

An accumulation of climatic stress events has led to years of reduced growth for sugar maple in southern Quebec, Canada

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Abstract. Understanding the influence of climatic variation on forest dynamics is of great ecological and economic interest, and is essential to prescribe silvicultural interventions that will facilitate ecosystem acclimation to global change. However, the retrospective identification of climatic events responsible for the inter-annual variation of tree growth is challenging, notably because both their duration and their subsequent effects can be highly variable in time. In this study, we aimed to (1) quantify empirically the effect of climatic stress events on the short- and long-term growth dynamics of sugar maple trees; (2) compare the effects of different types of climatic events, that is, drought and thaw–freeze; and (3) compare the effects of climatic stress events to those of traditional monthly level climate metrics. To achieve this, we paired cross-dated tree-ring series to monthly and daily-level climate metrics over more than 50 yr in two distinct regions of southern Quebec. While the analysis from monthly level metrics first suggested a weak and non-stationary relationship between climatic conditions and tree growth, the analysis from daily-level metrics showed that climatic stress events, and more particularly thaw–freeze events, were strongly related to the growth of sugar maple trees. Our results suggest that the synergic influence of cumulative climatic stress events, which was exacerbated by insect outbreaks during the early 1980s, induced an important shift in the growth dynamics of sugar maple and in its response to variation in climatic conditions. These results highlight the potential negative impact of global climate change on our capacity to predict stand productivity accurately, especially if climate-sensitive growth models are based on projections of future monthly metrics. Because adverse climatic events are expected to increase both in frequency and in severity over the next decades, a general decrease in the growth rate of sugar maple is apprehended in southern Quebec.

Key words: climate change; climate-smart silviculture; drought; frost; growth decline; insect outbreaks; thaw–freeze.

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INTRODUCTION

Forest ecosystem dynamics are affected by global climate change through the general increase in annual temperature, the frequency and severity of acute climatic events, and changes in natural disturbance regimes (Bell et al. 2004, Iverson et al. 2008, Allen et al. 2010, Dai 2013). In eastern North

America, a shift in composition toward slow-growing species that are more adapted to climate-induced stresses has already been observed (Zhang et al. 2018). Such shifts in forest composition and productivity will affect forest ecosystem dynamics and bring uncertainty about long-term forest growth (Zhang et al. 2018, SCAF 2018). A refined understanding of species-specific vulnerability to

climatic stressors is thus required not only to better anticipate the effects of climate change on forest ecosystems but also to ultimately help devise and implement adaptive measures (D'Amato et al. 2013, Allen et al. 2015, Nolet and Kneeshaw 2018).

An important challenge related to the quantification of such vulnerability is that climatic stresses, which may vary in duration, can also induce legacy effects that may far outlast the event itself (Anderegg et al. 2015). For example, severe droughts are known to induce growth reductions that can last for several years (Anderegg et al. 2015, Vanoni et al. 2016, Nolet and Kneeshaw 2018). The time resolution that must be used to detect both the causal factors and the induced response is therefore highly variable. Also, such legacy effects can lead to interactions with additional stressors and produce compound events that may ultimately lead to a long-term growth decline of trees and induce changes in the ecosystem dynamics (Nolet and Kneeshaw 2018).

Sugar maple (*Acer saccharum* Marsh.) is a key species both ecologically and economically in the northern hardwoods forest of northeastern North America. This late-successional species dominates a vast bioclimatic zone and is used for maple syrup production as well as being appreciated by the furniture and flooring industries. These attributes make it a well-studied species, especially with the current concerns about its response to climatic stressors (Oswald et al. 2018). Although sugar maple is a slow-growing species and is thus supposedly fairly resistant to climate-induced stresses, its vulnerability to climate change was evidenced by (1) niche model predictions suggesting an important decrease of its future potential habitat under projected climate scenarios (Iverson et al. 2008); (2) a significant growth decline observed across the range of the species over the last decades (e.g., Duchesne et al. 2003, Bishop et al. 2015, Nolet and Kneeshaw 2018); and (3) a higher vulnerability to climatic stressors than other companion species (Nolet and Kneeshaw 2018).

Despite the sensitivity of sugar maple to environmental conditions, results attempting to relate climatic variables to sugar maple growth dynamics seem somewhat contradictory (see Lane et al. 1993, Yin et al. 1994, Payette et al. 1996, Tardif et al. 2001, Gavin et al. 2008, Bishop et al. 2015). While some studies have observed moderate to

strong relationships between sugar maple growth and climate variables (Lane et al. 1993, Yin et al. 1994, Tardif et al. 2001), others have observed weaker relationships, which were generally associated with a non-stationary sensitivity to climate conditions over time (Payette et al. 1996, Gavin et al. 2008, Bishop et al. 2015). This lack of consistency between results may partly be explained by the inclusion of only monthly level climate metrics into modeling efforts, which may miss the effect of more acute events (Graumlich 1993). For example, novel metrics designed to capture the effects of climatic stress events, that is, periods of unusual warmth in January and August, were significantly related to the crown conditions of sugar maple trees over a 25-yr period (Oswald et al. 2018). Climatic stresses such as periods of drought and thaw–freeze events were also linked to decreases in the short- or long-term growth of this species (e.g., Graumlich 1993, Payette et al. 1996, Gavin et al. 2008, Nolet and Kneeshaw 2018). Despite such observations, the effects of climatic stress events have yet to be included in sugar maple growth models.

In this study, we paired cross-dated tree-ring series to daily climate metrics to quantify the effects of short-term climatic stresses on the growth dynamics of sugar maple trees from two distinct regions in southern Quebec. The growth response of individual trees to climatic stressors was investigated using a complementary set of four growth indices computed from tree-ring series covering a period of more than 50 yr. More specifically, we aimed to (1) quantify empirically the effect of climatic stress events on the short- and long-term growth dynamics of sugar maple trees; (2) compare the effects of different types of climatic stress events, that is, drought and thaw–freeze; and (3) compare the effects of stress events to those of traditional monthly level climate metrics.

MATERIALS AND METHODS

Sampling sites

Trees were sampled in two different areas on private woodlots owned by Domtar in southern Quebec, Canada. The first area (45°90' N, 70°80' W) was located in the Estrie administrative region, near the town of Saint-Malo, while

the second area (45°15' N, 71°55' W) was located in the Beauce administrative region, near Saint-Martin. These regions are both part of the eastern sugar maple-yellow birch bioclimatic subdomain, which is characterized by mean annual temperatures between 2.5° and 4°C, mean annual precipitation between 915 and 1100 mm and a growing season of 145–165 d (Saucier et al. 2009). The topography of this bioclimatic subdomain is characterized by hills and slopes, and the main surface deposits are shallow or deep tills (Grondin et al. 2007). The sampling sites were located in naturally established uneven-aged northern hardwood stands dominated by sugar maple, followed by yellow birch (*Betula alleghaniensis* Britt.) and red maple (*Acer rubrum* L.), with a smaller presence of American beech (*Fagus grandifolia* Ehrh.), black cherry (*Prunus serotina* Ehrh.), basswood (*Tilia americana* L.), hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), balsam fir (*Abies balsamea* (L.) Mill.), red spruce (*Picea rubens* Sargent), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). A period of insect defoliation was reported in this area during the early 1980s, which temporarily reduced the overall growth of sugar maple stands during the following decade (Payette et al. 1996; Domtar Corporation, *personal communication*).

Data collection and tree-ring chronologies

The radial growth history was assessed from increment cores sampled on trees located in two sets of permanent sample plots (PSPs) that were established between 1998 and 2004 in our study regions (9 PSPs in Estrie, 5 PSPs in Beauce). Both sets of PSPs were established on nearby sites with mesic soil-moisture conditions, gentle slope, and similar altitudes. During the summer of 2016, an increment core was extracted from all dominant/codominant live sugar maple trees within the 11.28-m radius circular plots. Cores were taken at a height of 1 m above the ground surface in the direction of the plot center. A total of 154 sample cores were glued to wooden blocks before they were air-dried and gradually sanded (Tardif et al. 2001). Only unbroken cores, with remaining bark at their end, without signs of decay and with complete delineation of latewood boundaries were retained for further analysis. Annual ring width was measured with a Velmex micrometer (± 0.002 mm). To remove the age-

related trend and isolate the climatic signal, each individual tree-ring series was standardized using a spline function with a 66% frequency response (Cook and Peters 1981). One master standardized chronology per study region was constructed using these tree-ring series. Treating all plots from a region as one group allowed us to isolate a more comprehensive climatic signal in the region rather than a stand-specific signal (Nolet and Kneeshaw 2018). Highly correlated (r values > 0.3) tree-ring series were sequentially added to the master chronologies until they reached the recommended expressive population signal (EPS) of 0.85 (Wigley et al. 1984, Briffa and Jones 1990, Tardif et al. 2001). The resulting chronology in the Estrie region was composed of 21 trees with an EPS of 0.89 while that in Beauce was composed of 16 trees with an EPS of 0.87. The high EPS values in the two regions underline the high statistical robustness of the two chronologies and the adequate precision of the climatic reconstructions (Wigley et al. 1984).

Climatic data

Daily temperature and precipitation data were obtained from the climate stations nearest to both groups of sampling sites, with comparable altitude, a long time series of records and without a large amount of missing data (Payette et al. 1996, Lévesque et al. 2013). Missing data were estimated by linear regression using data from nearby stations (Lévesque et al. 2013). In Estrie, the nearest station was located in Saint-Malo (45°12' N, -71°30' W) at a distance of 8 km from the sampling sites. The climate stations of East Hereford (45°08' N, -71°50' W) and Coaticook (45°15' N, -71°88' W), located at 10 and 16 km from the sampling sites, respectively, were both used to estimate missing data. In the Beauce region, the nearest station without a large amount of missing data was located in Lac Mégantic (45°36' N, -71°52' W) at 25 km from the sampling sites. The climate station of St-Ludger (45°75' N, -70°68' W), located at 14 km from the sampling sites, was used to estimate missing data. When missing data occurred in all climate stations near a study region, values were estimated using the mean of that month (Tardif et al. 2001). The period covered by the climatic stations for both regions was 1963–2015.

Detection of climatic stress events

Climatic stress events were defined using an a priori approach based on previous results from the literature. Daily climate data were used to identify both thaw–freeze events and periods of drought. The severity of a thaw–freeze event was expressed using cumulated growth degree-days (GDD) during the thaw prior to a refreeze (Bourque et al. 2005). As defined by these authors, a biologically significant thaw started when the daily maximum temperatures reached 4°C during the winter, a threshold representing the point at which biological activity begins (Braathe 1995, 1996). Cumulative GDD were then calculated based on the daily mean temperature values above the 4°C threshold during the entire duration of the thaw event. The event deemed to have ended when the daily minimum temperature went below –4°C, a threshold corresponding to the air temperature below which the root–soil plate freezes in the absence of a snow cover (Bourque et al. 2005), and at which root and shoot metabolism is reduced (Zhu et al. 2000, 2001). For each individual year through the 1963–2015 period, the event with the maximum cumulative GDD was retained as a potential predictor of yearly growth variation.

Following a similar procedure, we defined a precipitation threshold for the identification of drought events. Our method considered the absence of precipitation, but also the fact that drought conditions are dependent on the evaporation demand, which in turn is affected by temperature. We thus based the identification of drought events on the supply and demand concept of water balance (Vicente-Serrano et al. 2010). This was achieved by using both the daily total precipitation and GDD records. First, as applied by Payette et al. (1996) in northern hardwood stands from the same bioclimatic zone, we used a daily precipitation threshold of 15 mm below which the growth of sugar maple trees is hindered if the condition is met for several consecutive days. Second, we took account of the evaporative demand by summing GDD from the initial day when the daily total precipitation was under 15 mm until the next day during which this threshold was exceeded. For each individual year through the 1963–2015 observation period, the event with the maximum value of this drought index was retained as a potential predictor of yearly growth variation.

Tree ring analysis

In addition to the ring width and the standardized growth chronologies described above, we computed two supplementary growth variables for further analysis. First, for each individual tree-ring series, we determined when an abrupt annual growth reduction occurred. Based on the method proposed by Das et al. (2007), an abrupt annual growth reduction was defined as a year-to-year negative percentage growth change (PGG) of more than 1 standard deviation from the mean of all the negative year-to-year PGG observed from all individual tree-ring series. In our study, this analysis showed that the mean of all negative year-to-year PGGs was 26% with a standard deviation of 19%. To remain conservative, we set a threshold of 50% PGG to mark years of abrupt annual growth reduction.

Second, we calculated a growth sensitivity index to assess year-to-year variability of each individual tree-ring series. The sensitivity index was expressed as the mean year-to-year variation over a 5-yr window of observation. The sensitivity S_t at year t was defined as follows:

$$S_t = \left| \frac{(RW_t - RW_{t-1})}{(RW_t)} \right| \quad (1)$$

where RW_t is the radial growth measured at year t , and RW_{t-1} is the radial growth measured the previous year. The sensitivity index at year t was then computed using the average values of S_t over a five-year period from year $t - 4$ to year t . Such an index has previously been related to the sensitivity of trees to annual climatic variability (Fritts 1976) and has been recognized as a good predictor of imminent mortality in sugar maple (Moreau et al. 2019). It was thus used in this study as a proxy for the evolution of tree vigor during the observation period.

Statistical modeling process

Monthly climatic trends.—As they represent summary metrics commonly used in dendroclimatic analyses (Oswald et al. 2018), the total monthly precipitation and mean temperatures were also used as potential predictors of mean annual growth in the two master standardized chronologies. A bootstrapped response function was calibrated for each month of the vegetation period of year $t - 1$ (June–December) and year t (January–September) through the entire

observation period. This approach was developed to test the significance of the regression coefficients while considering the autocorrelation between predictors (Fritts 1976, Tardif et al. 2001, Zhang and Biondi 2013). We also investigated the temporal variability of growth–climate relationships using response functions with a 25-yr moving window. These analyses were performed using the *bootRes* package in R (Zang and Biondi 2013).

Climatic stress events.—The growth response of individual trees to drought and thaw–freeze event during the 1963–2015 period was expressed using the individual standardized tree-ring series to eliminate the age-related trends. It was statistically modeled using a mixed-effects linear model with tree-level random effects. The fixed effects predictors were the yearly series of thaw–freeze and drought event indices. In a second model, we also modeled the effects of these predictors on annual standardized growth with a potential one-year lag. Models were developed using the *lme* function of the *nlme* package (Pinheiro et al. 2014) in R. The probability of a tree to experience an abrupt annual growth decline was modeled for all individual tree-ring series using a mixed-effects logistic regression with a tree-level random effect. The binomial distribution model included the relationship between the predictors (thaw–freeze and drought event indices) and a binary response indicating the occurrence or not of an abrupt annual growth decline. Again, we tested both the responses in the current year and with a possible one-year lag in separate models. The *glmmTMB* function of the *glmmTMB* package (Magnusson et al. 2017) was used for the mixed-effects logistic regression. As for the construction of the master chronologies, tree-ring series from the two regions were modeled in two different groups. Model assumptions, that is, the homogeneity of variance, normality of residuals, the presence of outliers, and the over-dispersion, were validated with a graphical analysis of the residuals.

RESULTS

Monthly climatic trends

In the Estrie region, none of the climatic variables had a significant effect on sugar maple growth, as represented by the bootstrapped response function coefficients computed with residual chronologies (Fig. 1A, B). In the Beauce

region, growth was only significantly and positively related ($P < 0.05$) to the precipitation during August of the preceding year (Fig. 1C, D). In both regions, most of the tested predictor variables had non-stationary relationships with sugar maple growth during the observation period. While the response function coefficients of several variables were rather inconsistent from year to year, others changed steadily over time (Fig. 2). For example, in the Estrie region, temperature in April, September, and precipitation in June changed from having negative to positive effects over the last decades (Fig. 2A). Similarly in the Beauce region, the effect of temperature in April steadily shifted through the observation from negative to positive, while that of May and June shifted from null to positive (Fig. 2B).

Severe climatic events

The most severe climatic events, defined as a shift of at least 1 standard deviation (SD) from the mean value of all annual maxima of cumulated GDD, are presented in Table 1. In the Estrie region, the most severe thaw–freeze events occurred in 1981 and 2010, while the most severe drought events were detected in 1973, 1978, and 1979. In the Beauce region, the most severe thaw–freeze events were recorded in 1981, 2003, and 2010, while the most severe drought events occurred in 1970, 1971, and 1980. Overall, the severity of the climatic events tended to be slightly higher in Estrie, particularly for drought events.

Several growth reductions were observed in the standardized master chronologies of both regions, particularly from the beginning of the 1980s. In the Estrie region, the 1983 drought and the 1986 and 2010 thaw–freeze events all corresponded with low values of standardized growth (Fig. 3A). The growth index value was also low in 1995, but this was unrelated to any of the climatic stress events we identified. Overall, the growth index from individual tree-ring series decreases significantly with increasing cumulated GDD during thaw–freeze ($P < 0.0001$; Fig. 4A) and drought ($P = 0.032$; Fig. 5A) events. However, growth was unrelated to climatic events that had occurred in the previous year. In the Beauce region, low values of the growth index were observed in 1981, 1984, 1986, 2003, and 2010, all of which except 1984 coincided with

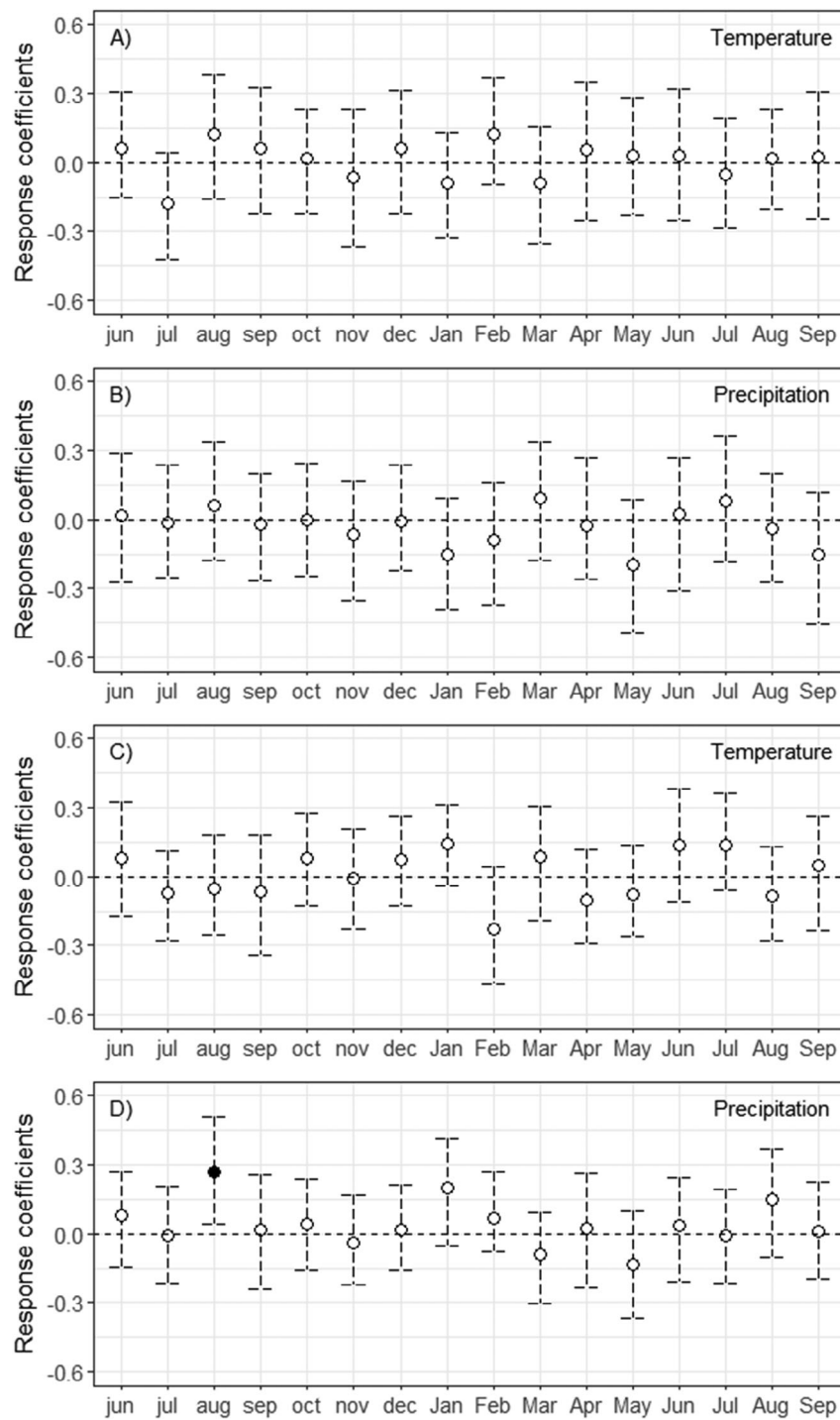


Fig. 1. Bootstrapped response function coefficients computed between sugar maple residual chronologies and the monthly climatic variables over the 1963–2015 period for (A) temperature and (B) precipitation in Estrie and (C) temperature and (D) precipitation in Beauce. The lowercase letters on the *x*-axis indicate the months of the year prior to growth (year-1), while the uppercase letters indicate months of the years of growth. Statistically significant correlation coefficients ($P < 0.05$) are represented by solid circles.

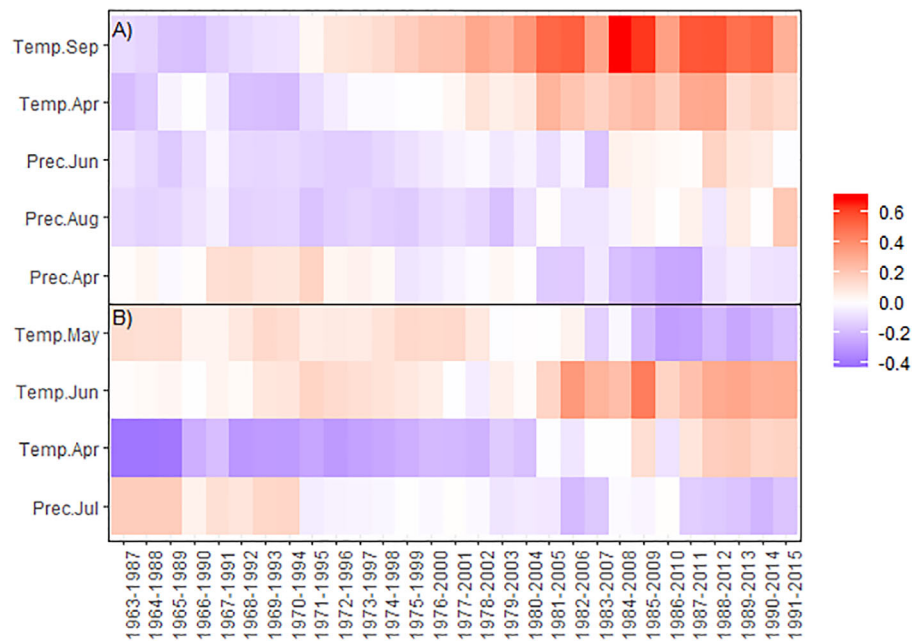


Fig. 2. Non-stationary relationship between sugar maple growth and monthly climatic predictors in Estrie (A) and Beauce (B) regions. The color scale represents the response function coefficients (dimensionless) that were calculated using a 25-yr moving window (see *Statistical and modeling process* for more details).

Table 1. Severe climatic events detected for the period 1963–2015 for the two study regions.

Region	Thaw–freeze				Drought			
	Year	Days	GDD	SD	Year	Days	GDD	SD
Estrie	1977	17	60	>1	1964	47	580	>1
	1981	24	148	>3	1965	40	497	>1
	1986	14	78	>1	1973	57	885	>2
	1987	11	77	>1	1977	39	543	>1
	2002	13	81	>1	1978	73	1007	>2
	2010	43	178	>4	1979	34	1145	>2
	2012	24	67	>1	1983	44	580	>1
					2005	41	571	>1
Beauce	1981	23	123	>2	1964	51	634	>1
	1986	14	75	>1	1965	61	735	>1
	1987	10	73	>1	1970	60	830	>2
	2003	33	146	>3	1971	61	819	>2
	2008	16	79	>1	1975	38	661	>1
	2010	45	161	>3	1980	68	844	>2
					1991	51	673	>1
					2000	46	596	>1
					2005	52	751	>1

Notes.: GDD is the maximum cumulated growth degree-days during a thaw–freeze/drought event, and days is the maximum cumulated days during a thaw–freeze/drought event. SD is the number of standard deviation shift from the mean GDD and days value. Years in bold indicated the most severe climatic events (a shift >2 standard deviation from the mean GDD and days value). Note that the maximum cumulated days are presented only to help describe the climatic events.

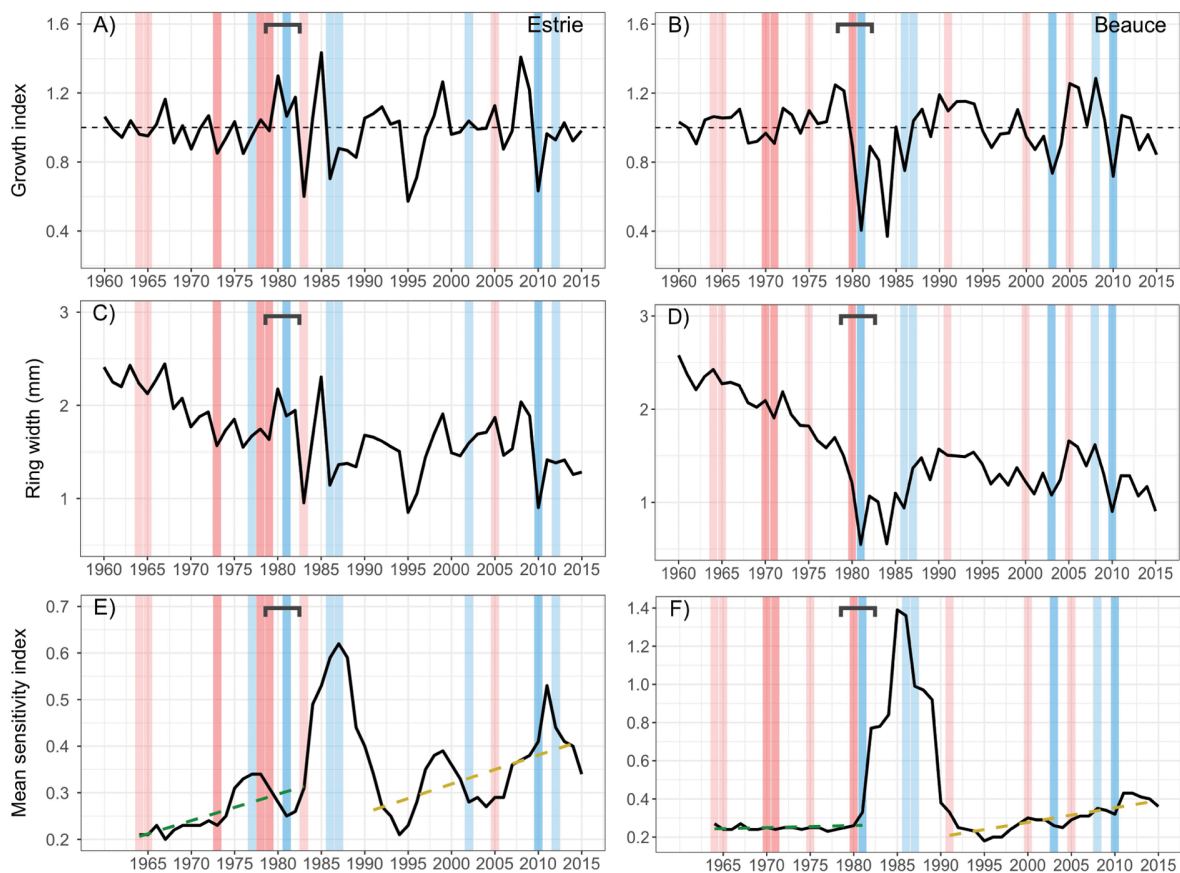


Fig. 3. Average growth index chronologies (A) in Estrie (nbr = 21, EPS = 0.89) and (B) in Beauce (nbr = 16, EPS = 0.87). Average ring-width (mm) chronologies (C) in Estrie and (D) in Beauce. (E) Growth sensitivity index calculated over a 5-year segment from all individual tree-ring series (E) in Estrie and (F) in Beauce. The linear relationship of the growth sensitivity index over time is illustrated by the green and yellow dashed lines. In Estrie (E), the slope and intercept values of the green dashed line are 0.0057 and 0.20, respectively (the period 1963–1983), and the slope and intercept values of the yellow dashed line are 0.0062 and 0.26 (from 1990 onward). In Beauce (F), the slope and intercept values of the green dashed line are 0.0011 and 0.24, respectively (the period 1963–1980), and the slope and intercept values of the yellow dashed line are 0.0077 and 0.20 (from 1990 onward). Note that (E) and (F) do not have the same y -scale. Red and blue vertical lines illustrate severe drought and thaw–freeze events ($SD > 1$), respectively, with darker lines representing the most severe events ($SD > 2$). The downward-pointing bracket indicates the insect defoliation period (1979–1982).

years of severe thaw–freeze events (Fig. 3B). The growth index decreased significantly with increasing cumulated GDD during a thaw–freeze event ($P < 0.0001$; Fig. 4B) and cumulated GDD during a drought event ($P = 0.0064$; Fig. 5B). In this region, the growth index was also significantly related to GDD during a drought event that had occurred in the previous year ($P = 0.0006$).

For both regions, the 1960–1970 period was characterized by a progressive reduction in ring width (Fig. 3C–D). This was then followed by several years of slow growth during the 1980s, a pattern that occurred after a rapid succession of severe stress events in the 1970s and early 1980s. This period marked the onset of a period of high irregularity in ring width characterized by several narrow rings interspersed with pulses of

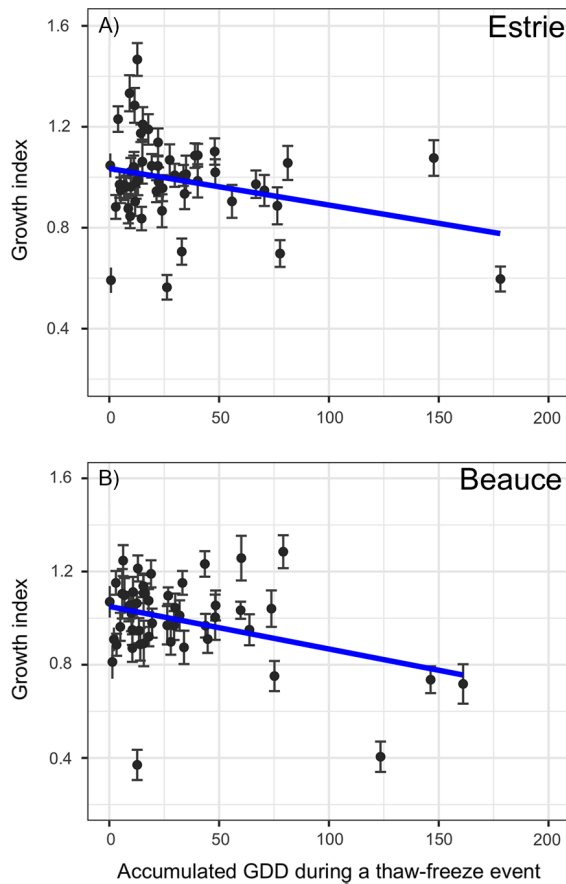


Fig. 4. Mean observed growth index as a function of the accumulated growth degree-days (GDD) during thaw–freeze event in Estrie (A) and Beauce (B), respectively. The blue lines correspond to the growth index predictions computed with the mixed linear models, with slope and intercept values of -0.0014 and 1.035 for (A), -0.0018 and 1.050 for (B), respectively. Each point is the average annual growth index, and bars correspond to the standard error.

increased radial growth. In the Estrie region, all trees experienced an abrupt growth decline during the 1983 drought event and the 1986–2010 thaw–freeze events. According to the logistic regression analyses, the probability of a tree to experience an abrupt growth decline increased sharply with an increase in cumulative GDD during a thaw–freeze event (Fig. 6A), while the effect was more moderate in the case of droughts (Fig. 6C). In the Beauce region, 94% of the trees experienced at least one abrupt decline from 1980 to 1986, while 35% of our sample trees also

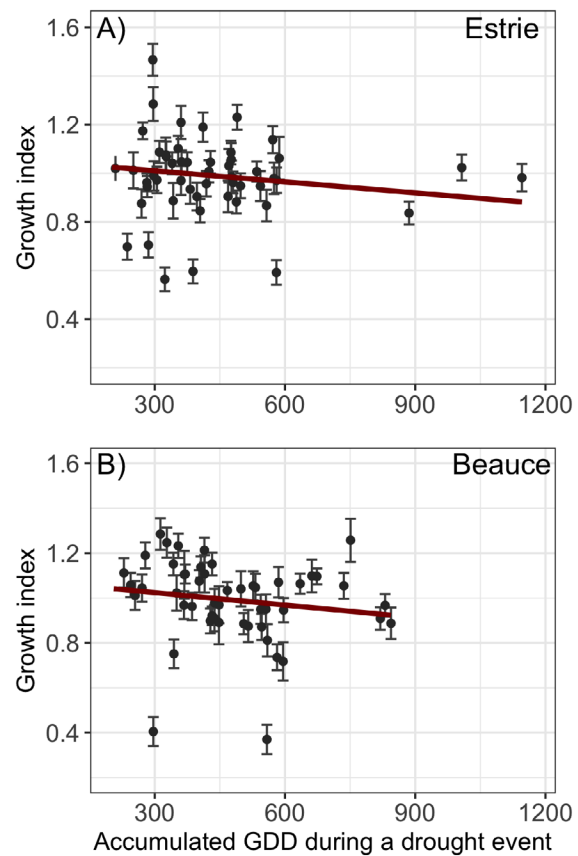


Fig. 5. Mean observed growth index as a function of the accumulated growth degree-days (GDD) during drought event in Estrie (A) and Beauce (B), respectively. The red lines correspond to the growth index predictions computed with the mixed linear models, with slope and intercept values of -0.0002 and 1.056 for (A) and -0.0002 and 1.079 for (B), respectively. Each point is the average annual growth index, and bars correspond to the standard error.

experienced a growth decline following the 2010 thaw–freeze event. For this region, only the cumulated GDD during a thaw–freeze event had a significant effect on the probability of a tree to experience an abrupt growth decline in the same year ($P < 0.0001$). In either region, the probability of an abrupt growth decline was unrelated to climatic events that had occurred during the previous year.

In the Estrie region, the growth sensitivity index increased progressively during the 1960–1980 period with a marked peak after the

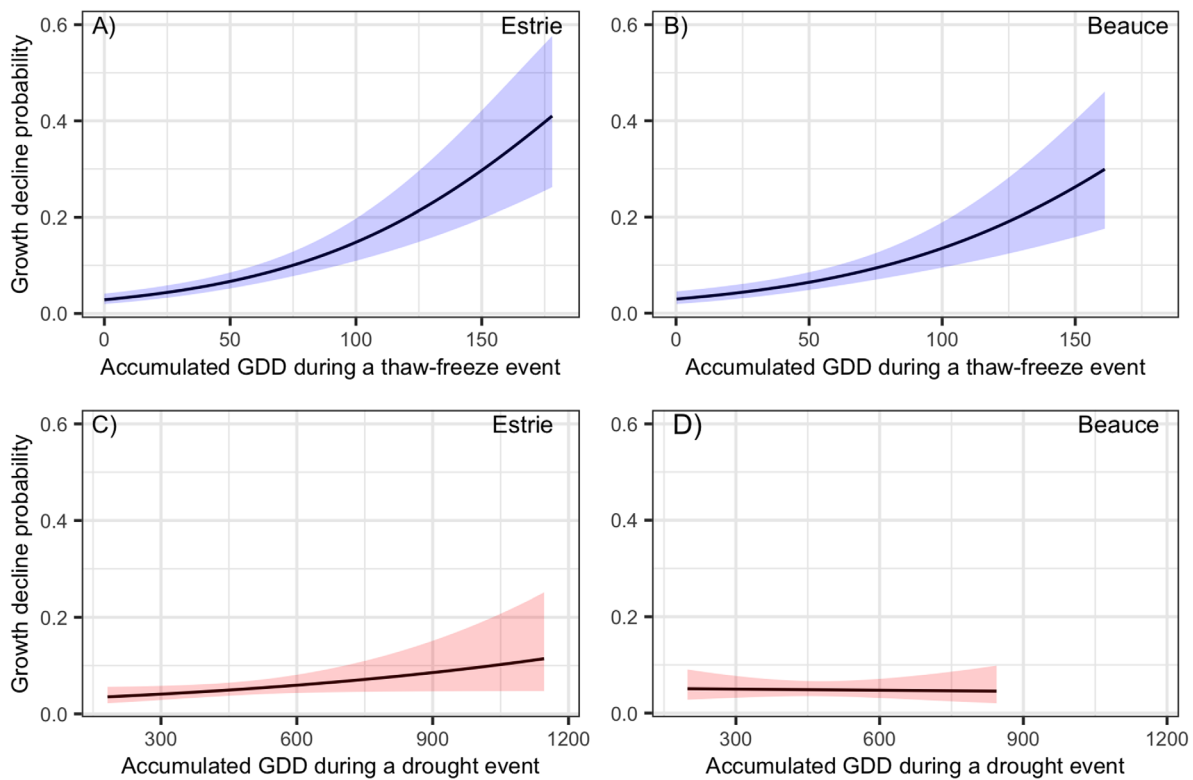


Fig. 6. Mean predicted abrupt growth decline probability as affected by accumulated growth degree-days (GDD) during thaw–freeze and drought event in Estrie (A, C) and Beauce (B, D), respectively. Confidence intervals of growth decline predictions (shaded area) were calculated with $\alpha = 0.05$.

severe drought event that occurred in 1973 (Fig. 3E). Following the thaw–freeze event of 1981, the growth sensitivity index increased abruptly, peaked in 1987 and then decreased until 1994. This was followed by a gradual increase in growth sensitivity until 2015. In the Beauce region, the growth sensitivity index remained stable during the 1960–1980 period until it increased abruptly following the drought and thaw–freeze events of 1980 and 1981, peaked in 1985, and then decreased until 1995. After this period, growth sensitivity increased slowly until 2011. For both regions, values of the growth sensitivity index were generally higher from 1995 onward compared to the 1960–1980 period.

DISCUSSION

Monthly climatic trends

Growth chronologies from this study had weak and non-stationary relationships with traditional

monthly climatic metrics over the 1963–2015 period, similarly to what was previously observed in sugar maple forests from southern Quebec (Payette et al. 1996) and the northeastern United States (Gavin et al. 2008, Bishop et al. 2015). The non-stationary relationships observed in this study are in line with observations that the responses of sugar maple trees to climatic conditions are currently changing in North America (Tardif et al. 2001, Bishop et al. 2015, Nolet and Kneeshaw 2018). This may partly explain why the overall relationships between climatic conditions and sugar maple chronologies were weak in the present study. It also suggests that any comparisons of such relationships between different periods should be avoided (Tardif et al. 2001, Bishop et al. 2015). The quantified effects of monthly climatic variables on annual growth are currently used for long-term climatic reconstruction and for modeling the future productivity of sugar maple forests in a changing climate (Tardif et al. 2001, Iverson

et al. 2008, Oswald et al. 2018). However, our results suggest that such metrics may not be appropriate for such purposes, especially in cases where yearly growth dynamics are of interest (Payette et al. 1996). Further studies are needed to identify more biologically meaningful metrics that do not break the climatic signal into arbitrary calendar-base units.

Climatic stress events

To our knowledge, this is the first study that could empirically quantify the impact of climatic stress events on the growth dynamics of sugar maple trees, a key species in the northern hardwoods forests of North America. Our results, along with the expected increase in the severity and frequency of adverse climatic events in upcoming decades (Bell et al. 2004, Bourque et al. 2005, Iverson et al. 2008, Allan et al. 2010, Dai 2013, Comerford et al. 2013, SCAF 2018), bring a new perspective on the challenge of estimating the effects of the ongoing global climate change on tree growth. They suggest that more attention should be given to stress events that are, by nature, highly variable in duration and severity, which can make them hard to detect and quantify. For similar reasons, their future occurrence is also difficult to predict.

In our study, long-lasting thaw–freeze events were particularly damaging to sugar maple as they induced abrupt growth declines in both study regions. Thaw–freeze events can affect trees through several physiological processes (Bourque et al. 2005). First, thaw–freeze events have been related to an increasing occurrence of xylem cavitation, which can reduce xylem conductivity, sap flow rate, and total sap volume (Robitaille et al. 1995, Zhu et al. 2000, 2001, Cox and Zhu 2003, Bourque et al. 2005). Second, in cases where the snow has melted during a long thaw, the return to freezing conditions can injure shallow roots through the freezing of cells and tissues. In turn, this can hinder root pressure development, limit the uptake of water and nutrients, and disrupt of other root processes (Robitaille et al. 1995, Zhu et al. 2000, Tierney et al. 2001, Cox and Zhu 2003, Comerford et al. 2013). Third, if the bud burst is triggered by the thaw, the newly emerging shoots are prone to dieback induced by the freezing of the

parenchyma cells (George and Burke 1986, Zhu et al. 2001). Damage to the root and shoot systems will cause a loss of carbon reserves, which in turn will force a reallocation of new resources to these tissues. Given that stemwood production is a low priority in the resource allocation of trees (Waring 1987), radial growth is expected to remain low in years following a severe climatic event until trees recover. Prolonged thaw–freeze events were identified as a key element in triggering severe episode of forest dieback in North America (Auclair et al. 1996) and were related to abrupt growth decreases preceding tree death for several species in European temperate forests (Vanoni et al. 2016). While some plants have shown adaptive frost stress memory, which leads to a progressively increased tolerance to successive stress events (Walter et al. 2013), we did not find evidence to support this in our data. The reduced growth index values and the high proportion of abrupt growth declines observed in both regions during thaw–freeze events from 1981 to 2010 suggest that sugar maple has a weak adaptive capacity to the frost injuries induced by such events.

In line with previous observations (e.g., Payette et al. 1996, Nolet and Kneeshaw 2018), our results also underscore the important impact of drought on the growth dynamics of sugar maple trees. It is very likely that severe drought events during the late 1970s weakened sugar maple trees and made them more vulnerable to the effect of the acute thaw–freeze event that occurred in 1981. In addition to being negatively related to the annual growth index in both study regions, we also observed a significant one-year lagged response between the occurrence of drought and the annual growth index in the Beauce region. This delayed growth response was also revealed by the significant effect of the August precipitation from the preceding year in the bootstrapped response function. Our results are in accordance with Vanoni et al. (2016), who showed that while frost injuries generally affect tree growth during the same year as the event occurred, the effects of droughts can be delayed by 1–5 yr. Again, such lagged effects are harder to detect and link directly to particular events, which may partly explain the weaker relationships observed in this study between sugar maple growth and droughts.

Impacts of cumulative stressors

The cumulative effect of adverse climatic events was not the only cause of the observed growth decline of sugar maple trees in this study. Indeed, forest tent caterpillar (*Malacosoma disstritia*) defoliation occurred in our study areas from 1979 to 1982 (Payette et al. 1996; Domtar Corporation, *personal communication*). Repeated defoliation over several years can cause severe radial growth reductions related to a decrease in carbon fixation and reserves (Hartman and Messier 2008). In addition to the repeated defoliations, severe drought and thaw–freeze events occurred consecutively between 1979 and 1981 in both regions. Our results suggested that the synergic influence of cumulative climatic events and insect outbreaks weakened sugar maple trees, which led to a growth pattern characterized by several abrupt growth declines and a marked increase in growth sensitivity that peaked 2–3 yr later during the mid-1980s. Moreover, the cumulative effect of these stressors may have played a major role in the inconsistent relationships between growth and monthly climatic conditions, possibly by weakening the capacity of sugar maple trees to take advantage of favorable climatic conditions (Graumlich 1993, Payette et al. 1996, Tardif et al. 2001, Nolet and Kneeshaw 2018). Finally, foliar nutrient deficits of calcium, potassium, and magnesium were also reported for sugar maple trees in our study area (Bal et al. 2015). Such nutrient deficits are known to predispose and contribute to sugar maple decline, thereby increasing its vulnerability to climatic and biotic stressors (Bal et al. 2015).

The period of severe growth decline during the 1980s corresponds to that already observed throughout the sugar maple range (Houle 1990, Payette et al. 1996, Hartmann and Messier 2008, Bishop et al. 2015, Nolet and Kneeshaw 2018). Such growth declines were observed in sugar maple trees from all ages and sizes (Bishop et al. 2015, Nolet and Kneeshaw 2018), indicating that the negative impact of cumulative stresses was not limited to older and larger trees. In many cases, this period of growth decline was related to sugar maple mortality from 2000 onwards (Moreau et al. 2019), which again underscores the importance of cumulative stresses and their detection to predict stand growth and vigor. Although a permanent growth recovery

sometimes occurred following the growth decline of the 1980s (Payette et al. 1996, Hartmann and Messier 2008), the irregular growth patterns observed in this study during the 1990s and the 2000s rather suggest a negative legacy effect of stressors from the 1980s (Anderegg et al. 2015). Similarly, Nolet and Kneeshaw (2018) observed a lack of growth recovery of sugar maple trees in western Quebec, which they attributed to irreversible damage related to massive vessel embolisms caused by severe droughts (Bréda et al. 2006). This situation could prove particularly problematic in older trees since sugar maple susceptibility to adverse climatic events may increase with age (Auclair et al. 1996).

Limitations of the study

In this study, we used a traditional dendroclimatological analysis that relied on standardized methods to construct stand-level chronologies. The strength of this approach is that using a small subset of highly correlated tree-ring series facilitates the detection of a strong and comprehensive climatic signal in the region of interest. Such an approach has been widely used in recent decades and has proven to be very effective for deepening our understanding of the relationship between tree growth and climate. However, one important drawback is that the use of small subsets of dominant/codominant trees limits the inference we can make about the effects of adverse climatic events on the growth dynamics of the overall population of sugar maple trees (Canham et al. 2018). Consequently, further testing and validation of our results are needed with additional chronologies covering the entire native range of the species.

MANAGEMENT IMPLICATIONS

Our results indicate that the effect of climate change on the radial stem growth of sugar maple is likely to be more influenced by the occurrence of acute climatic stresses than by changes in average monthly temperature and precipitation. Because drought and thaw–freeze events should become more frequent and severe in the future, we can anticipate a reduction in the growth of sugar maple. Considering the great ecological and economic importance of sugar maple in eastern

North America, climate-smart silviculture practices should be promoted to stabilize ecosystem services (D'Amato et al. 2013). To help implement remedial measures, it will be important to better characterize the vulnerability of all major companion species to climatic stressors. For example, sugar maple trees have a higher proportion of fine roots in the shallow organic soil horizon compared to companion species such as American beech and yellow birch (Fahey and Hughes 1994). Sugar maple may therefore have a higher vulnerability to root damage due to the soil freezing (Comerford et al. 2013). Differences between the vulnerability of tree species can influence the long-term competition dynamics in the stand. From a silvicultural perspective, characterizing tree species vulnerability to climatic stressors should also be integrated among tree selection criteria before partial cutting (Moreau et al. *unpublished manuscript*). Further research should also compare the resistance and resilience to climatic stressors between northern hardwood stands of different ages, densities, structures, species compositions, and vigor. Such information is required to meet the challenge of implementing adaptive forest management strategies that will maintain healthy and productive forest ecosystems despite rapid changes in climatic conditions.

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LITERATURE CITED

- Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.
- Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:1–55.
- Anderegg, W. R., et al. 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349:528–532.
- Auclair, A. N., J. T. Lill, and C. Revenga. 1996. The role of climate variability and global warming in the dieback of Northern Hardwoods. *Water, Air, and Soil Pollution* 91:163–186.
- Bal, T. L., A. J. Storer, M. F. Jurgensen, P. V. Doskey, and M. C. Amacher. 2015. Nutrient stress predisposes and contributes to sugar maple dieback across its northern range: a review. *Forestry: an International Journal of Forest Research* 88:64–83.
- Bell, J. L., L. C. Sloan, and M. A. Snyder. 2004. Regional changes in extreme climatic events: a future climate scenario. *Journal of Climate* 17:81–87.
- Bishop, D. A., C. M. Beier, N. Pederson, G. B. Lawrence, J. C. Stella, and T. J. Sullivan. 2015. Regional growth decline of sugar maple (*Acer saccharum*) and its potential causes. *Ecosphere* 6:1–14.
- Bourque, C. P. A., R. M. Cox, D. J. Allen, P. A. Arp, and F. R. Meng. 2005. Spatial extent of winter thaw events in eastern North America: historical weather records in relation to yellow birch decline. *Global Change Biology* 11:1477–1492.
- Braathe, P. 1995. Birch dieback-caused by prolonged early spring thaws and subsequent frost. *Norwegian Journal of Agricultural Sciences* 20:1–59.
- Braathe, P. 1996. Birch dieback caused by the effects of artificial spring frost on budburst and foliage. *Norwegian Journal of Agricultural Sciences* 10:1–6.
- Bréda, N., R. Huc, A. Granier, and E. Dreyer. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science* 63:625–644.
- Briffa, K. R., and P. D. Jones. 1990. Basic chronology statistics and assessment. Pages 137–152 in E. R. Cook and L. A. Kairiukstis, editors. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic, Norwell, Dordrecht, The Netherlands.
- Canham, C. D., L. Murphy, R. Riemann, R. McCullough, and E. Burrill. 2018. Local differentiation in tree growth responses to climate. *Ecosphere* 9:e02368.
- Comerford, D. P., P. G. Schaberg, P. H. Templer, A. M. Succi, J. L. Campbell, and K. F. Wallin. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. *Oecologia* 171:261–269.
- Cook, E. R., and K. Peters. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-ring Bulletin* 41:45–53.

- Cox, R. M., and X. B. Zhu. 2003. Effects of simulated thaw on xylem cavitation, residual embolism, spring dieback and shoot growth in yellow birch. *Tree Physiology* 23:615–624.
- Dai, A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change* 3:52–58.
- D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications* 23:735–1742.
- Das, A. J., J. J. Battles, N. L. Stephenson, and P. J. Van Mantgem. 2007. The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. *Canadian Journal of Forest Research* 37:580–597.
- Duchesne, L., R. Ouimet, and C. Morneau. 2003. Assessment of sugar maple health based on basal area growth pattern. *Canadian Journal of Forest Research* 33:2074–2080.
- Fahey, T. J., and J. W. Hughes. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *Journal of Ecology* 82:533–548.
- Fritts, H. C. 1976. *Tree rings and climate*. Academic Press, London, UK.
- Gavin, D. G., B. Beckage, and B. Osborne. 2008. Forest dynamics and the growth decline of red spruce and sugar maple on Bolton Mountain, Vermont: a comparison of modeling methods. *Canadian Journal of Forest Research* 38:2635–2649.
- George, M. F., and M. J. Burke. 1986. Low temperature: physical aspects of freezing. Pages 133–150 in *Woody plant xylem. Stress physiology and forest productivity*. Springer, Dordrecht, The Netherlands.
- Graumlich, L. J. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Canadian Journal of Forest Research* 23:133–143.
- Grondin, P., N. Jean, and D. Hotte. 2007. Intégration de la végétation et de ses variables explicatives à des fins de classification et de cartographie d'unité s homogènes du Québec méridional, Ministère des Ressources naturelles et de la Faune, Direction de la recherche forestière. Mémoire de recherche No 150.
- Hartmann, H., and C. Messier. 2008. The role of forest tent caterpillar defoliations and partial harvest in the decline and death of sugar maple. *Annals of Botany* 102:377–387.
- Houle, G. 1990. Growth patterns of sugar maple seedlings and mature trees in healthy and in declining hardwood stands. *Canadian Journal of Forest Research* 20:894–901.
- Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. Peters. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* 254:390–406.
- Lane, C. J., D. D. Reed, G. D. Mroz, and H. O. Liechty. 1993. Width of sugar maple (*Acer saccharum*) tree rings as affected by climate. *Canadian Journal of Forest Research* 23:2370–2375.
- Lévesque, M., M. Saurer, R. Siegwolf, B. Eilmann, P. Brang, H. Bugmann, and A. Rigling. 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Global Change Biology* 19:3184–3199.
- Magnusson, A., et al. 2017. Package 'glmmTMB'. R Package Version 0.2. 0. <http://cran.uni-muenster.de/web/packages/glmmTMB/glmmTMB.pdf>
- Moreau, G., A. Achim, and D. Pothier. 2019. A dendrochronological reconstruction of sugar maple growth and mortality dynamics in partially cut northern hardwood forests. *Forest Ecology and Management* 437:17–26.
- Nolet, P., and D. Kneeshaw. 2018. Extreme events and subtle ecological effects: lessons from a long-term sugar maple–American beech comparison. *Ecosphere* 9:e02336.
- Oswald, E. M., J. Pontius, S. A. Rayback, P. G. Schaberg, S. H. Wilmot, and L. A. Dupigny-Giroux. 2018. The complex relationship between climate and sugar maple health: climate change implications in Vermont for a key northern hardwood species. *Forest Ecology and Management* 422:303–312.
- Payette, S., M. J. Fortin, and C. Morneau. 1996. The recent sugar maple decline in southern Quebec: Probable causes deduced from tree rings. *Canadian Journal of Forest Research* 26:1069–1078.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1-117. <http://CRAN.R-project.org/package=nlme>
- Robitaille, G., R. Boutin, and D. Lachance. 1995. Effects of soil freezing stress on sap flow and sugar content of mature sugar maples (*Acer saccharum*). *Canadian Journal of Forest Research* 25:577–587.
- Saucier, J.-P., et al. 2009. *Écologie forestière. Manuel de foresterie*. 2e édition. Ordre des ingénieurs forestiers du Québec, Éditions Multimondes, Québec, Québec, Canada.
- Senate Committee on Agriculture and Forestry. 2018. *Feast or Famine: impacts of climate change and carbon pricing on agriculture, agri-food and forestry*. sencanada.ca/agfo
- Tardif, J., J. Brisson, and Y. Bergeron. 2001. Dendroclimatic analysis of *Acer saccharum*, *Fagus grandifolia*, and *Tsuga canadensis* from an old-growth forest,

- southwestern Quebec. *Canadian Journal of Forest Research* 31:1491–1501.
- Tierney, G. L., T. J. Fahey, P. M. Groffman, J. P. Hardy, R. D. Fitzhugh, and C. T. Driscoll. 2001. Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* 56:175–190.
- Vanoni, M., H. Bugmann, M. Nötzli, and C. Bigler. 2016. Drought and frost contribute to abrupt growth decreases before tree mortality in nine temperate tree species. *Forest Ecology and Management* 382:51–63.
- Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate* 23:1696–1718.
- Walter, J., A. Jentsch, C. Beierkuhnlein, and J. Kreyling. 2013. Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. *Environmental and Experimental Botany* 94:3–8.
- Waring, R. H. 1987. Characteristics of trees predisposed to die. *BioScience* 37:569–574.
- Wigley, T. M., K. R. Briffa, and P. D. Jones. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* 23:201–213.
- Yin, X., N. W. Foster, I. K. Morrison, and P. A. Arp. 1994. Tree-ring-based growth analysis for a sugar maple stand: relations to local climate and transient soil properties. *Canadian Journal of Forest Research* 24:1567–1574.
- Zang, C., and F. Biondi. 2013. Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. *Dendrochronologia* 31:68–74.
- Zhang, T., Ü. Niinemets, J. Sheffield, and J. W. Lichstein. 2018. Shifts in tree functional composition amplify the response of forest biomass to climate. *Nature* 556:99–102.
- Zhu, X. B., R. M. Cox, and P. A. Arp. 2000. Effects of xylem cavitation and freezing injury on dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw. *Tree Physiology* 20:541–547.
- Zhu, X. B., R. M. Cox, F. R. Meng, and P. A. Arp. 2001. Responses of xylem cavitation, freezing injury and shoot dieback to a simulated winter thaw in yellow birch seedlings growing in different nursery culture regimes. *Forest Ecology and Management* 145:243–253.