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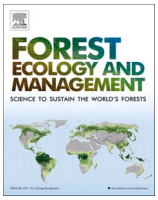

Tamm reviews

TAMM review: On the importance of tap and tree characteristics in maple sugaring

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A B S T R A C T

Maple sugaring mainly uses sugar and red maples (*Acer saccharum* and *Acer rubrum*) by tapping them for sap in the leafless-state across large portions of their ranges. How much sap exudes from a tap hole and how sweet this sap is, can vary substantially. Year-to-year variation in sap yield and sugar content can be primarily traced to differences in meteorological conditions that drive sap runs. Yet, how much of the total variation in sap yield and sugar content is linked to the year, site, species, tree, or tap has not been investigated systematically.

Here, we reviewed the literature and also compiled a dataset of sap yield and sugar content from gravity taps on 324 red and sugar maples. The compiled data originates from multiple studies at ten sites across a large proportion of the ranges of sugar and red maple and stretches over eleven years. Using about 15 000 data points on sap yield and sap sugar content, we analysed the importance of tap and tree characteristics, such as height of the tap hole on the stem or diameter at breast height. We also review previous research on the importance of tap and tree characteristics in maple sugaring. Moreover, we partition variability in the data to attribute it to species, site, tree, year, and tap characteristics.

Our results indicate that species, site and tree characteristics are the three largest sources of variability with regards to sap yield and the sap's sucrose concentration. However, differences between years and tap characteristics, which were found to be comparatively minor sources of variability in sap yield and the sap's sucrose concentration, have attracted far more attention in the past. We advocate for the continuation and expansion of systematic measurements of sap characteristics across a network of sites to further improve our understanding of maple sugaring. Such an understanding will be instrumental to prepare maple sugaring operations against the imminent effects of the climate and biodiversity crises and ensure their sustainability to perpetuate this traditional activity.

1. Introduction

Maple sugaring is a rapidly growing industry in North America with more than 60 million taps in 2022. Maple sugaring relies mostly on mature maple trees. During the freeze–thaw cycles, a positive pressure develops in the xylem of maples due to physicochemical interactions between the sap and the specific anatomical traits of the xylem (Ceseri and Stockie, 2013; Graf et al., 2015; Schenk et al., 2021). This positive pressure, that is driven by freeze–thaw cycles, allows the extraction of sweet maple sap when tapping the stem. For each tap, the extracted volume and its soluble sugar content determine the total maple sugar yield. This maple sugar can be transformed into a variety of products; most notably maple syrup.

Variations in the amount and sweetness of the sap have been studied extensively over the past century, in particular in relationship to weather, tap and tree characteristics. However, results with regard to the role of tap and tree characteristics on sap yield and sugar content were often contradictory, site-dependent, or inconclusive (Blum, 1973; Gregory and Wargo, 1986; Jones et al., 1903; Koelling and Blum, 1967; Kolb et al., 1992; Laing and Howard, 1990; Larochelle, 1998; Leaf and Watterston, 1964; Morrow, 1963; Morselli et al., 1978; Perkins et al., 2021; Rapp and Crone, 2015; Taylor, 1956; Wallner and Gregory, 1980; Wilmot et al., 1995).

In the past, most of the literature focused on the relationships of

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meteorological conditions with sap yield (Ceseri and Stockie, 2013; Graf et al., 2015; Tyree, 1983). Meteorological variables have been linked to both sap yield and sugar content (Duchesne and Houle, 2014; Houle et al., 2015; Pothier, 1995; Rapp et al., 2019). Variations in sap yield and sugar content due to non-climatic factors, such as tap, tree, and site characteristics, have long been suggested as an additional source of variation (Taylor, 1956), yet they have received much less attention. Previous studies on tap and tree characteristics were often limited to single sites, small sample sizes (typically $n < 30$), thus their results were often inconclusive and/or they were published in the grey literature. Despite many hypotheses being raised and disseminated over the years, we still lack solid theoretical and empirical foundations of the effects of tap and tree characteristics on maple sugaring. To-date, there is no review or *meta*-analysis of the importance of taps and trees in maple sugaring synthesising our knowledge.

Here, our aim is two-fold. First, we present existing literature on the effects of tap and tree characteristics on the total volume of maple sap that can be extracted from a tap during a sugar season (hereafter referred to as sap yield) and the sap's sucrose concentration by weight. Sap sucrose concentration (henceforth sap sugar content) constitutes more than 99% of total sugars in maple sap and can be reliably and easily estimated from refractometry in the field (Gregory and Hawley, 1983). Second, we carry out a *meta*-analysis involving about 15 000 data points on sap yield and sap sugar content on 324 trees belonging to the two most commonly exploited species for maple sugaring (259 sugar maples [*Acer saccharum* Marsh.] and 65 red maples [*Acer rubrum* L.] from ten sites across northeastern North America (Fig. 1). The dataset combines records from the literature and additional collections made for this study and represents a large part of the distribution of both sugar and red maple (Fig. 1). All included data comes from trees, that were gravity tapped once a year with one, two, or three tap holes per season for up-to eleven years. This *meta*-analysis allowed to (i) quantify the variability in sap yield and sugar content that can be ascribed to species, years, sites, trees, and taps and (ii) assess the importance of a selection of tap and tree characteristics on maple sap production for which we had sufficient ancillary data.

In the following sections, we first present current knowledge on water and solute transport during the sugaring season (Section 2), our methods (Section 3), and the specific effects of various characteristics of tap holes (Section 4) and trees (Section 5) on sap yield and sugar content. In order to provide guidelines for sustainable management practices, we require knowledge on the sources of the variability in maple sugar yields. Therefore, we finish the review by briefly discussing the different sources of variability in sap production and how they may change in the future due to interactions between tree physiology, maple sugaring, and shifts in climate and disturbance regimes (Section 6).

2. Mechanisms underlying sap yield and sap sugar content: Water and solute transport in the leafless state of maples

The positive stem pressure necessary for maple sugaring can only develop in the leafless state, when water transport inside the stem is not governed by cohesion-tension. Nonetheless, water and solute transport is still reliant on the same wood anatomical structures with resistance to flow determining the dominant direction of transport (Fig. 2). As a diffuse-porous species, vessels are homogeneously distributed in the transversal plane in maples (Fig. 2c & d), where bulk water transport occurs predominantly in vessels of the outer portion of the xylem (Pappas et al., 2022). While water transport follows primarily the longitudinal orientation of these xylem conduits, the vessels within and across tree rings are connected, thus enabling some circumferential and radial transport (Wason et al., 2019).

Contrary to other species, maples retain a relatively high concentration of soluble sugars in the xylem towards the end of dormant period (Larochelle et al., 1998). Red maples reach a seasonal maximum of soluble sugar concentrations in the xylem during the winter (Furze et al., 2019) with higher concentrations occurring close to the bark (Furze et al., 2020). During the sugaring season, extracted sap sucrose presumably originates from local nonstructural carbon reserves in adjacent parenchyma cells or hydrolised starch reserves in the roots. The extracted soluble sugars may be up to a decade-old (Muhr et al., 2016) and they are transported by concentration and temperature gradients between the roots and canopy (Sperling et al., 2017).

During maple sugaring, the sweet xylem sap exudes from freshly cut holes in the xylem, commonly a drilled hole, due to the positive stem pressures developing as a result of freeze–thaw cycles. The positive pressure is a purely physiochemical phenomenon, whose mechanism is well constrained (Ceseri and Stockie, 2013; Graf et al., 2015). The build-

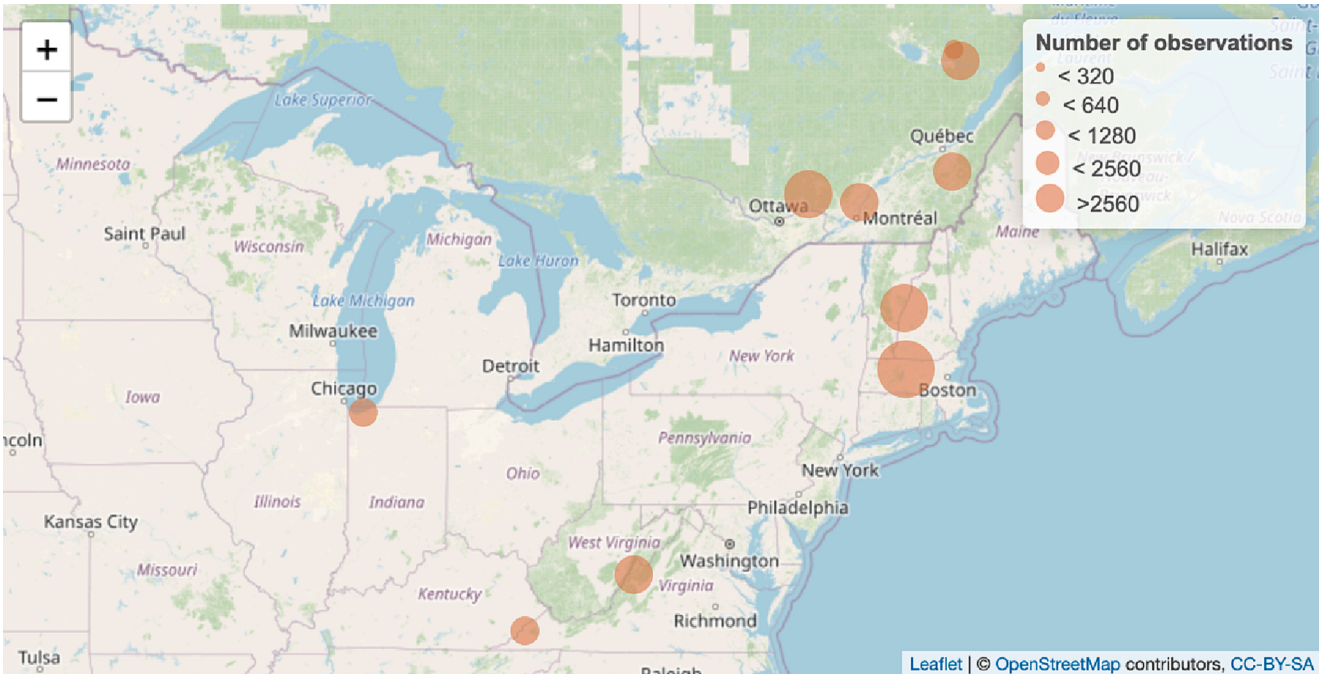

Fig. 1. Map of ten sites included in the analysis. Each dot represents a sample site with the dots size indicating the number of observations of sap yield per site.

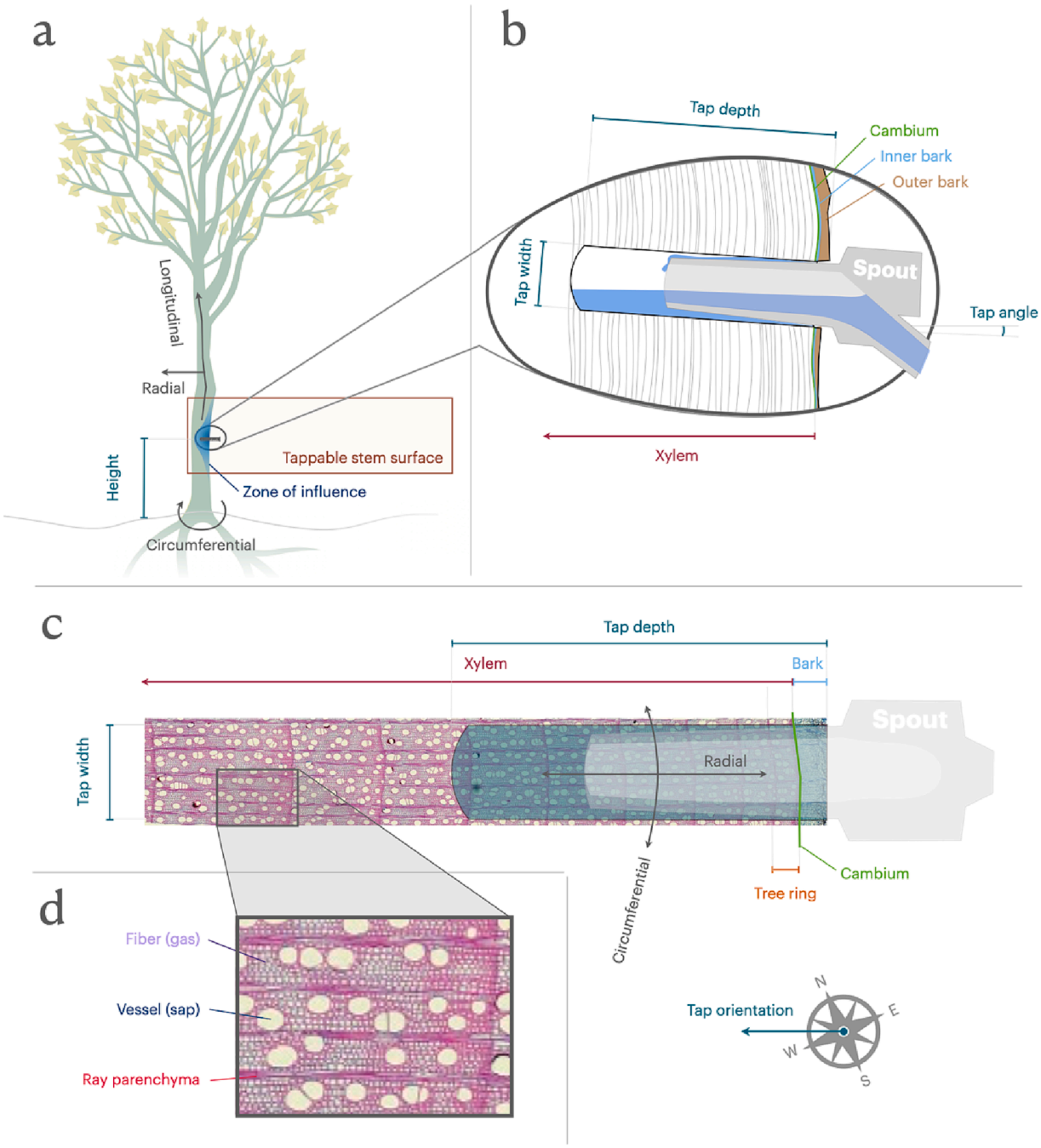

Fig. 2. Conceptual framework of the review at four different scales illustrating the spatial configuration of wood, tap, and tree characteristics. (**a**) At the tree scale, a certain area of the stem is easily tappable (circa 1–3 m), thus the tapping height on the stem typically falls within this tappable stem surface (orange rectangle). Transport of water and soluble sugars can happen either longitudinally, radially, or circumferentially (gray arrows), with longitudinal movement prevailing. This results in an asymmetric zone of influence of each tap (blue polygon). (**b**) Close-up of tap hole with spout illustrating the tap hole depth, width, and angle. (**c**) Top-down view of radial cut (i.e., transversal) through the tapping area in a red maple illustrating the tap orientation (i.e., direction pointing into the tap hole). (**d**) macro-view of maple wood anatomy indicating normally gas-filled fibers, sap-filled vessels, and ray parenchyma. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

up of positive stem pressure relies on physical characteristics of the xylem in conjunction with freeze–thaw dynamics. Air in the lumina of fibers is compressed during freezing and water is sucked from vessels into the adjacent fibers, where it sublimates forming ice. This ice has a highly negative chemical potential drawing more water out of the vessels (Cavender-Bares, 2005). Consequently, a negative pressure is established in the vessels. This negative pressure will vary longitudinally with a gradient of osmotic potential that presumably results in water uptake from the soil, which is transported across the interconnected network of vessels. This transport most likely follows the lower resistance to sap flow along a longitudinal path, although some radial and circumferential flow can also occur. While water is sucked from vessels into fibers during freezing, sucrose remains in the vessels due to the impermeability of fiber cell-walls to high-molecular weight solutes (Tyree, 1995). During a subsequent thaw, gas and ice in fibers expand and melt, respectively (Tyree, 1983). The combined pressure from expanding gas and osmotic pressure due to the high sucrose concentrations in the vessels, results in water moving back into the vessels from

the adjacent fibers, creating a positive pressure (Tyree, 1995). Slower freeze–thaw cycles will arguably result in a slower build-up of, but ultimately larger pressure differences (Tyree, 1983). Overall, the positive pressure experienced during each freeze–thaw event, and the consequent sap exudation from the tap hole, is related to the resistance to water transport (e.g., xylem anatomy, such as vessel size and interconnectedness), the concentrations of high-molecular weight solutes (e.g., locally available sucrose and mobilizable nonstructural carbon reserves), and the thermodynamics of phase transitions during the freeze–thaw cycle.

When tapping a tree for maple sugaring, the tap hole constitutes an injury that allows air and micro-organisms to enter and possibly contaminate the xylem. To limit the risk of propagation of foreign agents, the tree compartmentalises the wound (Shigo and Marx, 1977), which is often accompanied by changes in the wood's colour (Shigo, 1986). Each tap also has a zone of influence (i.e., xylem volume from which it can draw water and sugar), which is presumably larger in larger trees due to the reduced curvature of the stem and it arguably expands with the application of vacuum to the tap hole. The zone of influence determines the sap yield, as it constrains access to water and soluble sugars, yet it also appears to be proportional to the resulting compartmentalised wood (Renaud, 1998; van den Berg et al., 2016). Therefore, we can expect a trade-off between sugar yield and wounding. In other words, the size of the tap hole is related to both the wound's size (i.e., its volume and the surface of the opening in the bark) and the total sugar yield (i.e., its size of the zone of influence).

3. Methods

3.1. Data set

We compiled various publicly available and newly collected data sets of daily sap flow and sugar content for our analysis. First, we used data from the AcerNet network for five sites in the USA (Stinson, 2017). We excluded Harvard Forest from the AcerNet data, because more comprehensive data for Harvard Forest was added (Rapp et al., 2021), which would have partially duplicated the AcerNet data. Further, we used data from four additional sites in Quebec that have not been published to date (Table 1). When available or possible to derive, we included the following variables: site, tap, tree, date, time, latitude, longitude, altitude, species, daily sap yield and sugar content, number of taps per tree, tap hole depth, tap hole width, tap orientation (i.e., cardinal direction pointing into the tap), tap hole height on the stem, distance from previous tap holes or injuries, tapping date, date of tap removal, and diameter at breast height. We aggregated the daily sap yield and sap sugar content to obtain total sugaring season sap yield and mean sugar content for each tap. Taps that recorded no sap flow (n = 3) were removed from the data set. This left us with 16 624 data points on sap yield and 14 930 data points on sugar content for 324 trees (259 sugar and 65 red maples) from ten sites. Trees had one, two, or three taps per year and measurements were performed between one and eleven years (Table 1).

3.1.1. Additional sites

Newly collected data came from four additional sites. For three of these sites (l'Assomption, Saint-Émile-de-Suffolk, and Vallée-Jonction), daily sap yields were collected from buckets by either using a volumetric cylinder or by weighing the buckets and subtracting the bucket weight. Sap weights were converted to volumes using a sap density of 2% sucrose (see Rapp et al., 2019). Standard buckets were installed with 5/16″ spouts at the beginning of the sugaring season and protected from rain by covers. Sap sugar contents were measured using digital refractometers (e.g., PAL-alpha, Altago Co. ltd., Fukui, Japan) directly from the tap and from the buckets. For the Monts-Valin site, an automated precipitation gauge was installed and daily and seasonal sap yield were aggregated from the 15-min interval data. Sap sugar content was not measured at this site. For all four sites, sap measurements were conducted across the entire sugaring season.

3.2. Statistics

3.2.1. General approach

We estimated the effects of individual variables, such as number of taps, by building a parsimonious univariate regression model for each variable that could use all available data to fit either the distribution of sap yield or sap sugar content using a hierarchical Bayesian approach. The models all included population-level effects, such as interannual differences (*year*) or species-specific differences (*species*), as well as nested categorical group-level effects for *site* and *tree*. We built all models using the *brms* package (Bürkner, 2017) in R (R Core Team, 2019) and ran them on four chains with 6000 iterations. The code to reproduce this analysis is publicly available at https://github.com/TTRademacher/acer-web. Given the central limit theorem and the fact that the distributions of mean sugar content over the entire sugaring season is an average of discrete events, the distribution of mean sugar content over the season should approach a normal distribution. Sap sugar content can also not be negative, hence we modelled sap sugar content as a truncated normal distribution. In contrast total sap yield is multiplicative, as it is a function of discrete sap run events times the mean sap yield per run, as such it is best approximated as log-normal distribution (Limpert et al., 2001). Conveniently, the log-normal distribution cannot be negative, as sap yield have to be zero or larger. In the following, we reported either the estimated mean effects and their standard error in the format $\beta_x \pm \sigma_x$ or the estimated effects and their credible interval, *sensu* McElreath (2016), between the 2.5th and 97.5th percentile in the format $\beta_x[\beta_{2.5}; \beta_{97.5}]$. For all models, we made sure that models mostly converged and were well-mixed. We visually examined the posterior distributions and their errors to make sure they were

Table 1
Sites from which data was included in the *meta*-analysis. "Site" gives the site name, "Lat" and "Lon" the approximate latitude and longitude of the site, "Alt" the approximate altitude in meters, "Species" lists the species present (ACSA = Acer saccharum and/or ACRU = Acer rubrum), "Trees" gives the number of distinct trees that were tapped on each site, "Taps" provides the average number of tap holes per year, and "n" is the total number of observations of sap yield for the site across, taps, trees, and years.

Site	Lat	Lon	Alt	Species	Trees	Taps	Years	n
L'Assomption	45.8	−73.5	22	ACSA	33	33	2022	791
Dartmouth Organic Farm	43.7	−72.2	271	ACSA, ACRU	27	36	2014–2017	1769
Divide Ridge	37.0	−82.7	634	ACSA, ACRU	46	52	2016, 2017	350
Harvard Forest	42.5	−72.2	338	ACSA, ACRU	30	49	2012–2022	8391
Indiana Dunes National Lakeshore	41.6	−87.1	198	ACSA	24	25	2016, 2017	427
Monts-Valin	48.6	−70.9	220	ACSA, ACRU	2	2	2022	75
Québec	48.4	−70.7	243	ACSA, ACRU	30	30	2014–2017	1092
Saint-Émile-de-Suffolk	46.0	−74.9	233	ACSA	60	60	2020, 2021	2067
Southermost Maple	38.2	−79.7	838	ACSA, ACRU	42	73	2014–2017	670
Vallée-Jonction	46.4	−70.9	252	ACSA	30	30	2022	992

normally distributed (i.e., no obvious confounders were omitted from the model). In the following, we describe the tested and reported models for each variable.

3.2.2. Individual model specifics

There were several variables for which we could not fit any models due to the lack of suitable data or the lack of variability within the available data, notably tap hole depth, tap hole width, and growth. For all other models, we used the entire dataset unless stated otherwise.

For the number of taps (n_{taps}), tap orientation (φ), the height of the tap on the stem (h), and diameter at breast height (dbh), we fitted log-linear distributions for seasonal sap yield (y_s) and truncated normal distributions for seasonal mean sugar content (c_s) with a lower boundary of 0:

$$y_s \sim \ Log\ Normal(\mu_s, \sigma_s)$$

$$c_s \sim \ Normal_{+}(\mu_s, \sigma_s)$$

For the tap number models, we excluded a single data point from the single tree with three taps. The distributional means (μ_s) for the models looking at the effects of the number of taps were linear combinations of a global intercept (α), indexed effects for *year*, *species* (*spp*) and the number of taps (n_{taps}), and a nested effect for *site* and *tree:*

$$\mu_s = \alpha + \beta_{year[y]} + \beta_{spp[e]} + \beta_{site[s]} + \beta_{tree[st]} + \beta_{n_{taps}[i]}$$

For both models we also fitted a second model integrating a population-level diameter at breast height effect, such that:

$$\mu_s = \alpha + \beta_{year[y]} + \beta_{spp[e]} + \beta_{site[s]} + \beta_{tree[st]} + \beta_{n_{taps}[i]} + \beta_{dbh} dbh$$

For sap yield, we used the following weakly informative priors:

$$\alpha \sim \ Log\ Normal(0, 50)$$

$$\beta_{year[y]} \sim \ Normal(0, 2)$$

$$\beta_{spp[e]} \sim \ Normal(0, 2)$$

$$\beta_{site[s]} \sim \ Normal(0, 2)$$

$$\beta_{tree[st]} \sim \ Normal(0, 2)$$

$$\beta_{n_{taps}[i]} \sim \ Normal(0, 1)$$

$$\beta_{dbh} \sim \ Normal(1, 2)$$

$$\sigma_s \sim \ Exponential(1),$$

whereas we changed the intercept prior for sugar content to:

$$\alpha \sim \ Normal(2, 1)$$

For the tap orientation, the linear combination included of a global intercept (α), indexed effects for *year* and *spp*, a nested indexed effect for *site* and *tree,* and a spline for tap orientation ($s(\beta_\varphi)$):

$$\mu_s = \alpha + \beta_{year[y]} + \beta_{spp[e]} + \beta_{site[s]} + \beta_{tree[st]} + s(\beta_\varphi)$$

To test for a potential interactive effect of latitude (*lat*) and tap orientation we also fitted the following combination:

$$\mu_s = \alpha + \beta_{year[y]} + \beta_{spp[e]} + \beta_{site[s]} + \beta_{tree[st]} + s(\beta_\varphi * lat)$$

Furthermore, we divided the sugaring season into an early- and a late-season using the median day of sap flow for each tree. We then aggregated early- and late-season totals for sap yield and averaged sap sugar content over each period to fit distributions to each sub-season.

For the model investigating the effect of tap orientation on sap yield, we used the following weakly informative priors:

$$\alpha \sim \ LogNormal(3.7, 10)$$

$$\beta_{year[y]} \sim \ Normal(0, 2)$$

$$\beta_{spp[e]} \sim \ Normal(0, 2)$$

$$\beta_{site[s]} \sim \ Normal(0, 2)$$

$$\beta_{tree[st]} \sim \ Normal(0, 2)$$

$$\beta_{n_{taps}[i]} \sim \ Normal(0, 1)$$

$$\beta_{dbh} \sim \ Normal(0, 2)$$

$$\sigma_s \sim \ Exponential(1),$$

whereas we changed the intercept prior for the model of sugar content to:

$$\alpha \sim \ Normal(2, 1)$$

For height of the tap on the stem (h) and *dbh*, we fitted means using the respective formulae for both sap yield and sap sugar content:

$$\mu_s = \alpha + \beta_{year[y]} + \beta_{spp[e]} + \beta_{site[s]} + \beta_{tree[st]} + \beta_{dbh} dbh + \beta_h h$$

$$\mu_s = \alpha + \beta_{year[y]} + \beta_{spp[e]} + \beta_{site[s]} + \beta_{tree[st]} + \beta_{dbh} dbh$$

Again, we used the following weakly informative priors for sap yield models:

$$\alpha \sim \ Log\ Normal(3.7, 10)$$

$$\beta_{year[y]} \sim \ Normal(0, 2)$$

$$\beta_{spp[e]} \sim \ Normal(0, 2)$$

$$\beta_{site[s]} \sim \ Normal(0, 2)$$

$$\beta_{tree[st]} \sim \ Normal(0, 2)$$

$$\beta_h \sim \ Normal(0, 2)$$

$$\beta_{dbh} \sim \ Normal(0, 2)$$

$$\sigma_s \sim \ Exponential(1),$$

whereas we changed the intercept prior for the models of sugar content to:

$$\alpha \sim \ Normal(2, 1)$$

We also tried a non-linear spline for the *dbh* effect, which resulted in quasi-linear fit. For the sake of parsimony, we therefore reported results for the above model with a linear term. *Nota bene*, resulting fits are non-linear even with a linear term for sap yield due to the log-normal link function. To make the results more easily interpretable to the reader we provided examples of the effect from posterior draws, such as comparisons between a 30-cm tree and an 80-cm tree. For between-species differences we used the same model as for *dbh* to account for potential differences in the size distributions of each species.

4. Effects of tap characteristics on sap yield and sugar content

Clearly, tap hole properties are a crucial feature for sustainable maple sugaring, as they can both affect wounding and maple sugar yield (Section 2). Whether sap is extracted by gravity or under vacuum, normally a cylindrical tap hole is drilled into the tree prior to the sugaring season into which a spout is inserted. Tap hole characteristics,

whose effect on sap yield and/or sugar content have been postulated in the past, can be separated into effects of the geometry of the tap hole (width, depth, and shape), the number and positioning of tap holes on the stem (number of taps, orientation, height on stem, distance to previous tap holes), and the date of tapping and/or spout removal. Here, we review the effects of the tap hole's (4.1) depth, (4.2) width, (4.3) the number of taps, (4.4) the tap hole's orientation, (4.5) its height on the stem, and (4.6) the distance from previous injuries. We conclude this section (4.7) by discussing additional and less studied tap characteristics, such as method of tapping, shape of the tap hole, angle of the tap hole, insertion of spouts, and time since tapping.

4.1. Tap hole depth

While the physical process responsible for sap flow during the growing season (cohesion-tension) is different from the freeze–thaw induced positive pressures, sap flow relies on the same infrastructure in both cases. Given that any radial transport during the sugaring season is presumably utilizing, thus constrained by the same connections between vessels, the radial profile of sugar season sap flow is likely similar to that of growing season sap flow. During the growing season, the radial profile of sap flow is known to decrease with depth for maple (Pappas et al., 2022). Consequently, sap yield would increase with depth, but the incremental increase of sap yield would decline progressively in deeper tissues and ought to stop at the heartwood boundary (i.e., analogous to the radial profile of growing season sap flow; Fig. 3a).

According to pioneer studies, sap yield increases with tap hole depth up to a certain threshold (Gibbs, 1969; Morrow, 1963). However, the increases in sap yield are low above roughly 3.8 cm with modern production techniques (Perkins et al., 2021). As argued above, the exact threshold is likely related to sapwood thickness, but this remains to be tested. For sugar maple, there appears to be a linear relationship between sapwood area and stem diameter (Raulier et al., 2002), which could partially explain the strong observed effect of tree diameter at breast height (*dbh*) on sap yield (see Section 5.1). Unfortunately, the range of reported tap hole depths around the conventional 5 cm is very

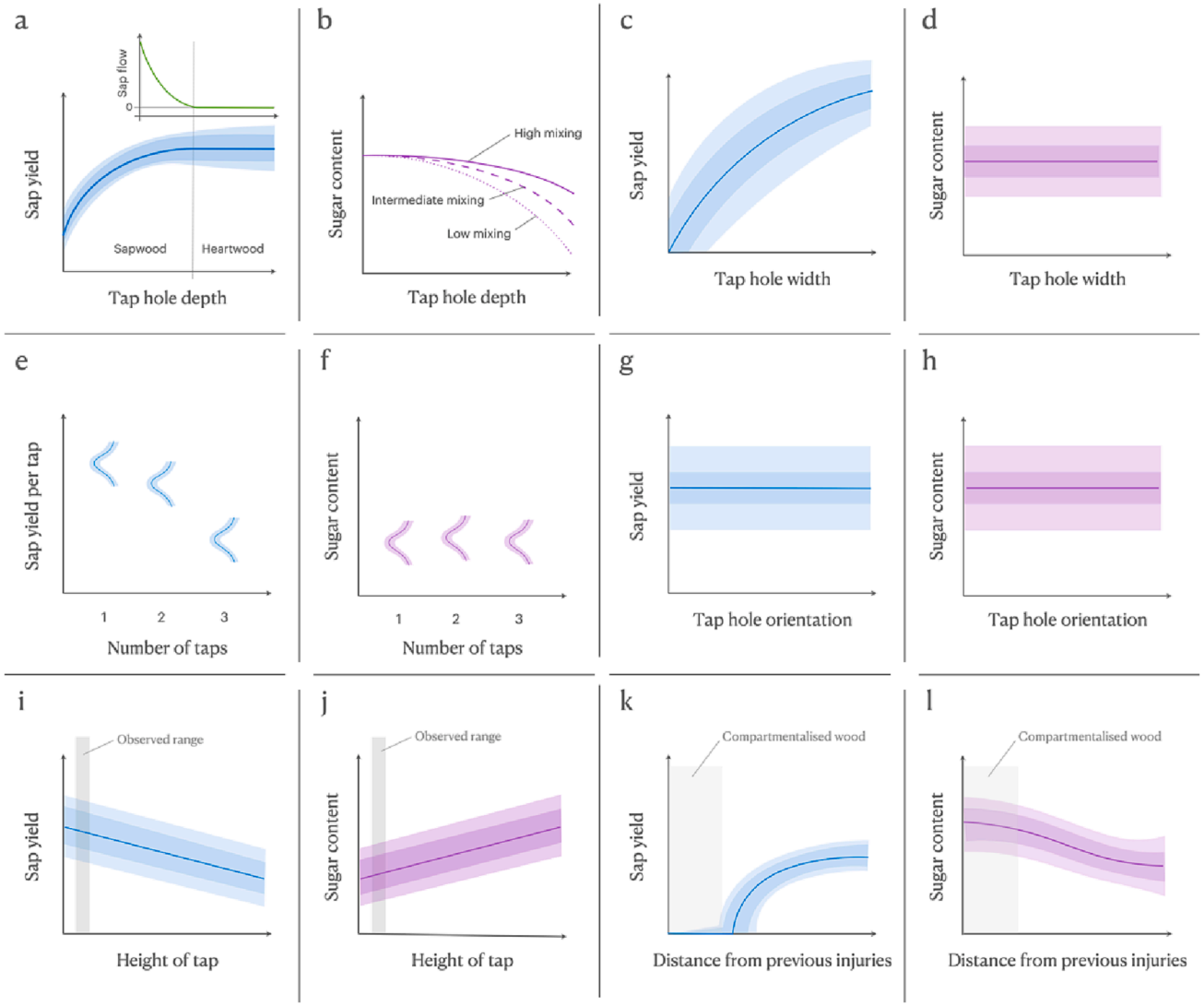

Fig. 3. Visual hypotheses of the relationships between sap yield (blue curves) or sugar content (purple curves) and tap characteristics: (**a** & **b**) tap hole depth, (**c** & **d**) tap hole width, (**e** & **f**) number of taps, (**g** & **h**) tap hole orientation, (**i** & **j**) height of tap hole on the stem, and (**k** & **l**) distance from previous injuries. The lines show the mean expected effect with shading illustrating the effects distribution. The insert in **a** shows (**a**) typical radial sap flow profile of maple trees with the dotted line indicating a hypothetical sapwood/heartwood boundary. The hypothesised effect of tap hole depth on mean sap sugar content is shown in (**b**) for three scenarios of radial mixing: high mixing (solid line), intermediate mixing (dashed line), and low mixing (dotted line). In (**i**) and (**j**), the typical and very restricted range of tapping height on the stem, due to practical considerations, is illustrated with the gray rectangle. In (**k**) and (**l**), the gray rectangle corresponds to the zone of compartmentalised wood from the previous injury. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

small with 4.2 to 6.3 cm. Thus, we cannot draw any additional conclusions from our *meta*-analysis. In addition to the low variability of reported tap hole depths, the usual method of drilling the tap hole with a drill guide does not account for variations in bark thickness or operator error. However, bark thickness varies substantially in maples. Bark thickness measurements from one of our sites (n = 30) varied between 5 and 14 mm; resulting in effective range of tap depths between 3.5 and 5.8 cm at the site. This variation in bark thickness has long been argued to represent a potential confounding factor when testing for effects of tap depth (Koelling and Blum, 1967). Accounting for bark thickness and sapwood depth seems particularly important with regards to understanding the exact depth thresholds at which sap yield tapers off. An important practical consideration with regards to tap depth is that tap depth in conjunction with growth rates also determine when a new tap can be drilled into the same stem section without overlapping with an old tap, thus incurring a yield penalty. Consequently, decisions on tap hole depth need to integrate knowledge on growth rates and sap flow to ensure the sustainability of maple sugaring.

Sap sugar content relies on previously stored and remobilised reserves in the form of soluble sugars and their accessibility. As nonstructural carbon concentrations decrease with radial distance from the bark in red maples, at least during the growing season (Furze et al., 2020), it could be argued that mean sugar content would therefore decrease with tap hole depth. Furthermore, nonstructural carbon concentrations are particularly low in heartwood, which is, *inter alia*, characterized by parenchyma cell death (Spicer, 2005). In fact, the residing nonstructural carbon in heartwood may not be metabolically available (Stewart, 1966). This would suggest that mean sugar content is highest in shallow tap holes and decreases particularly strongly when tap holes protrude into the heartwood, as the additional depth does not provide access to additional nonstructural carbon. Nevertheless, the fact that water and solutes can move across ring boundaries in maples (Wason et al., 2019) and that maple sap can contain even decade-old carbon (Muhr et al., 2016) suggest that some outward mixing of nonstructural carbon (e.g., towards the bark) is happening. Carbone et al. (2013) found evidence of such outward-mixing. The stronger this mixing is, the smaller would be the effect of tapping depth on sugar content (Fig. 3b). Our *meta*-analysis did not allow to improve our estimates of the degree of outward-mixing, as the range of tap hole depths in the compiled data was very small. In conclusion, tap hole depth may marginally affect mean sugar content depending on the degree of radial mixing, which remains to be determined.

4.2. Tap hole width

Wider tap holes cut across a larger total cross-sectional area facilitating longitudinal transport (Fig. 2c). Together with sap flow, the total cross-sectional area is a primary determinant of sap transport capacity. All else being equal, a wider tap hole should provide access to a larger cross-sectional vessel area (Fig. 3c) and ought to result in increased sap yield over the sugaring season. Tap hole width has indeed been shown to correlate positively with sap yield under gravity and vacuum extraction (Lagacé et al., 2015; Perkins, 2019). While these studies strongly suggest that sap yield does increase with tap hole width, they require additional validation, mainly because of their limited sample size (i.e., one or two sites, one species, four to six trees per treatment). Unfortunately, past studies have virtually exclusively used current industry standards (i.e., 5/16″ drill bits and spouts), hence there is virtually no variability with regards to tap hole width in the compiled data. Consequently, we can neither present additional evidence in support, nor against the above hypothesis.

Sugar concentrations within the region that can be drawn upon for sap extraction vary little longitudinally and/or circumferentially (Furze et al., 2020, 2019). Consequently, tap hole width should not affect the mean sap sugar content. However, soluble sugars ought to move substantial distances as solutes in the transported and exuded sap. In fact, long distance transport, exceeding a meter, is necessary, as exuded sap volume exceeds locally available water resources (e.g., water content of the volume of wood that is compartmentalised). Despite the import of distal sugar, as solutes in sap, the sap sugar content is unlikely to vary

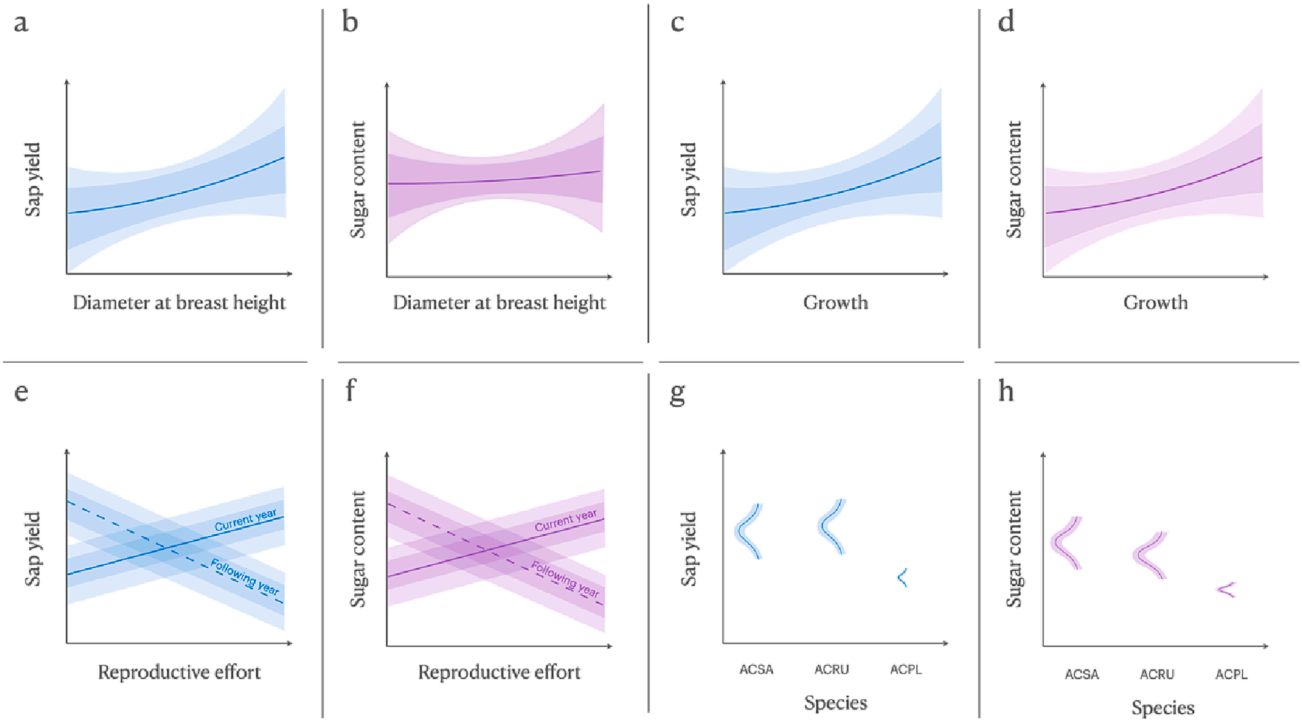

Fig. 4. Visual hypotheses of relationships between sap yield (blue curves) or sugar content (purple curves) and tree characteristics: (**a** & **b**) diameter at breast height, (**c** & **d**) growth, (**e** & **f**) reproductive effort, and (**g** & **h**) species. The lines show the mean expected effect with shading illustrating the effects distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

substantially with tap hole width as sugar concentrations are similar around and along the stem. As mentioned above, all available data used 5/16″ drill bits and spouts, preventing additional insights into the effect of tap hole width on sugar concentration. More systematic efforts to characterise the effects of tap hole width are desirable as this variable can easily be altered by maple sugar producers with various spout and tubing sizes becoming commercially available (e.g., 3/16″, 5/16″, and 1/4″).

While the tap hole width and associated spout size can be altered relatively easily, this needs to be done carefully as it comes with various caveats. Mismatched tubing sizes can potentially cause flow reversals, resulting in the build-up of microbes and bacteria, which can affect sap quality negatively (Ball, 2007; Garcia et al., 2020; Lagacé et al., 2019). Most importantly, wider tap holes result in larger injuries and disproportionally increase the volume of wood that is compartmentalised (Lagacé et al., 2015; Renaud, 1998; van den Berg et al., 2016). Consequently, wider tap holes may compromise the long-term sustainability of the maple sugaring operation. Equally, the tap hole width determines the wound surface, that needs to grow over by callus formation. Reducing tap hole width seems to shorten the time to wound closure (Lagacé et al., 2015), thus minimising infection risk (Allard, 1998). In the absence of additional evidence, reducing tap hole width seems a useful tool to reduce injury with only a small yield penalty attached, especially for vacuum systems where the probability of leaks may increase with tap hole width.

4.3. Number of tap holes per tree

It is common practise to add a second or even third tap to a single tree if the tree is sufficiently large (e.g., *dbh* > 40 cm for second and *dbh* > 60 cm for third tap). The underlying rationale is that as long as the additional tap hole does give more access to vessel cross-sectional area, that cannot otherwise be drawn upon, it will increase the sap yield. However, tap holes must be positioned in different parts of the stem to avoid overlapping zones of influence, which would draw on the same transport infrastructure and cause a larger fused wound. Spacing taps sufficiently is difficult on small stems, especially over multiple years due to their limited tappable stem surface. Consequently, the number of taps is only recommended above a certain size threshold (e.g., *dbh* > 40 cm).

An early study concluded that adding more than one tap hole to a single tree increases the total sap yield for that tree by about 20% for the second and third tap hole, which constitutes a 40% or 55% reduction of sap yield per tap hole with two or three taps, respectively (Morrow, 1963). This study was based on 111 sugar maple trees from four sites across nine years. Using data from 324 sugar and red maple trees from ten sites across eleven years, we find no clear decrease in sap yield per tap for a second tap hole when not accounting for tree size ($\beta_{n_{taps}[2]} = 0.02 \pm 0.42$). However, as the number of taps was not a randomised treatment in any of the composite data sets, we need to account for tree size, because a second tap was only installed on larger trees. When we account for tree size (i.e., include a population-level effect of *dbh*), we do see a reduction in sap yield per tap of similar magnitude to interannual variation, albeit very uncertain ($\beta_{n_{taps}[2]} = -0.12 \pm 0.51$). Another caveat with the compiled data is that it is exclusively from gravity taps. However, increased vacuum appears to further reduce any gains obtained from each additional tap hole (Grenier et al., 2008; Lagacé et al., 2015; Perkins et al., 2021), as it increases the zone of influence of each tap hole. Although our analysis is not conclusive, the compiled data suggests that tapping a tree more than once, inflicts additional wounding endangering the long-term sustainability of maple sugaring without a proportional increase in sap yield.

As each additional tap hole increases the total zone of influence, it is also likely to provide access to previously untapped nonstructural carbon reserves. However, the mean sap sugar concentration is unlikely to vary substantially between taps, as nonstructural carbon concentrations vary little longitudinally and circumferentially in the tappable stem surface due to continuous mixing of new and old nonstructural carbon reserves (Keel et al., 2007, 2006; Richardson et al., 2015). In addition to the observed reduction of sap yield per tap, adding a second tap hole did have a small, yet uncertain positive effect on sugar content ($\beta_{n_{taps}[2]} = 0.03 \pm 0.37$ °Brix), when accounting for *dbh*. This supports the hypothesis, that sugar content does not change with the number of taps.

Additional tap holes seem to provide only marginal increases in sap yield without affecting the sugar content according to the evidence reviewed and presented here. In contrast, most tapping guides still recommend adding a second and third tap hole beyond a certain size threshold (e.g., *dbh* > 40 cm for second tap). In the light of the current evidence, we question the validity of this recommendation, but systematic investigations that address the uncertainties in our analysis around the long-term sustainability of using more than one tap per tree are still required. Such investigations should explicitly consider location of the tap hole on the stem, including estimations of potential overlap between zones of influence with current and previous tap holes.

4.4. Tap hole orientation

Maple sugaring is mostly practised between the 40th and 50th parallel in the Northern Hemisphere, where insolation peaks in southern exposures. Predictable variations in insolation can cause substantial circumferential differences in stem temperatures in sugar maples (Reid et al., 2020). Such local variation in stem temperature may arguably lead to resulting variations in freeze–thaw dynamics depending on tap hole orientation. Nevertheless, it is not likely that sap yield is affected by the orientation of the tap hole on the stem, given the plasticity of sap transport (e.g., Dietrich et al., 2018) and the fairly large zones of influence, although maple wood is known to be sectorial (Ellmore et al., 2006; Orians et al., 2004).

Early studies observed that northern taps have lower yields (Jones et al., 1903; Wiegand, 1906), although another study only confirmed this sap yield difference in some years (Morrow, 1963). The author argued that southern taps have higher sap yields early in the sugaring season, while northern taps have higher yields later in the season (Morrow, 1963). However, tests of these hypothesis have only been conducted on very small cohorts (n > 15) of often open grown trees (Tucker, 1990). Here, our *meta*-analysis did not reveal a clear effect of tap orientation on sap yield when considering the entire sugaring season ($\beta_{\varphi} = -0.53 \pm 0.71$). Even when dividing the season into an early- and a late-season and accounting for site latitude, we found an inconclusive and counterintuitive trend of sap yield increasing in the early-season with northernly exposure (in the order of 5 litres per season) and no detectable effect of orientation in the late season, whether we accounted for site latitude or not ($\beta_{\varphi} = -0.34 \pm 0.67$ or $\beta_{\varphi} = -0.01 \pm 0.01$, respectively). Overall, the presented evidence suggests that the tap hole orientation does not affect sap yield.

Sap sugar content is also unlikely to vary with the cardinal direction of the tap hole, because circumferential differences in nonstructural carbon reserves are probably very small in trees. Indeed, we found no effect of tap hole orientation on sugar content with $\beta_{\varphi} = 0.85 \pm 0.96$. In conclusion, there is little evidence to support any effect of tap hole orientation on neither sap yield, nor sugar content. Yet, local stem temperatures and their effects on sap yield and sugar content may also vary with slope, aspect, stand density, and even community composition (e.g., presence of evergreen conifers), thus such site-specific factors should be included in future work trying to advance our understanding of the effect of tap hole orientation on maple sugaring. The lack of a strong effect of tap orientation on sap yield and sugar content permits tapping using the entire circumference of tappable stem surface (e.g., regular vertical and horizontal offset or multi-level tapping) without a production penalty; even at particularly high or low latitudes.

4.5. Height of tap on the stem

Heat diffusion, thus freeze–thaw dynamics, will vary with insolation and turbulence across strata in the maple grove. Moreover, tapering of stems and branches towards their apices equally reduces thermal mass, surface to volume ratios, and wood anatomy (e.g., vessel lumen size). Due to better heat diffusion, smaller thermal mass and higher surface to volume ratios higher up in the crown, higher strata (smaller branches) are generally better coupled with the atmosphere than lower ones (large branches and stems). These variations in coupling may affect freeze–thaw dynamics with consequences on sap yield, likely leading to more, but shorter, freeze–thaw events higher in the canopy. Positive pressure and sap yield have been shown to be related to the velocity of the freeze–thaw cycle with slower cycles increasing the pressure and sap yield (Tyree, 1983). Moreover, water to refill vessels during the freezing comes ultimately from the roots, thus rehydration has to combat gravity and ought to vary with stem height. As a secondary result of rehydration originating in the roots, the water column above a tap hole is also smaller the higher a tap hole is located. Finally, anatomical properties, such as vessel size, are smaller with height on the stem, which may also cause reductions in sap yield. Due to a combination of the differences in freeze–thaw cycles, rehydration dynamics, and anatomical properties, regions higher up on the stem ought to yield less sap per run.

Sap yield has, indeed, been reported to decrease with tap hole height (Wiegand, 1906). We were able to compile data of tap height on the stem for 526 taps holes ranging from 50 to 188 cm above ground. Even within this relatively small range of values, we find a small effect of tap hole height on sap yield (e.g., order of 5 litres less between a tap at 60 cm versus 180 cm over the season). Although this supports the hypothesis that sap yield decreases with tap hole height, it is clearly very weak evidence given the small range of heights in the compiled data.

Maple trees have higher nonstructural carbon concentrations in branches than at breast height (Furze et al., 2019), indicating that regions higher on the stem have access to more nonstructural carbon reserves. Consequently, sugar content could be expected to increase higher up the stem, leading to increases in sugar content with the height of the tap hole on the stem. In contrast to sap yield, sugar content has been reported to increase with tap hole height up to at least 14 m (Tucker, 1990). Equally, we found a positive effect of tap hole height on sugar content, albeit it being diminishingly small (i.e., 0.01° Brix difference between 60 cm and 180 cm) with the same caveat as for sap yield, that the range of investigated tap hole heights was very small in our compiled data.

Additional, measurements that vary more substantially in height are required to substantiate these relationships between tap hole height and sap yield or sugar content. Yet, there is a reason why reported heights vary little. Tapping above or below a certain range of heights (roughly 1 to 3 m, i.e., the easily tappable stem surface in Fig. 1a) is unpractical. Nonetheless, current knowledge suggests that maple sugaring could possibly be practised much higher up the stem without sizeable yield penalties. Tapping higher (or lower) on the stem can provide access to parts of the stem that are not riddled with wounds from previous tap holes. In particular, in maple groves with previously unsustainable tapping practises, tapping higher or lower on the stem is a valid option to reduce the risk of creating compound wounds.

4.6. Distance from injuries

Compartmentalised wood, resulting from tap holes or other types of wounds, substantially reduce local water transport. As a result, any overlap between the tap hole's zone of influence with previously compartmentalised wood (e.g., previous tap hole or other injury) will be non-functional for water transport. Thus, if the zone of influence overlaps with already compartmentalised wood, this is likely to reduce sap yield (Fig. 3i). The necessary distance to avoid a negative effect of a previous injury on the current tap is likely to vary with resistance to transport around the injury (i.e., be smallest longitudinally). As compartmentalisation requires energy and resources to form, *inter alia*, tyloses, local nonstructural carbon is likely going to be remobilised. While some of the locally available soluble sugar is then used to fuel compartmentalisation, some may be left over and isolated. If this is the case, sugar content close to previous injuries might even be slightly elevated, as it can tap into these otherwise unavailable resources, but taper off with distance from the wound (Fig. 3j).

We have found no data to address these hypotheses, despite their importance for sustainable maple sugaring operations. To sustainably tap a maple tree, tap holes need to be spaced out sufficiently. In fact, tapping into compartmentalised wood should be avoided at all costs, as wounds in close proximity fuse, thereby substantially increasing the volume of compartmentalised wood (van den Berg et al., 2016). Efforts to better understand the factors determining the size of the zone of influence and its relationship to the volume of compartmentalised wood are needed.

4.7. Other tap characteristics

While we were able to review and analyse some data concerning important tap characteristics, there are other characteristics that are not reported in the published literature to date. Notably, the effect of the angle at which the tap is drilled has not been investigated. Yet, it is common knowledge that a negative angle causes a build-up of sap inside the tap hole. Such a puddle of sap could increase the risk of infection, encourage fungal growth, lead to the accumulation of micro-organisms in general, and should therefore be avoided. The effects of time since tapping, as a proxy for occlusion of the tap hole by micro-organisms, may be studied in this context in the future. However, any such study should account for confounders; primarily variations in freeze–thaw dynamics between sap runs. We also found no published literature on the effects of the shape of the tap holes and tapping methods. Virtually all commercial taps are drilled nowadays and tapping guidelines typically recommend using sharp drill bits to create clean cuts, leaving a cylindrical hole. However, mini-chainsaw could be used to cut rectangular slots, such as for ribbonized sapflow sensors (Jones et al., 2020), or specifically-designed punching tools to cut tap holes of various shapes.

5. Effects of tree characteristics on sap yield and sugar content

Due to different life histories, maples can vary substantially in shape and form. Differences in life history and morphology result from and combine with micro-environmental fluctuations in maple groves to cause considerable variation in sap yield and sugar content between maple trees from the same stand. However, evidence from one site suggests that sap yield and sugar content are related; that is trees that have higher sap yields also have sweeter sap (Marvin et al., 1967). Other authors have confirmed that trees within a stand rank consistently with regards to sugar content over the years (Larochelle, 1998; Marvin et al., 1967; Taylor, 1956; Wilmot et al., 1995). While some trees seem to provide consistently more and sweeter sap, the causes for these between-tree differences remain partially unknown. Here, we review the effects of the tree's (5.1) size (i.e., diameter at breast height), (5.2) vigour, as measured by radial growth, (5.3) reproductive effort, and (5.4) species on sap yield and sugar content. Finally, we conclude this section (5.5) by discussing additional tree characteristics, that may affect both sap yield and sugar content.

5.1. Tree size

Tree functioning varies substantially with tree size. For example, allocation of resources varies systematically between seedlings and mature trees (Hartmann et al., 2018). Increasing distances of source and sink tissues in larger trees may even lead to marked differences in locally available reserves (Rademacher et al., 2022). How exactly resources

allocation dynamics scale with size in maple trees is, however, still unknown. Nonetheless, larger trees certainly have a larger zone of influence for each tap, as the curvature of the stem is reduced (Fig. 2a). Although any resulting effect should be asymptotic due to progressively smaller increments in the zone of influence with size. Consequently, it is reasonable to assume that sap yield increases with tree size (Fig. 4a). Tree size can be measured in multiple ways with diameter at breast height (*dbh*) being the most commonly measured size attribute. Because *dbh* captures the size of the tree at a relevant height for maple sugaring, is easily measured and commonly reported, we used it as a proxy for size.

Stem diameter has previously emerged to be related to sap yield and sugar content (Blum, 1973; Grenier et al., 2007; Larochelle, 1998; Wilmot et al., 1995). We can confirm this relationship for sap yield, as we find a strong non-linear relationship between sap yield and *dbh* for data from 574 taps on 123 trees over elven years, that varied in *dbh* from 16.0 to 86.2 cm. According to our fitted model, a tree with an 80-cm *dbh* yields on average roughly 80 litres per season, while an otherwise equal tree of 30-cm *dbh* (controlling for site, year, species, etc.) only yields about 26 litres.

Equally, we see an increase of 0.1 Brix per 10 cm of *dbh*. Such a relationship between tree size and sap sugar content could explain why trees tend to maintain their ranking of sap sugar content from year to year (Marvin et al., 1967; Taylor, 1956), as larger trees would generally provide sweeter sap. In conclusion, we provide additional strong evidence that larger trees do provide more sap and some, albeit weaker, evidence indicating that sugar content may also increase with tree size. These relationships might even be stronger when other measures of size, such as crown attributes, are used, as they might better capture carbon acquisition.

5.2. Tree vigour and growth

Tree vigour is an integrative concept of functional performance. Growth, efficient water transport, and larger energy reserves are arguably all measures of tree vigour (Chave et al., 2009; Poorter et al., 2010; Trumbore et al., 2015). While vigour is tricky to quantify, radial or diameter growth has been used extensively as a proxy for vigour (Dobbertin, 2005). Given the presumed correlations of water transport efficiency, nonstructural carbon reserves, and radial growth, more vigorous trees may generally be expected to have both higher sap yields and sugar contents (Fig. 4c & d).

Maple trees that grow faster tend to have a larger proportion of ray cells (Gregory, 1977), which are crucial for local nonstructural carbon storage and transport. Whether such systematic variation in xylem anatomy with growth is also true for vessels and fibers, remains to be determined. However, ray cell proportions are not correlated with sweeter sap in sugar maples (Garrett and Dudzik, 1989). Furthermore, growth has already been reported to positively correlate with both sap yield and sugar content (Laing and Howard, 1990; Marvin et al., 1967; Moore et al., 2020; Morselli et al., 1978), even though this relationship seems very weak in some sites (Blum, 1973; Grenier et al., 2007). As sap sucrose concentration itself is a driver of the development of positive pressure under thawing (Johnson et al., 1987), presumably sap yield is also related to sap sucrose concentration. Consequently, more vigorous trees with higher sap sucrose concentrations arguably provide sweeter sap and higher sap yields (Gabriel and Seegrist, 1977; Noland et al., 2006). However, this assumes implicitly that sap sucrose concentrations are associated with tree vigour, which remains to be determined as soluble sugar concentrations seem to be maintained homeostatically in red maples (Rademacher et al., 2022). We did not find published data to further probe these hypotheses. It has to be noted that growth (and arguably vigour) of sugar maple is strongly linked to available soil nutrients, particularly calcium (Bal et al., 2015; Ouimet et al., 2017; Schaberg et al., 2006; Wilmot et al., 1996). Thus, disentangling vigour effects on sap yield and sap sugar content will require long-term measurements across soil nutrient gradients. Conversely, tapping normally does not seem to affect growth in the long-run (Pothier, 1996), although growth can decline in some sites (Copenheaver et al., 2014; Isselhardt et al., 2016). However, this effect of tapping on growth does neither seem to be pervasive, nor clearly related to soil fertility (Ouimet et al., 2021). A recent study, showed that the negative effect of tapping (and high vacuum extraction) on growth are limited to small trees (Ouimet, 2022). Nevertheless, poor tapping practises are likely to lead to growth reductions.

In addition to radial growth, leaf nutrients, which are another proxy for vigour, have also been linked to sap sugar content (Leaf and Watterston, 1964), although a more recent study has shown that this relationship can be very weak (Wilmot et al., 1995). Interestingly, neither leaf area (Tucker, 1990), nor crown size (Blum, 1973; Grenier et al., 2007) show strong relationships with sap sugar content. Possibly, relative (i.e., proportional allocation) but not absolute amounts of carbon assimilation are driving sap sugar content. This hypothesised importance of relative allocation is further supported by the fact that defoliation, which primarily affects absolute carbon assimilation, does not affect sap sugar content (Gregory and Wargo, 1986; Kolb et al., 1992), but crown dieback - a sign of low vigour – did reduce sap yields (Wilmot et al., 1995). Ice storm damage have also been linked to lower sap yields and sugar contents (Noland et al., 2006), although this might be a direct consequence of the damage and not related to carbon allocation and/or tree vigour. Competition, which can drive changes in carbon allocation, does not seem to affect sap yield or sugar content (Pothier, 1995). Overall, there is some evidence for a positive relationship between tree vigour and sap yield and sugar content, but current evidence suggests a rather small direct effect.

5.3. Reproductive effort

Sugar and red maple are both mast seeding species, that invest a substantial fraction of their reserves on seed production every two to five years (Cleavitt et al., 2011; Garrett and Graber, 1995; Graber and Leak, 1992; Graignic et al., 2014; Houle, 1999; Jensen et al., 2012). Mast seeding is highly variable interannually and tends to be synchronised across populations (Kelly & Sork, 2002). Masting may be related to and possibly even triggered by the amount of nonstructural carbon reserves (Han and Kabeya, 2017). As nonstructural carbon reserves are equally drawn upon by maple sugaring, reproductive effort should modulate sap yield and sugar content.

For sugar maples, masting has been related to higher syrup production in the same year (prior to the masting event) and lower syrup production the following year using data at the regional scale in Vermont (Rapp and Crone, 2015; Fig. 4e & f). The authors even suggested that high nonstructural carbon reserves may trigger mast seeding in maples (Rapp and Crone, 2015). An alternative (sink-driven) hypothesis for the reported pattern maybe that increased sink activity during mast years, due to higher numbers of vegetative and reproductive buds, requires additional remobilisation of nonstructural carbon reserves in spring leading to more and sweeter sap in the same year, as the sugaring season precedes the masting event. Independent of whether nonstructural carbon reserves trigger mast seeding or mast seeding triggers remobilisation of nonstructural carbon reserves, the energetic demands of mast seeding seem to have repercussions on nonstructural reserves, reducing sap yield and/or sugar content in the year following a mast seeding event. This relationship has yet to be confirmed at the local scale using phenological and syrup production data from individual trees at the same site, which would also allow to disentangle whether sap yield, sugar content, or both are responsible for the observed changes in syrup production. If masting and maple sugaring draw on the same nonstructural carbon resources, sap sugar content will probably contribute more to the observed relationship between masting and syrup production.

5.4. Species

Maple sugaring overwhelmingly relies on sugar maples, but red and black maples (*Acer nigrum*) can be locally important species. However, other maple species, such silver maple (*Acer saccharinum*), Manitoba maples (*Acer negundo*), and even Norway maples (*Acer platanoides*), can also be tapped and exploited. As these species hail from the *Acer* genus and are phylogenetically and physiologically close relatives (Gao et al., 2020), which can sometimes hybridize (Saeki et al., 2011), it is commonly assumed that the sap exudation mechanism is identical to sugar maple. Despite their physiological similarity, maple species have distinct traits (e.g., wood anatomy), that are likely to affect maple sugaring. Species from other genera, such as birches (*Betula*), illustrate that positive stem pressure and sap exudation in a leafless state can even have completely different underlying mechanisms (Hölttä et al., 2018), as birches do not even require freeze–thaw cycles (Merwin and Lyon, 1909). While the underlying mechanism is likely to be similar in maple species, important differences in sap yield and sugar content are likely given the physiological difference (Fig. 4g & h). Finally, the combined economic profit imperative and prevalence of one species in the industry hints at sugar maple having higher sap yields and/or sugar content than other maple species. Nonetheless, no studies have investigated differences in sap yield and sugar content among species to our knowledge.

As the climate and biodiversity crises unfold, utilising the larger combined genetic and phenotypic pool of the *Acer* genus in maple sugaring provides opportunities for adaptation. To leverage various species traits in maple sugaring, we need to start by identifying existing differences. We were able to collect and compile data from three species: 259 sugar maples, 65 red maples, and a single Norway maple (which was excluded from the study). We found that sugar maples yield more and sweeter sap. Sugar maple sap is on average $0.51 \pm 0.58°$ Brix sweeter than red maple sap. Sap yield is estimated to be on average 32.5 litres for a 40 cm sugar maple, but only 24.3 litres for an equivalent red maple, assuming no net effects of *site*, *year*, and *tree*. The presented evidence strongly suggests that important between-species differences exist in sap yield and sugar content. Better understanding these differences and how these differences are modulated by climate, is crucial when advocating for the diversification of maple groves as an adaptation measure to the climate and biodiversity crisis. However, it should be noted that functional redundancy, such as the co-existence of several maples species, appears less beneficial for ecosystem service provision and resilience than introducing functionally diverse species (Brockerhoff et al., 2017). Consequently, sugaring operations ought to include functionally diverse companion species (e.g., oak, beech, poplar) to augment their resilience.

5.5. Other tree characteristics

The defining feature of trees is wood, which is equally the tissue that we drill into for maple sugaring. Given that the mechanism of sap exudation in a leafless state requires a specific wood anatomy (Section 2), it is reasonable to assume that anatomical properties will affect both sap yield and sugar content. For birch, clear links between wood anatomy and sap exudation have been shown recently (Zajączkowska et al., 2019). Some pioneering studies (Gregory, 1978, 1977; Morselli et al., 1978) have illustrated that maple trees with more and sweeter sap may have larger proportions of rays cells, but not a larger vessel area. However, a subsequent attempt to better quantify these links between sap yield or sugar content and anatomical properties has been inconclusive (Garrett and Dudzik, 1989). Nonetheless, anatomical differences may also explain part of the differences in sap yield and sugar content among species.

More generally, nonstructural carbon dynamics are also likely to play a pivotal role in determining sap yield and, especially, sugar content. The observed correlations between reproductive effort and sap yield and sugar content support such a link between nonstructural carbon dynamics and sap yield and sugar content. Sugars in maple sap can be up to a decade old, illustrating that fairly old reserves can be remobilised (Muhr et al., 2016). To understand interannual variation in sap yield and sugar content, we need to better understand these nonstructural carbon dynamics and how they vary from year-to-year. Recently, efforts have been made to understand the nonstructural carbon allocation and use in red maple (Chen et al., 2022), but many questions on how wood formation, reproductive efforts and nonstructural carbon dynamics – in particular during the leafless state - interact remain unanswered. While it is often presumed that healthy maple trees (possibly with larger nonstructural carbon reserves) provide more and sweeter sap, what is the best measure of health and/or vigour remains elusive and even measurements of local nonstructural carbon reserves are rare (but see Wong et al., 2003).

Finally, the role of roots has also received very little attention in the context of maple sugaring. Yet, healthy roots are crucial for maple sugaring, as they enable the uptake and transport of water from the soil to the stem in the build-up of positive pressure and the storage and remobilisation of distal nonstructural carbon reserves. Differences in root architecture and physiology may partially explain, between-tree, between-species, and even between-site differences in sap yield and sugar content. Efforts to understand why some trees provide more and/or sweeter sap, could facilitate the search for and breeding of high-yield cultivars. More importantly, this knowledge may prove critical to decide when to rest a tree for the season to avoid stressing it too much and exhausting crucial energy reserves.

6. Sources of variability in sugar yield and other important questions

The various effects of tap and tree characteristics on sap yield and sugar content are by no means the only source of variation. To be able to determine any influence of tap and tree characteristics, we had to account for variability between sites and years. Year-to-year variability is known to be a strong constraint on sap yield (Blum, 1973; Larochelle, 1998; Tucker, 1990), yet our data suggests that species, site, and tree characteristics all introduce more variability in sap yields than differences between years ($\sigma_{spp} = 1.06 \pm 0.64$, $\sigma_{site} = 0.98 \pm 0.27$, $\sigma_{tree} = 0.58 \pm 0.04$, $\sigma_{year} = 0.32 \pm 0.09$, $\sigma_{tap} = 0.07 \pm 0.05$, respectively). While this indicates that between-year variability is the second smallest source of variability in sap yields (among the sources included in our model), we caution against strong conclusions, as the model structure might confound some interannual variability for site-specific variability. To reliably differentiate between site- and year-specific variability, data from additional sites and years will be instrumental. Nevertheless, the overall pattern is identical with regards to sources of variability in sap sugar content (*i.e.*, $\sigma_{spp} > \sigma_{site} > \sigma_{tree} > \sigma_{year} > \sigma_{tap}$), suggesting that sap yield and sugar content might have largely similar drivers. For both sap yield and sugar content, the two smallest source of variability (i.e., variability among years and taps) have received by far the most attention, while tree characteristics and even more so site characteristics are relatively under-studied sources of variability. As such further investigating species, site, and tree characteristics holds substantial promise to understand differences in sap yield and sugar content.

There are a few obvious starting points for determining the importance of various site and tree characteristics. At the site-level, nutrients - primarily calcium - have been related to either vigour or directly to sap yields and sugar content (Bal et al., 2015; Ouimet et al., 2017; Schaberg et al., 2006). Adding site *meta*-data, such as soil nutrient levels, soil texture, and topographic indicators, to future data collections would permit a more detailed break-down of these site-level effects. As new forests are starting to be exploited in a rapidly growing industry, understanding the effects of site characteristics on sap yield and sugar content would help to select optimal sites. With regards to the influence of tree characteristics, many metrics have been tested in the past including growth history (Grenier et al., 2007), crown size (Tucker,

1990), and wood anatomy (Gregory, 1978, 1977). However, little work has be conducted on the effects of competition or the allocation, size and dynamics of nonstructural carbon reserves; especially during the leafless state. Understanding nonstructural carbon dynamics in mature trees remains challenging (Rademacher et al., 2019), but given methodological advances in physiological measurements we do now possess the tools to further probe for drivers of variability in sap yield and sugar content between trees. With the additional collection of comprehensive data on tap, tree, and site characteristics, we could integrate them in a single analytical framework to partition relative contributions of variability.

6.1. *Currently unquantifiable sources of variability*

Despite our best efforts, data about certain potential drivers of variability remains rare and therefore evaded systematic inclusion in our analyses. For example, methods and equipment of extraction, such as high-vacuum tubing, have been studied in isolation (Lagacé et al., 2019; Wilmot et al., 2007), but there was no data to include them here. While high-vacuum sap extraction does not seem to affect tree health in the short-run (Lagacé et al., 2019), better understanding of the tree's underlying nonstructural carbon dynamics is needed to rule out nefarious interactions with disturbances that also affect nonstructural carbon reserves (e.g., drought and herbivory). In fact, disturbances are another important source of variability that has rarely been studied to our knowledge in the context of maple sugaring (but see Moreau et al., 2020; Pothier, 1995), despite their projected increases in frequency and intensity with climate change (Seidl et al., 2017). In particular, drought, pests and pathogens, storm related damages, and how they affect maple sugaring ought to be studied in the future. Similarly, there are no studies yet that attempted to quantify the effects of community composition, despite the fact that the composition is known to affect, at least, growth dynamics and micro-climate.

7. Conclusions

Maple sugaring operations will be affected by the climate and biodiversity crises. Producers already feel that they are lacking the knowledge to adapt to these crises (Legault et al., 2019). Science-based tapping guidelines and forecasts can help producers to adapt their tapping and forest management practices but require a solid foundation. Here, we showed that the sources of variability in sap yield and sugar content are in descending order of importance: species, site, tree, year, and tap. Most previous research focussed on the two smallest sources of variability. In this context, we posit that continuing systematic measurements across species, sites, trees, years, and taps are necessary to finally disentangle the influence of individual factors on sap yield and sugar content. To ensure the sustainability of maple sugaring operations in a changing environment, we advocate for a network of standardised long-term measurements focussing on the major sources of variability in sap yield and sugar content.

8. Data availability

All code to reproduce the analysis is publicly available at https://github.com/TTRademacher/acer-web. The data is a compilation of various data sources and includes some publicly available data sets, such as the Harvard Forest data (Rapp et al., 2021).

Author contributions

TR had the idea for the paper, compiled the data and analysed it. TR, MC, ÉB, SSK, and JR collected and prepared data. TR developed the ideas with input from JD, ÉF and SD. TR wrote the first draft and revised the paper according to co-author and reviewer comments. All authors provided feedback on the manuscript and contributed ideas.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Tim Rademacher reports a relationship with Producteurs et Productrices Acéricoles du Québec that includes: speaking and lecture fees.

Data availability

The data use in this publication is partially available at https://www.sciencebase.gov/catalog/items?q=acernet and at https://harvardforest1.fas.harvard.edu/exist/apps/datasets/showData.html?id=HF285.

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