydraulic conductivity, hydraulic vessel diameter, vessel lumen area, and had a marginal influence on tree-ring width. The second principal component (PC2), explaining 19.2% of the overall variance, was positively correlated with tree-ring width, potential hydraulic conductivity and vessel density (Fig. S6). PC2 was also negatively correlated with hydraulic vessel diameter and vessel lumen area. The distribution of the groups is heterogeneous, with tapped trees being more clustered in the bottom left quadrant, while the untapped trees are more spread out due to a higher variability.

2.5 Discussion

This study investigated the impact of gravity-based tree tapping on radial growth and anatomical and functional traits of xylem in sugar maple growing at the northern edge of its natural range in Quebec, Canada. Compared to the control, the trees tapped annually for sap collection exhibited a decrease in tree-ring width after the first year of sap production. Tree tapping had compounding effects on the overall conductivity, resulting from a lower vessel density, hydraulic vessel diameter, and potential hydraulic conductivity. These results support the initial hypothesis that tapping leads to reduced growth performance and stimulates anatomical responses in wood features within the stem that affect the functional performance of the xylem.

2.5.1 Tapping and tree ring width

Tapped trees showed a reduced annual radial growth after successive tapping years compared to untapped trees. Tapping is a human-induced disturbance to maples the effects of which are not fully understood, particularly regarding long-term growth patterns (Ouimet *et al.* 2021). During the first growing season after tapping, in 2018, tapped and untapped trees showed comparable growth. However, a reduction in growth was observed in all tapped trees from the second year of the treatment. This finding aligns with aspects of previous studies showing declines in growth performances after the first tapping year, or even later (Copenheaver *et al.* 2014; Isselhardt *et al.* 2016; Ouimet *et al.* 2021).

The significant reduction in tree-ring width observed after the first year of tapping may indicate that tapping induces a considerable stress on maple. During the active photosynthetic period, from leaf unfolding in spring to senescence in fall, atmospheric carbon is converted into carbohydrates (Muhr *et al.* 2016). These sugars support important sinks such as primary and secondary growth, and sustain a number of metabolic processes, and finally a fraction is stored during dormancy. Non-structural carbohydrates are kept in the parenchymatous tissues of wood and bark throughout winter (Chantuma *et al.* 2009; Dietze *et al.* 2014; Von Arx *et al.* 2015). During dormancy, trees rely on starch reserves for survival and cold tolerance (Wong *et al.* 2005). In late winter, these stored carbohydrates are mobilized in the form of soluble sugar, increasing sap sugar concentrations to 1-6% (Dietze *et al.* 2014; Muhr *et al.* 2016; Lagacé *et al.* 2019; Ouimet *et al.* 2021). In this framework, tapping practices affect the tree storage pool which sustains the sinks of carbon until photosynthesis from the new leaves is able to satisfy the carbon needs of the tree (Dietze *et al.* 2014; Hartmann et Trumbore 2016; Muhr *et al.* 2016). In detail, the decline in growth performance in tapped trees is likely due to the effect of tapping on the balance between carbon storage and immediate usage (Copenheaver *et al.* 2014; Isselhardt *et al.* 2016), and this impact emerges more clearly in the second year of tapping when the carbon reserves have been significantly depleted.

Our results align with other studies from other productions showing that the collection of resins from Masson pine (Chen *et al.* 2015), Aleppo pine (Papadopoulos 2013), and Maritime pine (Génova *et al.* 2014), as well as the tapping of rubber trees for latex production (Silpi *et al.* 2006; Chantuma *et al.* 2009), typically results in a sharp decrease in the trees' radial growth. At the beginning of spring, sugar is mobilized and translocated, providing the necessary energy and resources for bud break and the reactivation of growth (Lagacé *et al.* 2019; Ouimet *et al.* 2021). In this moment sap collection also takes place, likely intercepting soluble sugars during their translocation, forcing the tree to rely on older stored carbohydrates. This affects the overall carbon storage, which is likely subsequently replenished with freshly assimilated carbon at the expense of wood production.

Sap collection could potentially also affect the overall fitness of tapped trees, leading to a negative impact on tree crown vigor (Copenheaver *et al.* 2014). A reduction in the crown size contributes to a lower photosynthetic rate and, consequently, reduced carbon assimilation (Copenheaver *et al.* 2014). Additionally, the wound created by the tapping requires a mobilization of resources to be repaired which could be a significant factor affecting the growth performance (Copenheaver *et al.* 2014). It is still challenging to identify a precise cause for the observed reduction, and it is likely that all of these factors contribute, to some extent, to the overall decline in growth after the first year of tapping. This uncertainty highlights the need for a much more in-depth exploration of the effects of tapping on tree fitness and performance, especially to gain a clearer understanding of the long-term impacts of tapping on maple trees.

2.5.2 Tapping and hydraulic conductivity

Tapped trees exhibited a decrease in potential hydraulic conductivity due to reduced vessel density, without significant differences in the vessel's morphology characteristics. In particular, vessel lumen area showed no change in size based on treatments or years. It is well known that vascular plants can adjust the anatomy of vessel conduits under differing conditions, making vessels larger or smaller, to protect against embolism and meet physical strength needs (Wilmot *et al.* 2007;

Zanne *et al.* 2010; Lens *et al.* 2011; Carrer *et al.* 2015). However, maple species seem unable to respond to stressors through modifications in vessel size (Lens *et al.* 2011). This observation also aligns with what is recorded in Mediterranean maples, which showed no significant variation in vessel size when exposed to drought (Rita 2015).

Despite the lack of significant variations in vessel area, our results showed that the hydraulic vessel diameter was lower in tapped trees compared to the control. The hydraulic vessel diameter measures the average diameter of vessels contributing most to water movement (Sperry *et al.* 1994). For this reason, this trait is sensitive to small changes in vessel size of larger vessels (Sperry *et al.* 1994). Although closely linked, it is important to note that hydraulic vessel diameter only considers the vessels that are contributing to water movement, thus excluding the small vessels from the calculation (Cruiziat *et al.* 2002).

The hydraulic vessel diameter showed a significant difference between tapped and untapped trees. The years 2019 and 2020 show a difference in vessel size with tapped trees having the smaller hydraulic vessel diameter. Moreover, hydraulic vessel diameter is driven by an allometric relationship with tree size (Carrer *et al.* 2015; Buttó *et al.* 2021), and therefore remains relatively constant considering the low variability in untapped trees. Conversely, we find that tapping affects the size of the tree, and the hydraulic diameter remains lower when compared to untapped trees. The stable hydraulic vessel diameter represents a shift to decreased mechanical strength and increased efficiency within the stem during those years (Zanne *et al.* 2010; Lens *et al.* 2011).

Tapping induces a reduction in vessel density, which contributes to the observed decrease in potential hydraulic conductivity in tapped trees over the study years. In our study, vessel density remained consistent, not increasing the density of vessels per section area across years in tapped trees. In contrast, vessel density increased per year in untapped trees when new, thicker rings, had more vessels contributing to hydraulic conduction. The link between increased vessel density and increased xylem conductivity is well demonstrated in maple species (Rita 2015). Variations in wood anatomical characteristics, or in this case, the lack of the expected variations may represent an adaptive solution to balance hydraulic efficiency with structural support (Fonti *et al.* 2010). Likely, tapped trees under stress prioritize mechanical stability, while sacrificing hydraulic efficiency.

2.5.3 To flow or to grow?

Our results show that trees tapped for sap collection exhibited a quick reduction in growth performance compared to untapped trees. This study was performed by observing the effect of tapping on growth performances collecting sap utilizing a gravity tapping system. However, to maximize yield, modern producers are equipped with vacuum systems (Isselhardt *et al.* 2016; Lagacé *et al.* 2019; Ouimet *et al.* 2021), that can yield twice as much sap as gravity extraction (Lagacé *et al.* 2019). Considering the significant reduction in growth with gravity sap collection shown in this study, utilizing vacuum tapping and doubling the extraction rate could potentially further impact the growth performance of tapped trees. However, the vacuum technique has some physiological advantages, such as smaller diameter spouts reducing the amount of internal compartmentalization (Perkins *et al.* 2015), and more rapid repair of the taphole (Staats et Kelley 1996). However, further studies investigating the growth performances and more in general the global carbon budget of trees submitted to sap collection with or without vacuum systems are needed in order to understand the amplitude of the impact of this practice on maple fitness.

This study takes place at the northern limit of the maple range in northeastern North America. Previous studies assessing the impact of tapping on maple tree growth across latitudinal gradients have yielded contrasting results, demonstrating that the relationship between tapping practices and reduced growth still needs deeper investigation (Copenheaver *et al.* 2014; Ouimet *et al.* 2021). Considering the previous studies and our results, it is likely that at higher latitudes of the maple syrup production area, the shorter growing season, decreased photosynthetic activity, and cooler temperatures can contribute to the reduced growth performance compared to maple trees in warmer climates (Hartmann et Trumbore 2016). These pieces of evidence are important factors in potentially limiting the exploitation of sap production in the northern regions.

This study highlights the need for further research into the long-term impacts of tapping with a vacuum system, particularly under varying climactic conditions. While innovations like vacuum systems have significantly boosted production, their effects on the overall health and longevity of maple remain uncertain. Therefore, gaining new insights into the impact of tapping on growth performance is essential to refine current extraction practices while ensuring the long-term sustainability of the industry.

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2.7 Author contributions

H.M, S.R and R.S conceived and designed the study; H.M and S.R conducted data gathering; H.M analyzed the data and led the writing of the manuscript; S.R, R.S, F.G, M.H, contributed critically to the drafts; All authors have final approval for publication.

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2.9 Competing interests

The authors declare no competing interests.

2.10 Data and coding availability statement

Data associated with this paper will be available in Borealis, the Canadian Dataverse Repository, once accepted for publication.

2.11 Supplementary materials

Table S1. Diameter at breast height (DBH, 1.30m) and total height of the eight monitored trees.

Tree	Treatment	DBH (cm)	Tree Height (m)
1	Control	22.9	12.7
2	Control	29.1	12.1
3	Control	21.6	14.3
4	Control	20.9	10.8
5	Tapped	33.5	14
6	Tapped	21.2	13.6
7	Tapped	25.0	12.2
8	Tapped	33.8	10.5

Table S2.Effects of year and tapping on tree ring width in sugar maple trees sampled in Simoncouche, Quebec, Canada. The measurements were evaluated by mixed effect models. One and three asterisks indicate P < 0.05 and P < 0.001, respectively.

Fixed Effect	Estimate	Std. error	t-value
Intercept	240.89	15.75	15.29***
Year 2019-2018	-71.04	12.48	-5.69***
Year 2020-2019	-7.86	12.48	-0.63
Year 2021-2020	5.07	12.48	0.41
Tapping	-32.44	15.75	2.06*
Tapping * Year 2019-2018	-78.09	12.48	-6.26***
Tapping * Year 2020-2019	41.26	12.48	3.31***
Tapping * Year 2021-2020	-33.80	12.48	-2.71***

Table S3. Effects of year and tapping on vessel lumen area in sugar maple trees sampled in Simoncouche, Quebec, Canada. The measurements were evaluated by mixed effect models. One and three asterisks indicate P < 0.05 and P < 0.001, respectively.

Fixed Effect	Estimate	Std. error	t-value
Intercept	95.49	4.87	19.62***
Year 2019-2018	-0.92	4.95	-0.18
Year 2020-2019	2.24	5.27	0.43
Year 2021-2020	-0.29	5.28	-0.06
Tapping	0.87	4.87	0.18
Tapping * Year 2019-2018	8.55	4.95	1.73
Tapping * Year 2020-2019	0.87	5.27	0.17
Tapping * Year 2021-2020	-11.20	5.28	-2.11*

Table S4. Effects of year and tapping on vessel density in sugar maple trees sampled in Simoncouche, Quebec, Canada. The measurements were evaluated by mixed effect models. One and three asterisks indicate $P < 0.05$ and $P < 0.001$, respectively.

Fixed Effect	Estimate	Std. error	t-value
Intercept	484.99	46.71	10.38***
Year 2019-2018	128.57	56.58	2.27*
Year 2020-2019	42.33	64.33	0.66
Year 2021-2020	-9.99	64.92	-0.15
Tapping	-52.48	46.71	-1.12
Tapping * Year 2019-2018	-89.30	56.58	-1.58
Tapping * Year 2020-2019	26.62	64.33	0.41
Tapping * Year 2021-2020	-10.94	64.92	-0.17

Table S5. Effects of year and tapping on potential hydraulic conductivity in sugar maple trees sampled in Simoncouche, Quebec, Canada. The measurements were evaluated by mixed effect models. One and three asterisks indicate $P < 0.05$ and $P < 0.001$, respectively.

Fixed Effect	Estimate	Std. error	t-value
Intercept	0.07	0.009	7.45***
Year 2019-2018	0.022	0.011	2.16*
Year 2020-2019	-0.001	0.011	-0.10
Year 2021-2020	0.007	0.011	0.65
Tapping	-0.019	0.009	-2.17*
Tapping * Year 2019-2018	-0.016	0.010	-1.53
Tapping * Year 2020-2019	0.014	0.011	1.32
Tapping * Year 2021-2020	0.000094	0.011	0.01

Table S6. Effects of year and tapping on hydraulic vessel diameter in sugar maple trees sampled in Simoncouche, Quebec, Canada. The measurements were evaluated by mixed effect models. One and three asterisks indicate $P < 0.05$ and $P < 0.001$, respectively.

Fixed Effect	Estimate	Std. error	t-value
Intercept	12.91	0.30	42.79***
Year 2019-2018	0.23	0.28	0.81
Year 2020-2019	0.07	0.29	0.24
Year 2021-2020	0.11	0.29	0.37
Tapping	0.35	0.30	1.17
Tapping * Year 2019-2018	0.69	0.28	2.46*
Tapping * Year 2020-2019	-0.21	0.30	-0.71
Tapping * Year 2021-2020	-0.50	0.30	-1.68

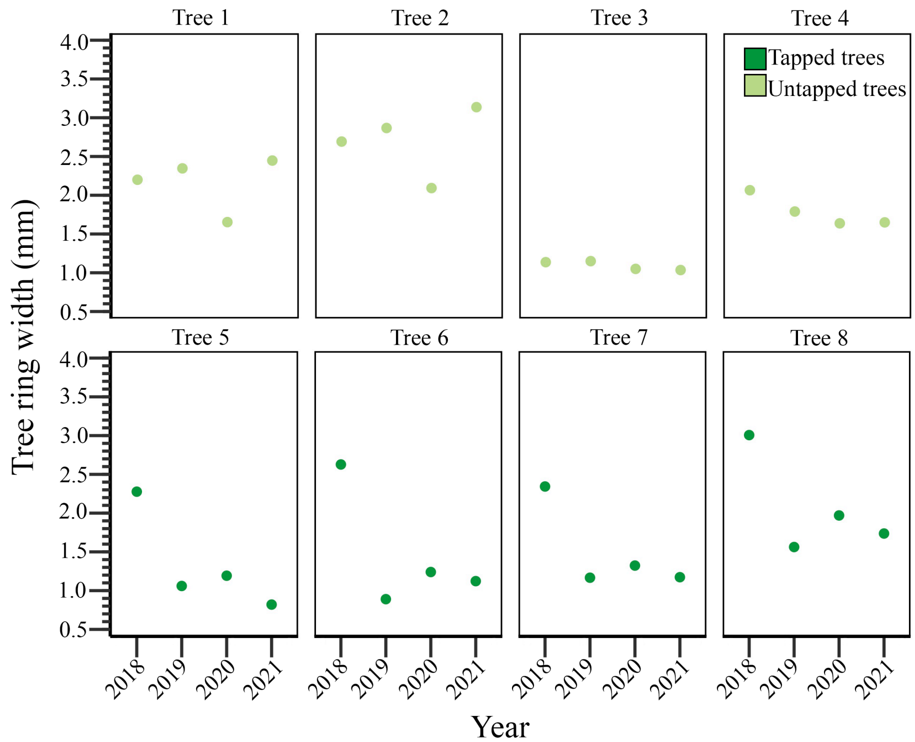

Figure S5. Average sugar maple tree ring width by each year, tree, and treatment in Simoncouche, Quebec, Canada

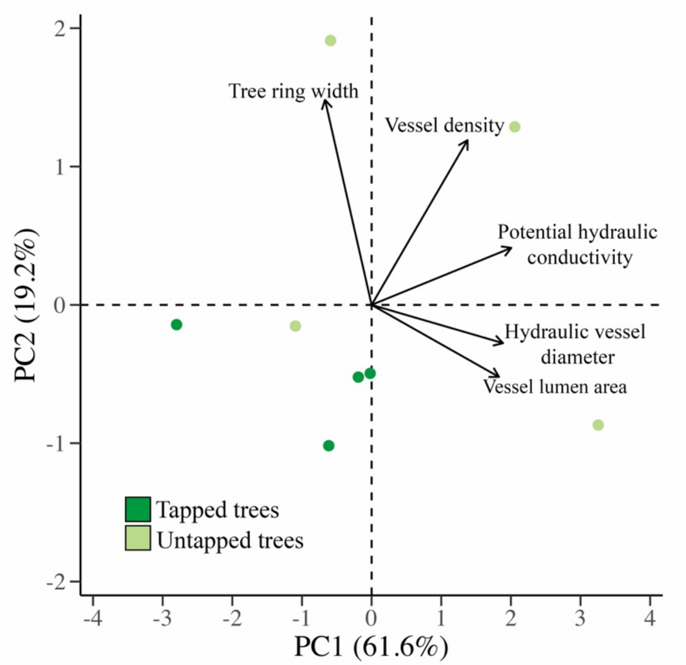

Figure S6. Variability between wood anatomical traits in tapped and untapped maples in Simoncouche, Quebec, Canada based on principal component analysis.

CHAPTER III

GENERAL CONCLUSION

This study provides insights into the impact of gravity-based tree tapping on sugar maple trees at the northern limit of their current range in Quebec, Canada. Through comparison of tapped and undisturbed maple trees we demonstrate that the sap exudation process significantly alters the physiology of the tree. Specifically, the decrease in average tree-ring width in the years after tapping demonstrates the stress and lack of carbon caused by tapping. The potential reallocation of resources within the tree also effects the xylem formation and resulting functional traits. Within the xylem of a tapped tree there is a reduction in vessel density, likely to prioritize structural stability over hydraulic efficiency. Overall, these findings suggest that physiological responses of maple trees to tapping and sap exudation are complex and require further studies.

Moving forward, this study highlights the importance and need for long term monitoring of both traditional gravity-based sap extraction and modern vacuum sap extraction methods. Utilizing similar methods to this study, a comparison of wood anatomical characteristics and functional characteristics from wood of the two extraction methods could result in a deeper understand of how the current tapping practices effect maple tree stands. A long-term monitoring study could also shed light on the influence of climate and its potential impact on wood formation. As the maple industry continues to expand, understanding the impacts of tree tapping will be vital in ensuring tapping practices remain sustainable and promote tree health for future generations.

REFERENCES

Boakye EA, Bergeron Y, Drobyshev I, Beekharry A, Voyer D, Achim A, Huang J-G, Grondin P, Bédard S et Havreljuk F. 2023. Recent decline in sugar maple (*Acer saccharum* Marsh.) growth extends to the northern parts of its distribution range in eastern Canada. Forest Ecology and Management, 545 : 121304.

Buttó V, Millan M, Rossi S et Delagrange S. 2021. Contrasting carbon allocation strategies of ring-porous and diffuse-porous species converge toward similar growth responses to drought. Frontiers in plant science, 12 : 760859.

Carrer M, von Arx G, Castagneri D et Petit G. 2015. Distilling allometric and environmental information from time series of conduit size: the standardization issue and its relationship to tree hydraulic architecture. Tree physiology, 35 : 27-33.

Chantuma P, Lacointe A, Kasemsap P, Thanisawanyangkura S, Gohet E, Clément A, Guilliot A, Améglio T et Thaler P. 2009. Carbohydrate storage in wood and bark of rubber trees submitted to different level of C demand induced by latex tapping. Tree physiology, 29 : 1021-1031.

Chen F, Yuan Y-j, Yu S-l et Zhang T-w. 2015. Influence of climate warming and resin collection on the growth of Masson pine (*Pinus massoniana*) in a subtropical forest, southern China. Trees, 29 : 1423-1430.

Chen Y, Rademacher T, Fonti P, Eckes-Shephard AH, LeMoine JM, Fonti MV, Richardson AD et Friend AD. 2022. Inter-annual and inter-species tree growth explained by phenology of xylogenesis. New Phytologist, 235 : 939-952.

Cirelli D, Jagels R et Tyree MT. 2008. Toward an improved model of maple sap exudation: the location and role of osmotic barriers in sugar maple, butternut and white birch. Tree physiology, 28 : 1145-1155.

Copenheaver CA, McCune RC, Sorensen EA, Pisaric MF et Beale BJ. 2014. Decreased radial growth in sugar maple trees tapped for maple syrup. The Forestry Chronicle, 90 : 771-777.

Cruiziat P, Cochard H et Améglio T. 2002. Hydraulic architecture of trees: main concepts and results. Annals of forest science, 59 : 723-752.

Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD et Vargas R. 2014. Nonstructural carbon in woody plants. Annual review of plant biology, 65 : 667-687.

Duchesne L, Houle D, Côté M-A et Logan T. 2009. Modelling the effect of climate on maple syrup production in Québec, Canada. Forest Ecology and Management, 258 : 2683-2689.

Fonti P, von Arx G, García-González I, Eilmann B, Sass-Klaassen U, Gärtner H et Eckstein D. 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytologist, 185 : 42-53.

Génova M, Caminero L et Dochao J. 2014. Resin tapping in *Pinus pinaster*: effects on growth and response function to climate. European journal of forest research, 133 : 323-333.

Gibbs CB et Smith HC. 1973. Cambial dieback and taphole closure in sugar maple after tapping. Research Note NE-155 Upper Darby, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station 4p, 155.

Gouvernement du Québec. 2018. Regulation respecting sugar bush management in forests in the domain of the State. Dans : Éditeur officiel du Québec Q éd., Gazette Officielle, Sustainable Forest Development Act.

Government of Canada. 2023. Statistical Overview of the Canadian Maple Industry. Minister of Agriculture and Agri-Food.

Guillemette F, Michaud-Larochelle S, Bédard S et Tremblay S. 2023. Assessing the effects of sugar maple tapping on lumber production. The Forestry Chronicle, 99 : 150-160.

Hartmann H et Trumbore S. 2016. Understanding the roles of nonstructural carbohydrates in forest trees–from what we can measure to what we want to know. New Phytologist, 211 : 386-403.

Isselhardt ML, Perkins TD, van den Berg AK et Schaberg PG. 2016. Preliminary results of sugar maple carbohydrate and growth response under vacuum and gravity sap extraction. Forest Science, 62 : 125-128.

JMP Statistical Discovery LLC. 2022. JMP® 17 Automation Reference. Dans : LLC JSD éd., JMP Statistical Discovery LLC, Cary, NC, USA.

Koelling MR, Laing F et Taylor F. 1996. Chapter 2: History of maple syrup and sugar production. Dans : North American Maple Syrup Producer's Manual Ohio State University (OSU).

Kurokawa S, Bhatt G, De Lima Santos G, Silvestro R, Delagrange S et Rossi S. 2024. Measuring natural sap production in sugar maple at daily temporal resolution. iForest - Biogeosciences and Forestry, 17 : 323-330.

Lagacé L, Camara M, Martin N, Ali F, Houde J, Corriveau S et Sadiki M. 2019. Effect of the new high vacuum technology on the chemical composition of maple sap and syrup. Heliyon, 5.

Lens F, Sperry JS, Christman MA, Choat B, Rabaey D et Jansen S. 2011. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. New Phytologist, 190 : 709-723.

Muhr J, Messier C, Delagrange S, Trumbore S, Xu X et Hartmann H. 2016. How fresh is maple syrup? Sugar maple trees mobilize carbon stored several years previously during early springtime sap-ascent. New Phytologist, 209 : 1410-1416.

Ouimet R, Guillemette F, Duchesne L et Moore J-D. 2021. Effect of tapping for syrup production on sugar maple tree growth in the Quebec Appalachians. Trees, 35 : 1-13.

Papadopoulos A. 2013. Resin tapping history of an aleppo pine forest in Central Greece. The Open Forest Science Journal, 6.

Perkins TD, Isselhardt M et Van Den Berg A. 2015. Recent trends in the maple industry III-changes in sap yield. The Maples News : 11.

Pires MA, Andrade RS et Iglesias M. 2021. Effect of Temperature on Physical Properties of Canadian Maple (*Acer saccharum* Marsh.) Syrup. J Bioeng Tech Appl Health, 4 : 30-36.

R Core Team. 2021. R: A language and environment for statistical computing (Version 4.1.2). R Foundation for Statistical Computing, Vienna, Austria.

Rademacher T, Cliche M, Bouchard É, Kurokawa SYS, Rapp J, Deslauriers A, Messier C, Rossi S, Dupras J, Filotas É et Delagrange S. 2023. TAMM review: On the importance of tap and tree characteristics in maple sugaring. Forest Ecology and Management, 535 : 120896.

Rapp JM et Crone EE. 2015. Maple syrup production declines following masting. Forest Ecology and Management, 335 : 249-254.

Rita A. 2015. Functional responses of Sycamore maple and Italian alder to the Mediterranean climate. Trees, 29 : 1907-1916.

Rossi S, Morin H et Deslauriers A. 2011. Multi-scale influence of snowmelt on xylogenesis of Black Spruce. Arctic, Antarctic, and Alpine Research, 43 : 457-464.

Silpi U, Thaler P, Kasemsap P, Lacointe A, Chantuma A, Adam B, Gohet E, Thaniswanyankura S et Améglio T. 2006. Effect of tapping activity on the dynamics of radial growth of *Hevea brasiliensis* trees. Tree physiology, 26 : 1579-1587.

Sperry JS, Nichols KL, Sullivan JE et Eastlack SE. 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology, 75 : 1736-1752.

Staats LJ et Kelley JW. 1996. Field evaluation of the IPL VacuSpout for maple sap collection. Northern journal of applied forestry, 13 : 171-174.

van den Berg AK, Perkins TD, Isselhardt ML et Wilmot TR. 2016. Growth rates of sugar maple trees tapped for maple syrup production using high-yield sap collection practices. Forest Science, 62 : 107-114.

Von Arx G, Arzac A, Olano JM et Fonti P. 2015. Assessing conifer ray parenchyma for ecological studies: pitfalls and guidelines. Frontiers in plant science, 6 : 166464.

Whitney GG et Upmeyer MM. 2004. Sweet trees, sour circumstances: the long search for sustainability in the North American maple products industry. Forest Ecology and Management, 200 : 313-333.

Wilmot T, Perkins T et Van den Berg A. 2007. Vacuum sap collection: how high or low should you go. Maple syrup digest, 19 : 27-32.

Wong B, Staats L, Burfeind A, Baggett K et Rye A. 2005. Carbohydrate reserves in *Acer saccharum* trees damaged during the January 1998 ice storm in northern New York. Canadian journal of botany, 83 : 668-677.

Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SE et Coomes DA. 2010. Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. American Journal of Botany, 97 : 207-215.

Zimmermann J, Link RM, Hauck M, Leuschner C et Schuldt B. 2021. 60-year record of stem xylem anatomy and related hydraulic modification under increased summer drought in ring- and diffuse-porous temperate broad-leaved tree species. Trees, 35 : 919-937.