Forestry: An International Journal of Forest Research, 2024, 1–13
https://doi.org/10.1093/forestry/cpae022
Original Article

Age and growth reductions increase the proportion of dark heartwood in sugar maple at the northern limit of its range

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Abstract

The wood of sugar maple (*Acer saccharum* Marsh.) in the northernmost part of the species range often exhibits high proportions of discoloured wood at the centre of the stems, which is referred to as dark heartwood. This defect significantly decreases the wood market value of the species, which, in turn, challenges the implementation of state-of-the art silvicultural treatments. The causes of dark heartwood are associated with trauma and the colder climate of the northern regions. In this study, we investigate factors influencing the occurrence of dark heartwood in sugar maple's northern populations, considering tree age, vigour, stem growth, and local climate. We also aimed to determine whether the proportion of dark heartwood is higher in northern stands compared to more southern ones. We collected samples from 302 sugar maple stems at 16 sites within two bioclimatic domains of Quebec, Canada, i.e. the balsam fir–yellow birch domain (representing the northern limit of the sugar maple range) and the sugar maple–yellow birch domain (representing a more southern location within the range). Our results indicate a positive relationship between dark heartwood proportions and stem age, as well as with the amplitude of the maximum growth reduction throughout the tree's lifespan and the length of the longest suppression period. We also observed significantly higher dark heartwood proportion for a given tree age in northern stands. The results suggest that silvicultural systems aiming to release suppressed crop trees through group selection using a cut-to-length system could favour the development of high quality timber.

Keywords: Sugar maple; dark heartwood; growth; tree quality; climate; discolored wood

Introduction

Sugar maple (*Acer saccharum* Marsh.) is an important species of the hardwood forests in eastern North America (Godman et al. 1990). This species is highly sought for sawing and other valuable timber products (Farrar 1995; Godman et al. 1990). The market value of its wood depends on its aesthetic quality, which is affected by the presence of defects such as dark heartwood (Erickson et al. 1992; Havreljuk et al. 2013). In sugar maple, dark heartwood is characterized by a reddish-brown colour, which contrasts with the normal pale, uniform colour of the wood (Havreljuk et al. 2013). The dark heartwood zone is usually concentrated at the centre of the stem's cross-section, and its shape can be either uniform (i.e. circular) or irregular (Erickson et al. 1992; Shigo 1966). Specifically, dark heartwood is an internal defect that progresses through the wood when a wound is created on a stem (Shigo 1966; Wernsdörfer et al. 2005). Unlike naturally occurring heartwood in some species, dark heartwood in sugar maple is purely attributable to traumatic causes (Shigo and Hillis 1973; Shigo and Marx 1977). Since the value of dark heartwood is lower than that of clear wood, its presence can have a substantial impact on the profitability of the forest value chain (Delisle 2019; Erickson et al. 1992).

Sugar maple trees in colder climates at the northern limit of the species' distribution range are more likely to contain large proportions of dark heartwood (Havreljuk et al. 2013; Wiedenbeck et al. 2004). In Quebec, the northernmost sugar maple stands are located on hilltops in the balsam fir–yellow birch bioclimatic domain (Després et al. 2014; Graignic et al. 2018; Guillemette and Bédard 2019; Saucier et al. 2009). Environmental conditions in these areas may contribute to a greater abundance of dark heartwood and wood decay (Burton et al. 2008; Havreljuk et al. 2013). The higher occurrence of dark heartwood in northern maple stands is a major barrier to the profitability of the wood value chain, and in turn to the application of state-of-the-art silviculture (Hassegawa et al. 2018). However, it remains unclear whether changing climatic conditions and/or the implementation of management solutions could potentially mitigate the occurrence of this defect. Despite increasing temperatures over recent decades due to climate change, a growth decline has been observed at the northern limit of the sugar maple range (Boakye et al. 2023). However, it remains to be determined to what extent this growth trend could be related to the development of dark heartwood.

The presence of dark heartwood has previously been associated with the radial growth rate of the stem, with higher

Handling editor: Dr. David Auty
Received: August 27, 2023. **Revised:** April 3, 2024. **Accepted:** May 2, 2024

proportions being linked to periods of rapid growth followed by suppressions at the margin of the colored area (Havreljuk et al. 2013). While some studies also suggest a positive correlation between dark heartwood and tree age (Havreljuk et al. 2013; Kaminski et al. 2019), others suggest instead that the ratio of stem size to that of the dark heartwood zone within the stem decreases with increasing diameter (Germain et al. 2015; Yanai et al. 2009). Other studies have found that moribund sugar maple stems tend to have a higher proportion of dark heartwood (Baral et al. 2013; Kaminski et al. 2019). There is little information on the potential effects of site characteristics on the proportion of dark heartwood, but Havreljuk et al. (2013) found a negative correlation between the average minimum temperature of a site and the proportion of dark heartwood within the stem.

Results from previous studies suggest that in colder climates at the northern limit of the sugar maple range, dark heartwood proportion could be higher than in more southern locations due to lower stem vigour, increased occurrence of external defects (e.g. cracks), and reduced stem growth (Burton et al. 2008; Guillemette and Bédard 2019; Havreljuk et al. 2013). However, the associations between local climate, stem vigour, and dark heartwood proportion observed in these studies have yet to be validated for sugar maple at the northern limit of its range because previous research has primarily focused on sugar maple stands located further south (Baral et al. 2013; Havreljuk et al. 2013; Kaminski et al. 2019).

In this study, we investigated the relationships between sugar maple dark heartwood occurrence and climatic variables at the site level, as well as links with tree vigour, age, and growth. Our analysis is based on a comprehensive sampling effort covering the northern part of the species' range throughout Quebec. We hypothesized that the proportion of dark heartwood would increase in old, non-vigorous trees, having experienced periods of growth suppression. Additionally, we hypothesized that stands in the balsam fir–yellow birch domain (i.e. at the northern limit of the species range) have a higher proportion of dark heartwood than more southern stands because of the colder climate.

Methods

Study sites and plot measurements

We sampled 16 sites (Table 1; Fig. 1) across two bioclimatic domains in Quebec: the balsam fir–yellow birch and the sugar maple–yellow birch (Saucier et al. 2009). In the balsam fir–yellow birch domain, the mean annual daily temperature ranges from approximately 1.5°C to 2.5°C, while in the sugar maple–yellow birch domain, the mean annual daily temperature ranges from approximately 2.5°C to 4.0°C. The sugar maple–yellow birch domain represents our southern sites where the maple stands are typically distributed throughout the area as a forest massif. In contrast, in the balsam fir–yellow birch domain, maple stands are more likely to be distributed in small populations in a landscape dominated by softwood species. Sugar maple stands at the northern limit of the species' range are typically located on hilltops with moderate drainage (Goldblum and Rigg 2002). This topographical location appears to offer a favorable microclimate for sugar maple as it is protected from cold air drainages that may occur towards the valley bottoms (Goldblum and Rigg 2010, 2002).

To control for topography, sites in both bioclimatic domains were sampled in similar topographical positions, i.e. on hilltops with moderate drainage. Our selected sites consisted of uneven-aged stands with mature sugar maple trees, where there was no documented history of severe anthropogenic or natural disturbances listed in government databases. Such disturbances would include any substantial alteration of stand structure attributable to the simultaneous mortality and/or removal of a significant proportion of trees in the stand. We ensured that the selected sites were evenly distributed across the studied bioclimatic domains, and we considered site accessibility to facilitate field sampling.

At each site, we established four plots with a radius of 11.28 m (400 m^2). For trees with a DBH of 30 cm or larger, the plot radius was adjusted to 14.10 m (625 m^2). We measured the DBH of all trees and used these measurements to calculate the stand basal area. The basal area of sample sites ranged between 23.6 and 34.8 m^2/ha, with an average of 28.3 m^2/ha, which is indicative of well-stocked stands unaffected by recent disturbances.

Stem classification

To investigate the extent to which the proportion of dark heartwood could be predicted by the presence or absence of external defects related to tree vigour, we classified all stems using the MSCR system developed by Boulet and Landry (2015). The system evaluates the risk of mortality according to the most severe category of defects occurring on the tree, including (1) fungal infection, (2) cambial necrosis, (3) bole deformations and injuries, (4) butt and root defects, (5) stem and bark cracks, (6) woodworms and sap wells, (7) crown defects, and (8) branching and pruning defects. A harvest priority is assigned based on the risk of mortality, categorizing it into one of four classes: moribund (M), survival (S), conserve (C), and reserve (R). For our analysis, we grouped the stems into two categories based on their vigour: high (CR) and low (MS) vigour as was done by Pothier et al. (2013).

Characterization of stem growth and dark heartwood

To induce variation in stem DBH and to sample the various diameter classes typically encountered in maple stands, we defined four diameter classes and aimed to sample three sugar maple stems in each class at every plot (Table 2). To select trees for core sampling, we chose the first three trees in each diameter class in a clockwise direction, starting from the north. To ensure capturing a portion of the variability in the cross-sectional shape of the stem and dark heartwood zones, we collected two cores at a height of 1.3 m above ground and at a 90° angle from each other on the selected sugar maple stems using a Pressler increment borer (Haglöf, Sweden). When there were fewer than three stems in the plot for a given diameter class, the sample was reduced by taking what was available. Overall, an average of 9 trees per plot (36 per site) were sampled (Table 2).

Before analysis, the samples were dried and sanded, and the rings measured using a Velmex ring gauge (± 0.002 mm, Velmex Inc., USA). To confirm the dating of the samples, we standardized the individual tree-ring series using COFECHA software (Cook and Peters 1981; Grissino-Mayer 2001; Holmes 1983). The robustness of all site chronologies was confirmed by the expressed population signals reaching over 0.85 after the first year that included all samples in each chronology (Wigley et al. 1984). To ensure the accuracy of the dated chronologies, we excluded cores for which dating could not be confirmed, often in trees with highly suppressed stem cores or young stems (302 trees). However, these cores were retained in the model developed to predict the proportion of dark heartwood within a stem. We also excluded samples with wood decay from the analysis of dark heartwood. This is because wood decay significantly compromises wood structure, prevents age estimation, severely restricts growth analysis in

Table 1. Characteristics of sampling locations

Location ID	Bioclimatic domain	Elevation range (m)	Mean annual daily temperature (°C)	Stand basal area (m^2/ha)
1	Balsam fir–yellow birch	329–370	2.0	30.1
2	Balsam fir–yellow birch	362–369	1.4	25.3
3	Balsam fir–yellow birch	436–457	1.6	23.6
4	Balsam fir–yellow birch	440–490	1.4	28.9
5	Balsam fir–yellow birch	462–492	1.4	24.2
6	Balsam fir–yellow birch	472–483	1.5	25.1
7	Balsam fir–yellow birch	535–565	1.2	34.8
8	Balsam fir–yellow birch	430–437	1.6	31.1
9	Balsam fir–yellow birch	429–452	1.8	32.9
10	Sugar maple–yellow birch	235–303	2.3	30.6
11	Sugar maple–yellow birch	469–496	2.6	29.1
12	Sugar maple–yellow birch	290–395	3.2	24.1
13	Sugar maple–yellow birch	316–328	2.9	32.7
14	Sugar maple–yellow birch	473–499	2.1	28.4
15	Sugar maple–yellow birch	340–363	3.1	25.7
16	Sugar maple–yellow birch	321–355	3.5	26.1

Mean annual daily temperatures were obtained through interpolation using surrounding weather stations and BIOSIM software.

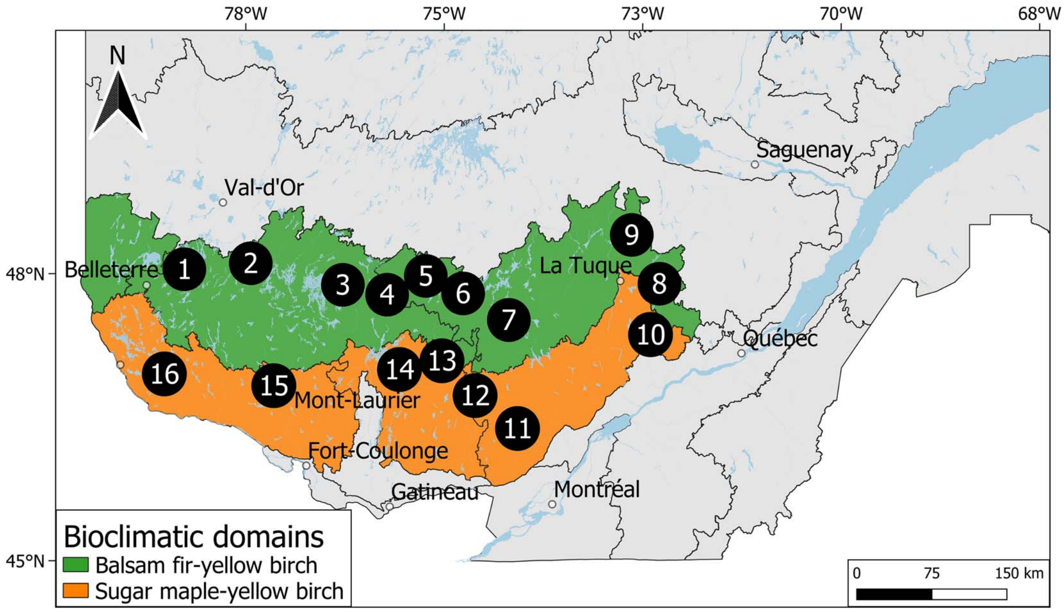

Figure 1. Location of the studies sites in the province of Quebec.

Table 2. Summary of sampled trees

DBH class (cm)	Total number of sampled trees	Number of trees with confirmed dating	Number of trees with age
9.1–19.0	256	88	151
19.1–29.0	189	132	81
29.1–39.0	107	75	30
39.1 +	174	129	28

The number of trees with confirmed dating comprises all decayed or non-decayed stems whose dating was statistically validated and used in the reference chronology. Tree age could not be estimated for samples containing decay; therefore, only trees without decay and with known ages were used for the dark heartwood analysis.

decayed areas, and strongly interacts with the proportion of estimated dark heartwood (Basham 1991). Following dating validation, we converted the ring width series into ring area using the *bai.in* function from the dplR package in R (Bunn et al. 2021), This function calculates ring area from the centre of the tree. When the sample did not reach the centre, as seen in instances where rot was present at the centre of the stem, the estimated missing length was incorporated into the calculation by the difference between the radius of the tree measured from its diameter and the length of the core sample. Unlike ring width, which naturally tends to decrease with an increase in stem circumference (Biondi and Qeadan 2008), ring area has the advantage to remain more stable over time.

To measure the radius of coloured wood, we performed an image analysis procedure similar to that of Havreljuk et al. (2013) on scanned core samples. This analysis allowed us to obtain a percentage of dark heartwood based on its radial length in the stem cross-section. We used the threshold function of the

ImageJ software for this step, which categorizes the pixels of an image into two categories (Abràmoff et al. 2005; Ridler and Calvard 1978). The threshold was automatically selected, with a unique value for each image. This approach limited experimenter bias, particularly at the dark heartwood boundary, which can often be diffuse and difficult to determine to the human eye. Furthermore, we employed the *remove outliers* function to reduce the noise resulting from the presence of conductive vessels within the wood, represented as white dots in the scanned image. This function automatically eliminates these white dots that could otherwise impact the threshold function. Given that the dark heartwood cross-sectional area is not consistently circular, we averaged the measurements from the two cores extracted from each tree.

Computation of growth indices from individual basal area increment series

We computed four indices to characterize the growth patterns of the sampled sugar maple stems. The first index was used to refine the analysis of growth reductions. The calculation of this index started with the calculation of the per cent-growth change (PGC), presented by Nowacki and Abrams (1997), which is typically used to detect growth releases but that can also be used to detect growth reductions (Das et al. 2007; Moreau et al. 2020c, 2020a). PGC was calculated by comparing the average basal area increment (BAI) in a period preceding any year of interest to the average increment in a period following that year (Equation 1):

$$PGC = \frac{M_2 - M_1}{M_1} \times 100 \quad (1)$$

where M_1 represents the mean BAI for the 5-year period preceding the year of interest, and M_2 represents the mean BAI over the subsequent 5 years. This process is iterative, and the same calculation was performed for all rings (Fig. 2). In the literature, the number of years considered around the year of interest typically vary between 5 and 10 years. A preliminary analysis showed that results were not very sensitive to the number of years included in the calculation. We opted for 5 years to account for medium-term variability (Black and Abrams 2004). We only retained the largest growth reduction in each tree (i.e. highest negative value of PGC) for subsequent analyses, which we refer to as the maximum growth reduction (MGR). By focusing on the most significant growth reduction, this index was deemed reliable to quantify the effect of the most traumatic event that a tree had sustained throughout its life.

Secondly, we calculated a suppression index (SUP, years) using the BAI (cm^2/year) to assess the probability of dark heartwood development in suppressed sugar maple trees. A suppression period is generally defined as several years during which the annual growth remains below 2 cm^2/year, for a minimum of 4 years (Canham 1985; Duchesne et al. 2003). However, adopting a more conservative approach, and considering that our sample is situated in a zone further north than those from the cited studies, we set a threshold of 1 cm^2/year. By employing this conservative threshold, we were able to focus our analysis on the most severe suppression periods. Ultimately, the longest suppression period was chosen for each stem.

The third index, SLR_{25}, was computed as the slope of the BAI over the 25 most recent years of growth. This index helped determine if the dark heartwood proportion was associated with the general growth trend of the last 25 years of the life of our sample stems. Previous studies have shown that moribund stems with declining growth can contain large proportions of dark heartwood (Baral et al. 2013; Shigo and Marx 1977).

Table 3. List of explanatory variables used in models describing the variation in dark heartwood proportion within tree stems

Variable	Description
Age (years)	Cambial age at 1.3 m
MGR (%)	Maximum growth reduction
SUP (years)	Period of suppression
Vigour	Vigour based on Boulet and Landry (2015)
SLR_{25}	Linear regression slopes of BAI values over 25 recent years
DBH (cm)	Diameter at breast height (1.3 m)
LogBAI (cm^2/year)	Log-transformed mean basal area increment
MAT (°C)	Mean annual daily temperature
DOM	Bioclimatic domain based on Saucier et al. (2009)

Table 4. Radial proportion of dark heartwood across age classes

Bioclimatic domain	Age class	Dark heartwood (%)
Sugar maple–yellow birch	30–59	42.55
	60–89	42.33
	90–119	48.87
	120 +	50.27
Balsam fir–yellow birch	30–59	30.31
	60–89	40.96
	90–119	50.02
	120 +	56.61

The fourth index was the averaged BAI (LogBAI, cm^2/year) over the entire lifespan of the trees. This variable was included in our analysis to assess whether stems with low average growth had a lower healing capacity and, consequently, a higher dark heartwood proportion (Germain et al. 2015). Prior to incorporating it into our models, we performed a logarithmic transformation on this variable due to the non-normal distribution of its residuals.

Climatic variables

To investigate the impact of the local climate on the development of dark heartwood, we extracted the site-specific mean annual daily temperature (°C) and total precipitation (mm) for the 1981–2010 period using the BioSIM software (Régnière et al. 2017). For each site, we used data from the four nearest weather stations to calculate the two climate variables (Régnière et al. 2017). Based on analyses including cross-correlations and correlations with the proportion of dark heartwood, we decided to include only the mean annual daily temperature (MAT) in the model (Table 3). This variable is also strongly linked to the concept of bioclimatic domains (Saucier et al. 2009).

Statistical analysis

We developed linear mixed models to describe the variation in dark heartwood proportion in sugar maple (Table 4). The selection of variables included in these models was based on their potential to explain the proportion of dark heartwood. They include growth indices, Age, Vigour, and DBH. We also incorporated bioclimatic domains and MAT as site-level predictors in our models and examined their interactions with other covariates. The interactions considered were those between MAT, DOM, DBH, and Age.

During the construction of candidate models based on the full model, we checked for high correlations between variables

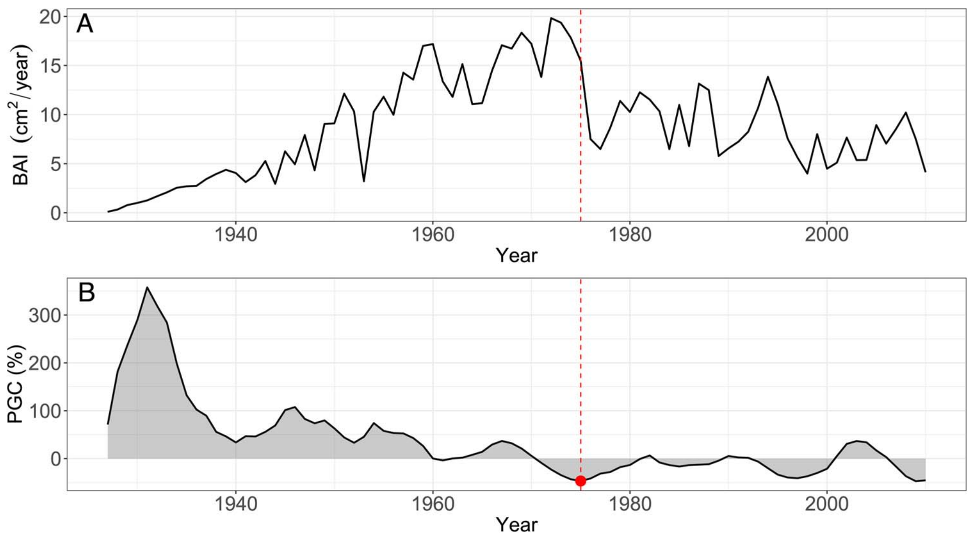

Figure 2. Process of calculating the MGR for a sample stem. (A) The BAI was calculated for all years of growth of the stem. (B) The PGC is calculated from the BAI for each year of growth, considering periods of 5 years before and after the year of interest. The point and the horizontal dashed line represent the largest drop (%) within the evaluated period, which corresponds to the MGR.

to avoid collinearity issues among predictor variables using the variance inflation factor (VIF) with a threshold of 5 (Zuur et al. 2010) (Supplementary materials, Table S1). The levels of correlation among candidate variables were low (VIF < 2) except between SUP and LogBAI, which was slightly higher (VIF = 2.30). However, model testing with and without these variables yielded consistent conclusions so both variables were retained as candidates in the model selection process. Cook's distances were used to verify extreme values, a quantile-quantile plot was used to check normality of the residuals, and a standardized residual plot was used to check the homogeneity of variances. We used the DHARMa package (Hartig and Lohse 2022) to generate the primary diagnostic plots (Supplementary materials, Fig. S1). Following these verifications, we observed a high level of correlation between stem DBH and LogBAI, and therefore these two variables were not included in the same models. A high level of correlation was also detected between MAT and DOM, so we also included them in separate models.

Then, to determine whether tree age or tree size is best related to dark heartwood proportion, we compared the performance of models including Age to those including DBH. Ultimately, 9 models resulting from these verifications were created. We used the glmmTMB package in R (R Core Team 2023) to fit the mixed models with a beta distribution, considering random effects on the intercept for both the site level and plots within a site (Brooks et al. 2023). The AICcmodavg package was used for model selection, based on the Akaike criterion corrected for small sample sizes (Burnham and Anderson 2002; Mazerolle 2020, 2006). This approach involves comparing various models to determine their relative predictive capabilities. An intercept-only model was included to ensure that it does not perform better than other, more complex models (Burnham and Anderson 2002).

These models were incorporated into a multimodel inference approach, following Burnham and Anderson (2002), to predict the impact of variables in interaction-free models. Then, as multimodel inference methods do not provide coefficient estimates and confidence intervals for models with interactions, we directly analyzed the interactions from the relevant models using a significance level of 5%. The predictions derived from models incorporating interactions were used to illustrate their effects.

To assess the synchronicity of MGRs, we determined the percentage of stems exhibiting their MGR in each decade. We utilized Tukey's HSD multiple comparison test to assess statistically significant differences in the occurrence of MGR among decades. Then, the mean BAI was computed and plotted by age class to visually examine growth patterns over calendar years. To validate our visual interpretation of the BAI patterns, we conducted a segmented regression analysis to identify the specific period when a growth shift occurred for each location (Zeileis et al. 2003). This analysis examines the temporal trend and detects changes, enabling us to identify a potential year for a shift in the growth trend for each age class, while considering the variability between stems of the same class (Bishop et al. 2015; Zeileis et al. 2003). A confidence interval was calculated based on the mean of all breakpoints. A linear model of BAI as a function of calendar years was subsequently applied to assess the statistical significance of the observed average growth trends following the breakpoint.

Results

Effect of growth, age, and vigour on dark heartwood proportion

The percentage of the stem's radius consisting of dark heartwood varied from an average of 35.38% for stems aged 30–59 years to 52.9% for stems aged 120+ across all measured samples; however, the range of variation across age classes was larger in the balsam fir–yellow birch domain (Table 4).

The best-performing model for predicting dark heartwood proportion in sugar maple included Age, Vigour, MGR, LogBAI, SUP, SLR_{25}, MAT, and its interaction with Age (model 1, AICc = −433.84, wi = 0.57). The model had an adjusted R^2 of 0.47, which decreased to 0.37 when calculated from the fixed effects only (Supplementary materials, Table S2). The second-best model, which incorporates the bioclimatic domain variable (DOM) instead of mean annual daily temperature (MAT), had a AICc difference of 1.58 (Δi) with the best model and a probability of 0.26 (wi) of being the best model among the set of candidates (Table 5).

Based on the 95% confidence intervals of the best model parameters, MGR (CI = −0.29 to −0.15), and Age (CI = 0.11 to 0.27) were found to have a significant impact on the dark heartwood

Table 5. Comparison of the multiple linear mixed regression models for sugar maple dark heartwood proportion

Model	ID	K	Df	AICc	Δi	wi	LL	R^2m	R^2c
Age + Vigour + MGR + LogBAI + SUP + SLR_{25} + MAT + MAT*Age	1	12	221	−433.84	0.00	0.57	229.48	0.37	0.47
Age + Vigour + MGR + LogBAI + SUP + SLR_{25} + DOM + DOM*Age	2	12	223	−432.26	1.58	0.26	228.69	0.37	0.46
Age + Vigour + MGR + LogBAI + SUP + SLR_{25} + MGR*LogBAI	3	11	222	−431.16	2.68	0.15	227.05	0.35	0.45
Age + Vigour + MGR + LogBAI + SUP + SLR_{25} + MAT	4	11	222	−425.99	7.85	0.01	224.47	0.34	0.45
Age + Vigour + MGR + LogBAI + SUP + SLR_{25} + DOM	5	11	222	−425.54	8.30	0.01	224.24	0.33	0.44
DBH + Vigour + MGR + SUP + SLR_{25} + MAT + MAT*DBH	6	11	222	−413.95	19.89	0.00	218.45	0.31	0.40
DBH + Vigour + MGR + SUP + SLR_{25} + DOM + DOM*DBH	7	11	222	−413.39	20.45	0.00	218.17	0.30	0.40
DBH + Vigour + MGR + SUP + SLR_{25} + MAT	8	10	223	−412.67	21.17	0.00	216.73	0.30	0.39
DBH + Vigour + MGR + SUP + SLR_{25} + DOM	9	10	223	−412.06	21.78	0.00	216.42	0.16	0.35
Intercept	10	4	228	−319.25	114.59	0.00	163.70	0	0.25

K is the total number of parameters (including an intercept and random terms), df is the degrees of freedom, Δi is the difference in AICc with the best model, wi is the probability that the model is the best among the whole set of candidates, LL is the Log-likelihood, R^2m is the marginal variance explained, and R^2c is the conditional variance explained. A description of the abbreviations used for the predictor variables is given in Table 3.

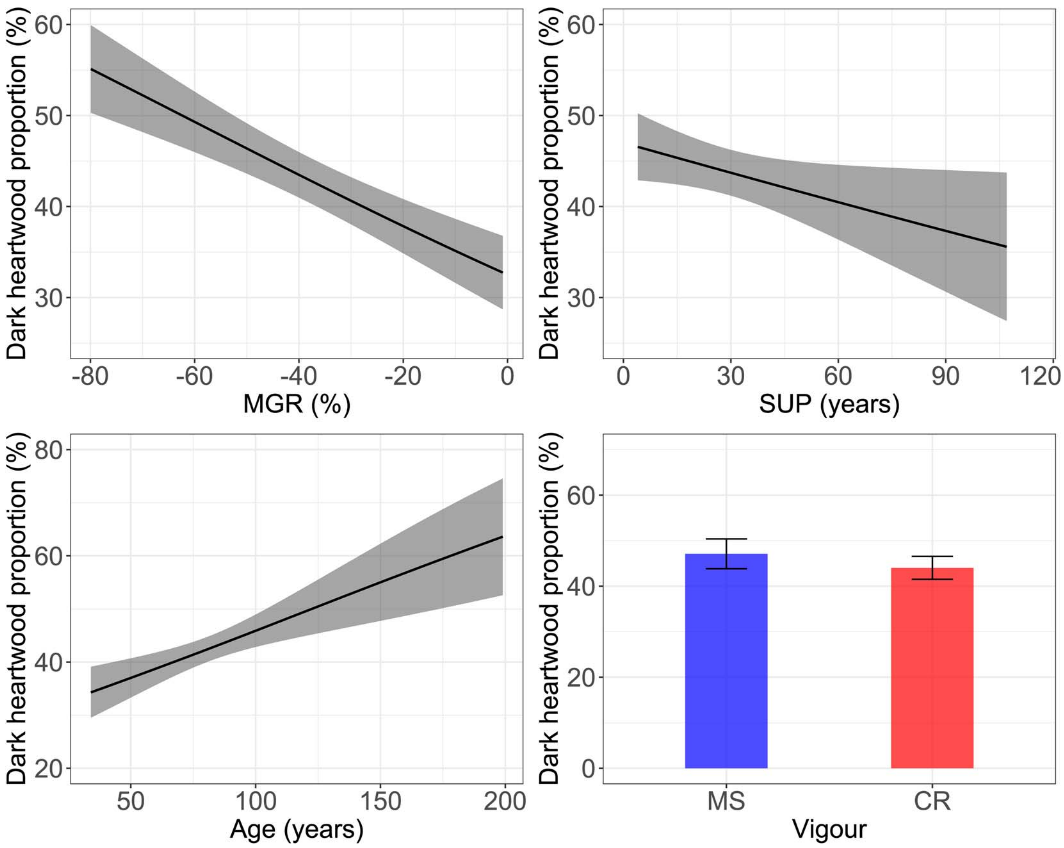

Figure 3. Fixed effects and marginal 95% confidence intervals for the best model predicting dark heartwood proportion with MGR, period of suppression (SUP), tree age, and vigour (MS represents non-vigorous trees and CR represents vigorous trees).

proportion (Fig. 3). The effect of SUP was weaker but remained significant (CI = −0.16 to −0.1). The effect of Vigour was found to be marginally significant (CI = 0 to 0.26), with non-vigorous stems tending to have a higher dark heartwood proportion (Fig. 3). The effects of MGR and SUP were negative, whereas the effect of Age was positive (Fig. 3).

Difference between bioclimatic domains

Models including Age performed better than those including DBH as a predictor (Table 5). The coefficients of the two best models had significant interactions between either Age and mean annual daily temperature (Fig. 4A; coeff = −0.09 ± 0.03; *P*-value <0.05) or Age and bioclimatic domain (Fig. 4B; coeff = 0.17 ± 0.06; *P*-value <0.05). The increase of dark heartwood with Age was faster in colder sites (Fig. 4).

MGRs over time

The greatest occurrence in MGRs occurred in the 2000s, affecting 39.4% of stems in the sugar maple–yellow birch domain and 32.8% of stems in the balsam fir–yellow birch domain (Fig. 5). Over 69.4% of the MGRs in the balsam fir–yellow birch domain and 73.9% in sugar maple–yellow birch domain occurred in the last 40 years. However, after 2010, the percentage of affected stems decreased substantially in both domains with only 6.1% in the balsam fir–yellow birch domain and 1.4% in the sugar maple–yellow birch domain.

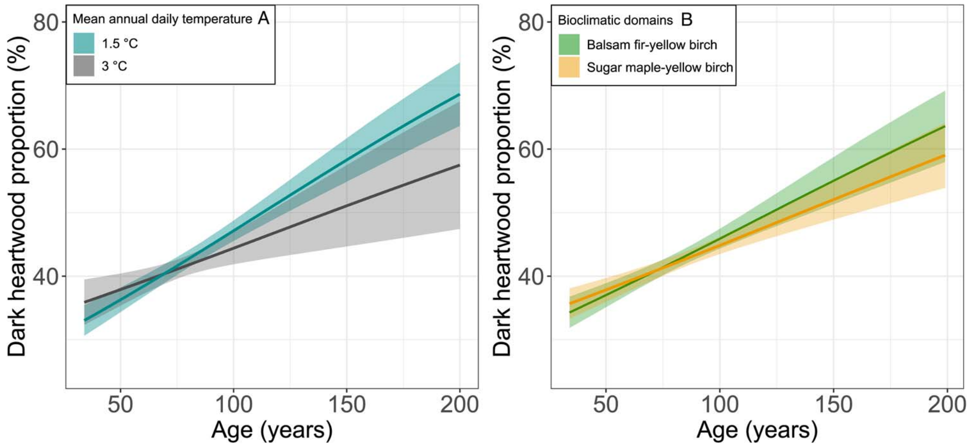

Figure 4. Predicted values of dark heartwood proportion and their standard error for a range of tree ages and different levels of mean annual daily temperature (A) and different bioclimatic domains (B).

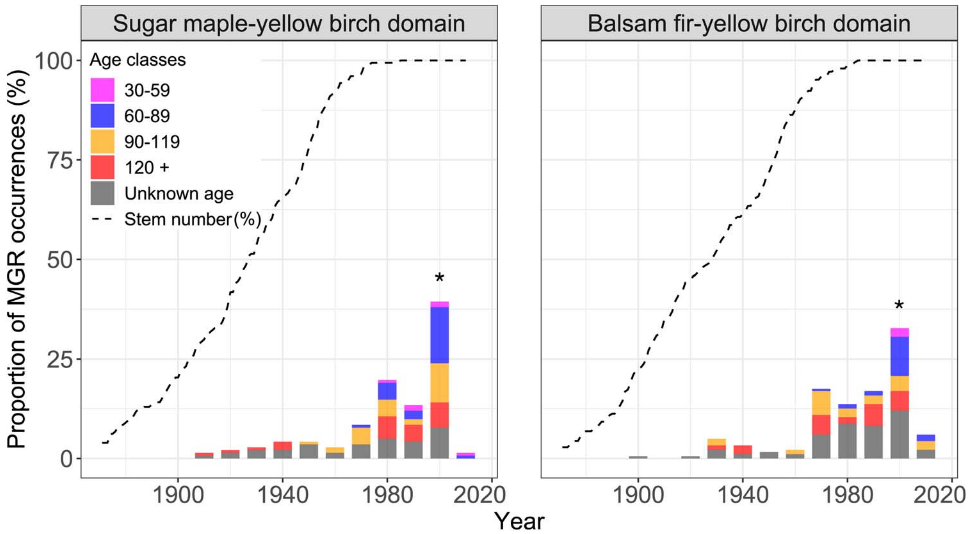

Figure 5. Percentage of stems that had their most important yearly growth reduction (MGR) occurring in each decade. The period when the most important proportion of MGRs occurred is represented by an asterisk. The proportion of MGR occurrences in a decade was calculated by dividing the number of MGRs in the decade by the total number of MGRs for all years. All stems with validated dating were included in this analysis and results were separated by bioclimatic domain. The dotted curve indicates the progression of the proportions of the total number of trees in the sample over time. The proportion increases over time due to the variation in tree age among samples.

In the balsam fir–yellow birch domain, mean BAI growth tended to stabilize and then decline after 1970, whereas the onset of decline was more variable in the sugar maple–yellow birch domain (Fig. 6). In both domains, trees aged 90 years and older experienced a decline in BAI after 1970, coinciding with the increase in MGR occurrences (Figs 5 and 6). This was also observed in stems of unknown age, in which the presence of decay at the core made the age estimation impossible. The balsam fir–yellow birch domain displayed the most negative growth slopes and the highest synchronicity for classes over 90. Conversely, the stems younger than 90 years exhibited the highest variability in breakpoints (Table 6). In the sugar maple–yellow birch domain, a sudden increase in BAI was observed just before the year 2000 in stems aged 60 years and older, which was thereafter followed by a rapid decline (Fig. 6).

Discussion

Overall, trees from all age classes contained proportions of dark heartwood above 30% on average, which can be considered an important impediment on timber quality. Results confirm our first hypothesis, which postulated that the proportion of dark heartwood would be positively correlated with low vigour, periods of growth suppression, and stem age. The fact that this association was marginally significant for tree vigour may be, in part, attributable to how the variable was defined. Tree vigour was assessed through the MSCR system in this study because it is the official system used in the province of Quebec. However, Moreau et al. (2023) have demonstrated that the MSCR system does not, in fact, provide a very accurate assessment of mortality risk or growth potential, which are two important indicators of tree vigour.

The robust positive relationship between stem age and the proportion of dark heartwood confirms previous findings from comparable research (Baral et al. 2017; Germain et al. 2015; Havreljuk et al. 2013) and indicates that tree age, rather than size, is a driver of dark heartwood proportion within sugar maple stems. We also found that the proportion of dark heartwood was strongly related to the MGR that a tree has experienced over its lifetime. This result refines the findings of Havreljuk et al. (2013), which

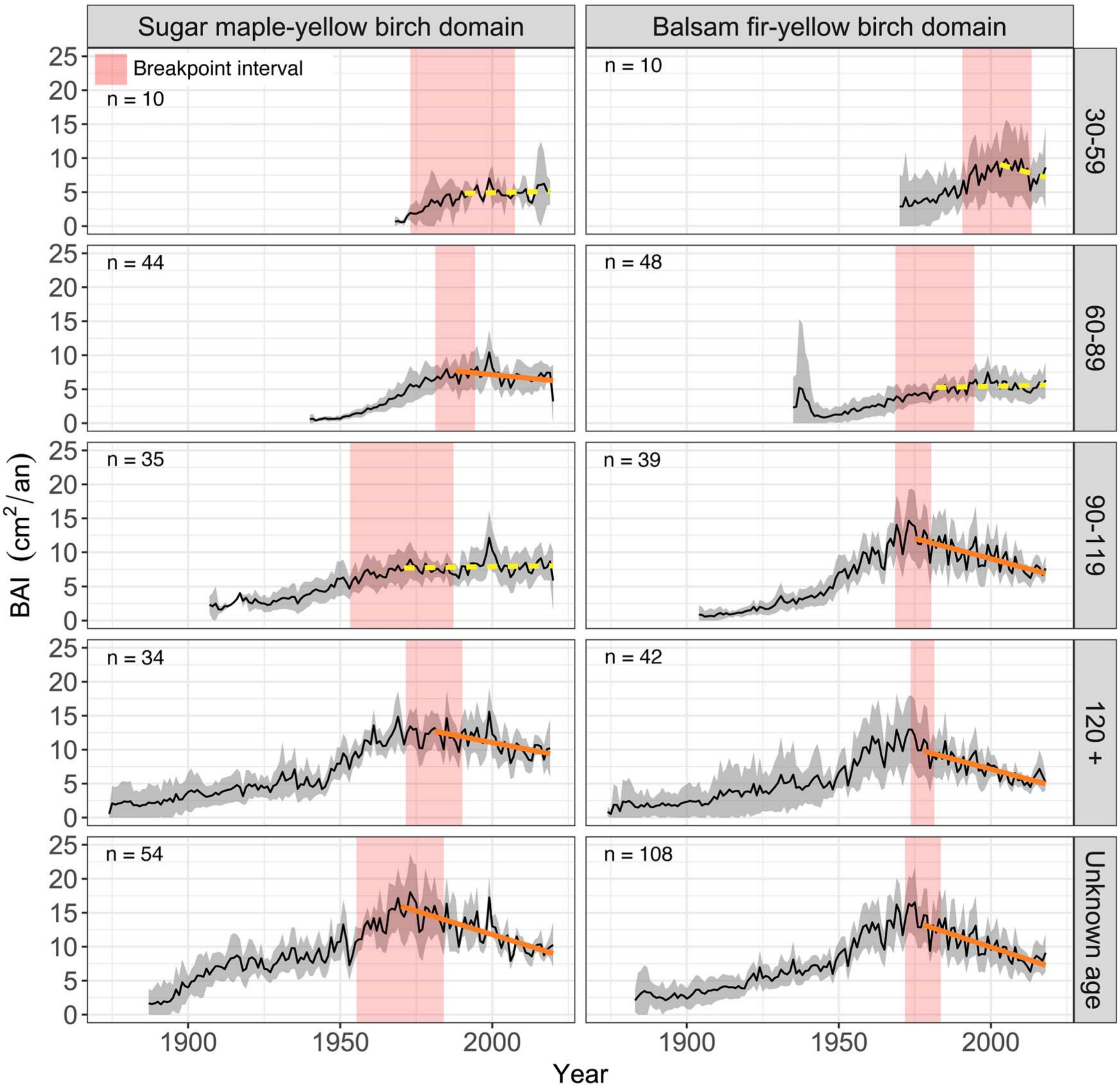

Figure 6. Average BAI by age class (i.e. 30–59, 60–89, 90–119, 120 and above), and for sample trees of unknown age. The black curve represents the mean growth calculated from all dated samples within each class, while the red zone depicts the confidence interval (95%) of the occurrence of breakpoints, indicating the moments of significant change in growth trend for each age class. The solid orange line indicates a statistically significant average growth decline following the mean breakpoint, while the dashed yellow line indicates a non-significant average growth trend, implying steady or no discernible trend in growth. The number of stems (*n*) per age class and bioclimatic domain is displayed in the top left corner for each subset.

Table 6. Descriptive results of the linear models applied to the different age classes and bioclimatic areas in the study

Bioclimatic domain	Age class	Breakpoint		Parametric coefficients		
		Mean	Std. error	Estimate	Std. error	P-value
Balsam fir - yellow birch	30–59	2002	6	−0.17	0.06	0.07
	60–89	1981	7	−0.05	0.01	0.36
	90–119	**1974**	**3**	**−0.13**	**0.02**	**<0.001***
	120 +	**1977**	**2**	**−0.13**	**0.02**	**<0.001***
	Unknown age	**1977**	**3**	**−0.18**	**0.02**	**<0.001***
Sugar maple - yellow birch	30–59	1990	9	0.03	0.02	0.57
	60–89	**1987**	**3**	**−0.04**	**0.02**	**<0.05***
	90–119	1970	9	−0.04	0.01	0.53
	120 +	**1980**	**5**	**−0.09**	**0.02**	**<0.001***
	Unknown age	**1969**	**7**	**−0.13**	**0.02**	**<0.001***

The table includes the mean breakpoint of all stems, which indicates the year when the growth trend changed, along with its corresponding standard error. The coefficient of estimated trend after the breakpoint, its standard error, and the significance probability (P-value) are also shown. The oldest stem encountered in the class of 120+ is 200 years, while the earliest decay-free year for stems of unknown age is 1833 (187 years).

focussed on growth changes at the margin of the dark heartwood. MGRs may be related to trauma, which, in turn, may lead to the development of dark heartwood by facilitating the penetration and progression of microorganisms into the stems (Baral et al. 2013; Germain et al. 2015; Havreljuk et al. 2013; Shigo and Hillis 1973). Our model selection analysis highlighted age and the MGR index as the primary drivers of the proportion of dark heartwood.

Our results also confirm our second hypothesis that, at a given age, trees in the balsam fir–yellow birch domain tend to have a higher proportion of dark heartwood compared to those from the sugar maple–yellow birch domain further south. The proportion of dark heartwood increased more rapidly with age in colder, more northern sites. Given that models incorporating the interactions of bioclimatic domains and mean annual temperature accounted for similar proportions of the variance, it appears adequate to utilize either variable depending on the specific circumstances. However, the limited number of sampling sites (i.e. 16) and the better AICc of the model including mean annual temperature (model 1) suggest predictions based on site-specific mean annual temperature, if available, would be preferable to those applicable to the full extent of a bioclimatic domain.

Growth trends appeared consistent in both bioclimatic zones until the 1970s. Following decades then marked the onset of a decline period characterized by a downward trend in growth primarily in older stems, but also present to a lesser extent in younger stems. This period is also marked by a high occurrence of MGRs. Using the same dataset as employed in the present study, Boakye et al. (2023) confirmed that sugar maple growth has been declining in recent decades over our study area. The overall synchronicity of the MGRs observed in this study and the initiation of the overall growth decline post-1970 suggests that traumatic events (such as droughts, late spring frosts, insect outbreaks) led to a loss of vigour. This, in turn, favored the production of dark heartwood proportions in our sample trees. This period also coincides with the emergence of declining growth trends reported in other studies on sugar maple growth (Duchesne et al. 2003; Moreau et al. 2020a; Nolet and Kneeshaw 2018), which have also characterized a broadscale dieback period for this species (Duchesne et al. 2002; Horsley et al. 2002; Long et al. 2009; Payette et al. 1996).

Several types of disturbances have been suggested as potential causal agents for sugar maple dieback, such as thaw-freeze events, forest tent caterpillar epidemics, acid rain, and their compound effects (Bishop et al. 2015; Cooke and Lorenzetti 2006; Duchesne et al. 2003; Moreau et al. 2020a). Several studies have already demonstrated that extreme climatic events, such as thaw-freeze events and droughts, might exert a more pronounced impact at the northern edge of the range of numerous species due to the inherently challenging environmental conditions in those regions (Chagnon et al. 2023; Goldblum and Rigg 2010; Zang et al. 2014). However, studies specifically investigating the connections between sugar maple and these extreme climatic events at its northern limit have not yet been undertaken. For instance, Moreau et al. (2020a) found that droughts and thaw–freeze events caused sudden growth declines. However, this study took place in southern latitudes, distant from the species' northern distribution limit.

In our study area, the nutritional quality of soils may have interacted with traumatic events and contributed to initiating this period of dieback. Previous studies have shown that nutrient-poor soils are associated with a lower resilience of sugar maple stems to traumatic events (Bal et al. 2015; Long et al. 2009). At the northern limit of the species' range, nutrient poor Canadian Shield soils (Goldblum and Rigg 2010) may have led to a higher synchronicity of growth declines than further south. Future research should aim to obtain a better understanding of the causes of such growth reductions, as well as the potential interactions among these factors. It should also aim to ascertain whether these traumatic events will become increasingly prevalent with climate change (D'Orangeville et al. 2018; Iverson et al. 2008; Moreau et al. 2020a).

The synchronicity of the breakpoints in growth trends measured in this study appeared to be higher and the subsequent growth declines steeper in trees >90 years of age from the balsam fir–yellow birch domain (i.e. at the northern limit of the sugar maple range). This suggests traumatic events were more concentrated in time and had a more severe impact on tree vigour at the northern limit of the range. The more prominent synchronization among older trees is in line with previous results showing that the response to traumatic events can vary according to tree age (D'Amato et al. 2013; Zang et al. 2014). Our results showed no significant differences in dark heartwood proportion according to the bioclimatic domain or the mean annual temperature of the site for trees younger than 90 years of age. This suggests that the higher proportion of dark heartwood at the northern limit of the range is not attributable to a direct effect of site-level variables but is rather the legacy of traumatic events that occurred at these latitudes in the 1970s and that mainly affected older stems. In other words, at these northern latitudes sugar maple trees have suffered a long, trauma-induced, and particularly intense period of dieback, which likely led to higher dark heartwood proportions among older stems.

We also found a negative but weak relationship between the proportion of dark heartwood and the length of the suppression period characterized by a BAI lower than 1 cm^2/year. This unexpected result indicates that suppressed stems generally develop a lower proportion of dark heartwood. This may be related to the fact that suppressed trees can exhibit a distinct susceptibility to traumatic events, as was observed for the forest tent caterpillar epidemic in the 1980s (Cooke and Lorenzetti 2006; Schowalter 2017) and for thaw-freeze or drought events (Clark et al. 2016). This is consistent with our finding of a different reaction to traumatic events between younger and older trees. Due to the uneven-aged structure of the stands, lower stems in our study occupied lower positions within the canopy. Suppressed trees have a lower leaf-to-sapwood ratio, which may limit transpiration and reduce drought vulnerability in these individuals (Clark et al. 2016; Niinemets 2010). The limited growth of suppressed stems may also limit the development of branches, which could be an advantage considering that dead branches are important entry points for dark heartwood (Belleville et al. 2011; Havreljuk et al. 2013). However, the limited effect of the suppression could be attributed to age, as older suppressed stems may display a higher proportion of dark heartwood due to their advanced age. In other words, slow growth implies that stems are inevitably older when reaching a merchantable diameter, a factor that was linked to a higher proportion of dark heartwood. Furthermore, although efforts have been made to study the critical period of stem suppression before their recruitment into the canopy (Canham 1985), our approach to associate suppression with growth remaining below the 1 cm^2/year threshold may be overly simplistic; such slow growth may have occurred in some trees even after their recruitment in the main canopy. Nevertheless, this indicator still allows us to confirm that stems with a long period of homogeneous growth, whether low or high, tended to be associated with lower proportions of dark heartwood. Future studies should delve more deeply into this variation in responses to traumatic events based on the social position, competition and age of the trees.

A marginally significant relationship was found between the MSCR vigour classification developed by Boulet and Landry (2015) and the dark heartwood proportion. A more precise assessment of the effects of individual defects (Havreljuk et al. 2014; Moreau et al. 2023, 2020b) might have improved the relationship between tree vigour and dark heartwood proportion. Despite this, our findings, along with those of previous studies, tend to confirm the traumatic nature of dark heartwood in sugar maple, as was observed in other hardwood species, such as white birch (*Betula papyrifera* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) (Belleville et al. 2011; Wernsdörfer et al. 2005). More research is required, however, to fully comprehend the interactions among dark heartwood, tree growth, climatic events, and other factors such as insect outbreaks (Moreau et al. 2020a).

One limitation of our study was the range of variation among our sample stands, which were characterized by low levels of disturbance and were located at similar topographical positions on the tops of hills. The high stem density within all plots might have constrained individual stem growth, potentially interacting synergistically with traumatic factors (Pothier 1996). Subsequent research could encompass sites affected by past disturbances and positioned differently topographically, as disturbances may result in accelerated individual tree growth, potentially curtailing the development of dark heartwood. However, this beneficial effect may be limited by the presence of larger branches associated with potentially larger wounds (Belleville et al. 2011; Havreljuk et al. 2013; Wernsdörfer et al. 2005), as well as by cutting wounds in managed stands (Moreau et al. 2019).

Silvicultural implications and concluding remarks

Our results provide valuable insights for enhancing sugar maple silviculture. A key question for silviculturists is whether stands at the northern limit of the sugar maple range may be managed to produce high quality timber. Our results demonstrate that dark heartwood proportion increases with the amplitude of growth reductions as well as with tree age, thus highlighting the importance of steady, vigorous growth (Moreau et al. 2019). The fact that younger stems contained similar proportions of dark heartwood at northern latitudes compared to stems of similar age in more southern sites suggests the production of high-quality timber is possible at northern latitudes. However, because the progression of dark heartwood with tree age was more pronounced in northern sites, it may be advisable to harvest stems at a younger age than what is generally prescribed further south. Additionally, combinations of factors that have led to growth decline and higher proportions of dark heartwood among older trees in northern sites appear to have been rare and isolated over the past decades. More work is, however, needed to estimate the likelihood of their occurrence in years to come.

Producing stems of a merchantable diameter at a younger age could help limit the loss of timber value caused by dark heartwood. Younger trees exhibited a lower susceptibility to the traumatic events that predominantly affected older trees since the 1970s, especially in the northernmost sugar maple stands. However, results have also shown that trees undergoing a long period of suppression also tend to have lower dark heartwood proportion. This suggests that silvicultural systems aiming to release suppressed crop trees through group selection using a cut-to-length system could minimize damage to residual stems and promote the development of high-quality timber. Trees intended for release must exhibit few defects and be vigourous to avoid potentially leaving genetically inferior and malformed saplings as future crop. Experiments evaluating the future growth potential of these trees should be implemented to test the effects of the proposed approach and its potential to decrease the proportion of dark heartwood in sugar maple stands. Lastly, our results do not imply that we should rely solely on suppressed stems to ensure the future of these forests; instead, our results suggest that the focus should be on promoting uniform growth for future sugar maple stems.

Given that the majority of northern hardwood stands are uneven-aged and comprise a high proportion of suppressed stems, understanding how these trees will respond to and maintain their quality after a partial cut, remains to be determined. The difference in quality between regeneration established following a treatment and that of suppressed advance growth remains to be validated. Key to the success of such silvicultural systems at the northern limit of the sugar maple range will be whether harvesting older, less vigorous trees combined with the release of crop trees can stop, or even reverse, the declining growth trends observed in these stands over recent decades. For this to materialize, processing pathways will be required for low quality timber. In this sense, a profitable forest value chain is essential to the implementation of state-of-the-art silviculture. Future research should investigate the causes of the observed growth declines observed in this study and evaluate the capacity of silvicultural treatments to reverse this trend in a rapidly changing climate.

Acknowledgements

We are grateful to Frédéric Mireault-Pelchat, Audrey Demers, Sébastien Dumont, and Gabriel Tremblay for their fieldwork and laboratory analysis contributions, as well as to the Tree-ring Laboratory at Laval University, managed by Ann Delwaide, for their laboratory analysis support. We also want to express our gratitude to the reviewers for their valuable comments, which have allowed us to enhance this article.

Author contributions

David Voyer (Conceptualization, Formal analysis, Methodology, Writing—original draft, Writing—review & editing), Guillaume Moreau (Methodology, Supervision, Writing—review & editing), Fabio Gennaretti (Methodology, Supervision, Writing—review & editing), Pierre Grondin (Conceptualization, Funding acquisition, Writing—review & editing), Steve Bédard (Conceptualization, Funding acquisition, Methodology, Supervision, Writing—review & editing), Filip Havreljuk (Conceptualization, Funding acquisition, Methodology, Writing—review & editing), and Alexis Achim (Conceptualization, Methodology, Supervision, Writing—review & editing).

Supplementary Data

Supplementary data are available at *Forestry* online.

Conflict of interest statement

None declared.

Funding

This study was funded by the Ministère des Ressources naturelles et des Forêts du Québec (project number 142332159) and by an NSERC (Natural Sciences and Engineering Research Council of Canada) Alliance project (grant number 142 332 159) directed by Yves Bergeron. This work was supported by the Discovery Grants program of the Natural Sciences and Engineering Research Council of Canada (grant no. RGPIN-2021-03553 to F.G.) and by the Canadian Research Chair in dendroecology and dendroclimatology (CRC-2021-00368 to F.G.).

Data Availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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