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Research paper

A heat wave during leaf expansion severely reduces productivity and modifies seasonal growth patterns in a northern hardwood forest

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A useful approach to monitor tree response to climate change and environmental extremes is the recording of long-term time series of stem radial variations obtained with precision dendrometers. Here, we study the impact of environmental stress on seasonal growth dynamics and productivity of yellow birch (*Betula alleghaniensis* Britton) and sugar maple (*Acer saccharum* Marsh.) in the Great Lakes, St Lawrence forest region of Ontario. Specifically, we research the effects of a spring heat wave in 2010, and a summer drought in 2012 that occurred during the 2005–14 study period. We evaluated both growth phenology (onset, cessation, duration of radial growth, time of maximum daily growth rate) and productivity (monthly and seasonal average growth rates, maximum daily growth rate, tree-ring width) and tested for differences and interactions among species and years. Productivity of sugar maple was drastically compromised by a 3-day spring heat wave in 2010 as indicated by low growth rates, very early growth cessation and a lagged growth onset in the following year. Sugar maple also responded more sensitively than yellow birch to a prolonged drought period in July 2012, but final tree-ring width was not significantly reduced due to positive responses to above-average temperatures in the preceding spring. We conclude that sugar maple, a species that currently dominates northern hardwood forests, is vulnerable to heat wave disturbances during leaf expansion, which might occur more frequently under anticipated climate change.

Keywords: cambial activity, dendroclimatology, dendroecology, drought stress, eddy covariance, heat stress.

Introduction

The Great Lakes, St Lawrence forest region, covers ~20 million hectares in the province of Ontario (Canada) and forms an important biogeographical unit that provides a multitude of ecosystem services and goods, such as wildlife habitat, recreation, carbon sequestration and sustainable timber production (Ontario Ministry of Natural Resources 2012). The forest composition in this region is characterized by a gradual transition from mainly temperate broad-leaved tree species located in the south to the more boreal and conifer-dominated forest ecosystems in the north. Yellow birch (*Betula alleghaniensis* Britton) and sugar maple (*Acer saccharum* Marsh.) are two valuable broadleaf tree species characteristic of northern hardwood forests in the Great Lakes, St Lawrence region. Over 60% of the

forest area in Ontario is used for timber production and in central Ontario, sugar maple alone accounts for 78.5% of the total harvest volume (Ontario Ministry of Natural Resources 2010, Kwiaton and Wang 2015). Despite their ecological significance and central role in the regional forest and wood sector, there is a lack of understanding of the response of productivity and seasonal growth dynamics of yellow birch and sugar maple to climatic events and anticipated environmental changes in the Great Lakes Basin (Plummer et al. 2006, Šeparović et al. 2013).

Drought sensitivity and adaptive capacity of yellow birch and sugar maple growth performance are subjects of controversy in the scientific literature. While several studies have identified water availability during summer as a predominating factor controlling radial growth response in sugar maple, yellow birch and

other species in the region (Tardif et al. 2001, He et al. 2005, Kwiaton and Wang 2015), it has also been suggested that climate warming in conjunction with increased precipitation could positively affect growth rates, in particular closer to the northern distribution limits of the tree species (Goldblum and Rigg 2005). In contrast, other studies have demonstrated that exceeding certain temperature thresholds might lead to declining growth rates in boreal forest ecosystems, if increased evapotranspiration demands due to rising temperatures are not compensated by sufficient amounts of additional precipitation (D'Arrigo et al. 2004). The non-linearity and divergences of past and present climate–growth relationships at northern latitudes might also be a result of confounding environmental factors such as increased winter precipitation or changes in the timing of snow melt (Vaganov et al. 1999, D'Arrigo et al. 2008).

A useful approach to monitor tree response to environmental changes with very high-temporal resolution is the use of precision dendrometers, which can measure the change of the radial or circumferential stem dimensions in intervals of hours or minutes (Drew and Downes 2009). Analyses of long-term time series of dendrometer data can increase our understanding of the short-, medium- and long-term responses of growth and carbon fluxes of forest ecosystems to environmental changes and extreme climatic events (Kahle 2006, Zweifel et al. 2010, van der Maaten 2013). The diurnal dynamics of swelling and shrinking monitored by dendrometer sensors are considered valuable ecophysiological indicators as they can be linked to daily growth rates, transpiration demand and the stem internal water status (Deslauriers et al. 2007, Swaef et al. 2015). By enabling the conversion of spatial scales of wood anatomical or wood density profiles to seasonal time scales, dendrometer data also allow detailed studies of the effects of environmental conditions on intra-annual variations in tree-ring structure and wood density (van der Maaten et al. 2012, Stangler et al. 2016). High-resolution data of stem dimensional variations as recorded by dendrometers also have the potential to provide insights into growth responses to severe short-term environmental stress such as the spring heat wave that hit central Ontario in late May 2010. At the peak of leaf expansion, three consecutive days of extremely high temperatures in May were linked to mortality, scorching and shedding of partially expanded leaves (Filewod and Thomas 2014). The 'leaf drop' phenomenon was predominantly observed on sugar maple, but other shade-tolerant tree species were also affected. The authors investigated various canopy processes of sugar maple after the leaf drop event and discovered altered morphology as well as reduced size, mass and nutrient content of the second flush of neo-formed leaves. Despite recovery of photosynthetic competence in July and August, a 65% decrease of photosynthetic capacity during June clearly demonstrated that short-term heat stress events can have severe and lasting impacts on forest productivity. In addition, the spring heat wave disturbance was attributed to high carbon

losses and significant reductions in net ecosystem productivity that were detected by eddy covariance measurements within the same research area (Geddes et al. 2014).

This study contributes a long-term time series of comparative precision dendrometer measurements of yellow birch and sugar maple between 2005 and 2014, which captures the 2010 heat wave in addition to other environmental stress events and inter-annual climatic variation. Specifically, we investigated the impact of contrasting environmental conditions such as the spring heat wave in 2010 and the summer drought in 2012 on main characteristics of seasonal growth patterns, such as growth onset, growth cessation, growth duration, timing and extent of maximum daily growth rate, average growth rates and tree-ring width. As temperature is known as a major stimulus for the onset of cambial activity (Gričar et al. 2006), we expected growth onset of both tree species to occur earlier under above-average temperatures during spring. Furthermore, we tested the hypothesis that the documented leaf mortality and reduced photosynthetic capacity of sugar maple, caused by the spring heat wave in 2010, led to significant reductions in growth rates, growth duration and tree-ring width. Since the 2012 summer season was classified as extraordinarily warm and dry (Environment Canada 2013), and sugar maple and yellow birch are known to be sensitive to summer drought, we also evaluated how both tree species responded with respect to growth rates and growth phenology during this drought year. By calculating chronologies for each investigated response variable, we also searched for lag effects in growth performance caused by environmental stress and tested for differences between the two tree species.

Materials and methods

Study site and experimental set-up

The study site is a mature, mixed, uneven-aged and managed forest stand located at an altitude of ~400 m above sea level (45°14'47.52"N, 78°34'48.45"W a.s.l.) in Haliburton Forest and Wildlife Reserve Ltd, a 32,000 ha privately owned forest estate in south eastern Ontario, Canada. The tree species composition is characteristic for northern hardwood forests in the Great Lakes, St Lawrence region, dominated by sugar maple and yellow birch intermixed with American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), black cherry (*Prunus serotina*), white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*). The soil type is a shallow cambisol derived from granite bedrock on a predominately flat terrain. For the period 1970–2000, mean annual temperature in the study region was 4.9 °C and mean annual precipitation was 1009 mm (Filewod and Thomas 2014).

In March 2005, 15 yellow birch and 13 sugar maple pole- to sawlog-sized sample trees were randomly selected in an area of 3.5 ha for monitoring with point-dendrometers that were mounted at 1.4 m above ground (Siegel 2012). The dendrometer type is based on a linear displacement transducer

(Trans-Tek Inc., Ellington, CT, USA) with a measurement resolution of close to 1 μm (van der Maaten 2013). Dendrometer data were collected in nine growing seasons between the years 2005 and 2014 with the exception of year 2006, when no monitoring took place due to technical problems. The measurements of stem radial displacement (SRD) were recorded in intervals of 15 min and stored by a data logger (23X, Campbell Scientific, Logan, UT, USA). Measurements were started after snow melt and well before the flushing of new leaves in spring, and the annual time series usually ended in autumn between the time of leaf coloration and leaf abscission.

Sampling of increment cores and tree-ring width measurements

In March 2015, an additional 15 yellow birch and 17 sugar maple trees were selected within the same area to complement the dendrometer data and to obtain annual increment measurements of 30 trees in total for both tree species (Table 1). All trees within this study were selected based on the following criteria: being dominant or co-dominant, free of logging damage or pathogen infestation, and having a bottom log with potential for veneer quality at the time of harvest. Increment cores that were 5 mm in diameter and 30–40 cm long were extracted from the sample trees using Hagl of borers. Sampling height was set at 1.3 m for all sample trees, except the dendrometer trees, which were sampled at the location of the dendrometer sensors at 1.4 m after the study was concluded and dendrometers were removed.

In the laboratory, the cross sectional surfaces of the air-dried increment cores were prepared with an ultra-precise diamond flycutter device (Spiecker et al. 2000). Tree-ring widths were measured from pith to bark with a resolution of 1 μm , using a combination of a reflected light microscope (Zeiss AxioTech vario 25 HD, $\times 25$ –500 magnification, Carl Zeiss AG, Jena, Germany) with a high precision X/Y-Table (Physik Instrumente (PI) GmbH & Co. KG, Karlsruhe, Germany). Visualization and subsequent cross-dating of the tree-ring series were performed using the software package PAST4 (Knibbe 2004).

Characterization of the climate anomalies in 2010 and 2012

The climate data used in this study were provided by the Canadian Forest Service and estimated at daily resolution for the

coordinates of our research plot based on spatial spline climate models (McKenney et al. 2011). As the daily models were not yet available for the year 2014, we used the meteorological data from the weather station in Haliburton (Environment Canada, 45°01'56.1"N 78°31'52.0"W, 330 m a.s.l., located ~24 km south of the research plot), to estimate the missing 2014 climate data using a linear regression based on the relationship with data from previous years. To quantify drought periods during growing seasons, we used the deterministic forest hydrological model WBS3 (Matzarakis et al. 2000). Based on an adjustment to the local site conditions, WBS3 provides daily simulations of the relative plant available soil water capacity derived from the meteorological input variables daily mean temperature and daily precipitation sum. Daily mean temperature was calculated as the arithmetic mean of daily maximum and minimum temperature.

This study focused on the seasonal growth dynamics and tree species performance in response to the spring heat wave in 2010 and summer drought 2012, 2 years with distinct climate anomalies that fell into our observation period. The spring heat wave in 2010 lasted for 3 days with daily maximum temperatures of 29.4 °C (24 May 2010), 31.5 °C (25 May 2010) and 32.3 °C (26 May 2010). In particular, the temperature peak on 26 May stands out as a heat anomaly of very low probability and an extreme climatic event (Figure 1a).

The drought anomaly during the summer of 2012 was characterized by a prolonged dry period in July with very low levels of relative usable soil water capacity and above average maximum temperatures (Figure 1b and c). After a short recovery, the soil water content decreased again to low levels during the second half of August and reached a local minimum in the beginning of September. With the exception of the second half of May, the year 2010 had above-average levels of soil water availability for much of the growing season. For the statistical analysis, we grouped the years according to the prevailing climatic conditions: 2010 was categorized as a 'spring heat wave' anomaly, 2012 was categorized as a 'summer drought' anomaly and all other years of the dendrometer monitoring period were grouped and categorized as 'reference' years as the prevailing climatic conditions in these years were moderate in comparison. The year 2006 was excluded in the dendrometer data analysis as no data were available due to technical problems.

Table 1. Sample sizes, mean age and mean diameter at breast height (DBH) of the study trees grouped by tree species.

Tree species	All trees			Dendrometer trees		
	No. of trees	Age (years)	DBH (cm)	No. of trees	Age (years)	DBH (cm)
Yellow birch	30	54.0 (10.1)	25.8 (4.5)	15	51.7 (7.4)	25.3 (5.1)
Sugar maple	30	80.3 (34.7)	25.3 (5.9)	13	79.1 (39.8)	23.7 (5.3)

Age refers to cambial age at breast height (1.30–1.40 m) as determined by increment cores (time of data acquisition: spring 2015); standard deviations are presented in parentheses.

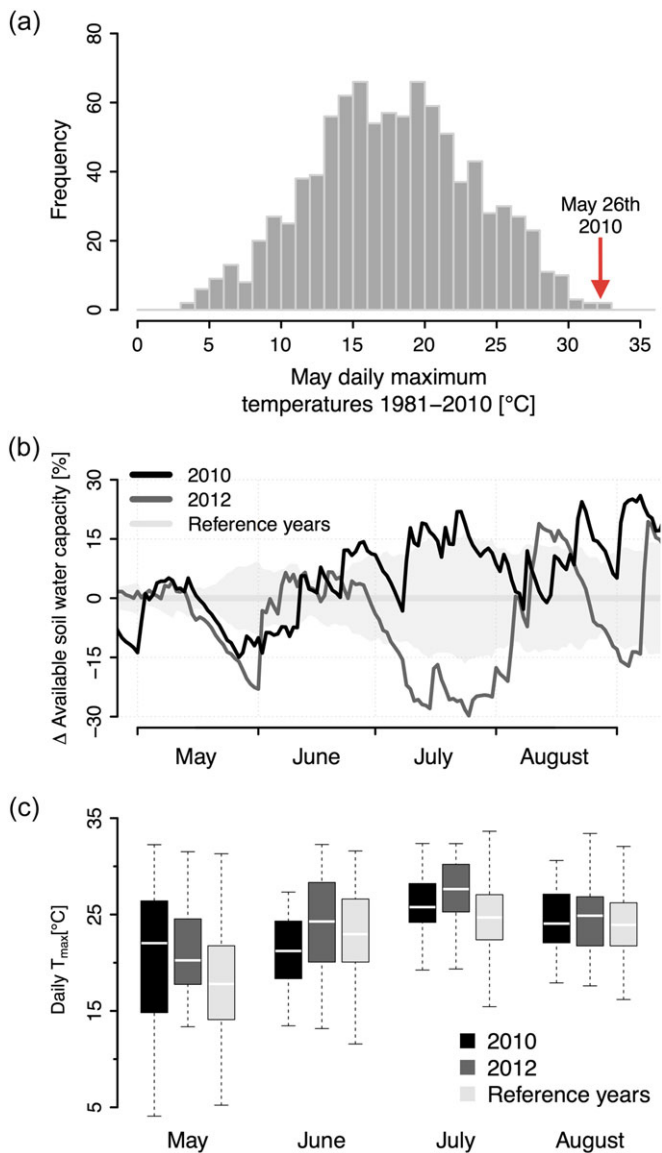


Figure 1. (a) Histogram of daily maximum May temperatures provided by the daily climate models for the baseline climate period 1981–2010 ($n = 930$). The gray arrow indicates the daily maximum temperature of 26 May 2010. (b) Simulated daily relative plant available soil water capacity during the year 2010 (spring heat wave) and 2012 (summer drought) as a deviation of the mean conditions of the reference years (2005, 2007, 2008, 2009, 2011, 2013 and 2014) with 95% confidence intervals displayed as transparent ribbons. (c) Monthly variation of daily maximum temperatures for the years 2010 and 2012 as well as for the reference years.

Statistical data analysis and modeling

All calculations and data analyses were performed in the R programming environment (R Development Core Team 2015). This study used the dendrometer time series and tree-ring width measurements to provide for each tree and calendar year estimates of growth phenology (onset, cessation, duration of radial growth, time of maximum daily growth rate) and productivity (tree-ring width, monthly and seasonal average growth rates, maximum daily growth rate), and to compare the values of these

variables between tree species and growing seasons with contrasting climatic conditions (2010, 2012 and reference years).

It is generally agreed that the low-frequency trend in the seasonal course of the SRD data between late spring, i.e., after the period of frost shrinkage, and early autumn is mainly controlled by secondary growth processes within the stem (Duchesne et al. 2012). However, as dendrometers only detect variations in the radial (or circumferential) stem dimension rather than measuring radial growth directly, the exact and unambiguous assessment of intra-annual growth dynamics based on dendrometer measurements is discussed controversially (Mäkinen et al. 2008). As clear evidence of cambial cell divisions and secondary growth processes can only be gained by complementary methods such as the pinning technique or the extraction of micro-cores, we emphasize that all investigated response variables of our statistical models except tree-ring width have to be considered as proxies rather than direct measurements.

To estimate the onset of radial growth (t_{on}) for each tree and calendar year, we first calculated a signal-to-noise ratio (SNR) for each day of year (DOY) t , based on the following formula:

$$SNR_t = \frac{\text{mean}(SRD_t) - \frac{1}{t-j} \sum_{j \leq k < t} \max(SRD_k)}{\text{sem}(\max(SRD_j), \dots, \max(SRD_{t-1}))} \quad (1)$$

where SRD is a vector of all daily measurements of SRD, j is the starting DOY of each annual time series and k are all days of year starting from j and prior to t . The abbreviations max, mean and sem refer to the daily maximum, arithmetic mean and the standard error of the mean of SRD, respectively. Growth onset was expected to have occurred when SNR_t irreversibly crossed the predefined threshold of 4. Once the SNR remained constantly above this predefined level, we assumed the rehydration of the stem internal water storage after the winter period to be completed and interpreted the subsequent steady increase in SRD as being controlled primarily by secondary growth processes.

To estimate the timing of the cessation of radial growth (t_{ce}), we fitted the dendrometer detrending algorithm, as described by Zweifel et al. (2005), to the upper 50% of the SRD raw data. The algorithm is a straightforward approach that extracts the growth component in the dendrometer data by fitting a convex polyline to adjacent local maxima, starting from the absolute maximum SRD value, backwards through the time series. A threshold for t_{ce} was defined, when the slope between adjacent local maxima decreased below $3 \mu\text{m day}^{-1}$. For the purpose of defining growth cessation, the slope of the convex polyline has the advantage of being robust against temporary growth depressions during the growing season, which therefore would not be misinterpreted as unusual early growth cessations. An example of the operating modes and respective outputs of the growth phenology algorithms can be found in Figure S1 available as Supplementary Data at [Tree Physiology Online](#).

To model the intra-annual dynamics of radial growth, we fitted a double sigmoid function (DSF) to the SRD data (Michelot et al. 2012, Stangler et al. 2016). This deterministic growth function is characterized by its flexibility in fitting unimodal as well as complex bimodal seasonal growth patterns, while still preserving robustness against short-term fluctuations of stem internal water status. To allow a better fit of the model to the initial stem size in spring, we slightly modified the equation by an additional asymptote (Duchesne et al. 2012):

$$y(t) = A + \frac{B}{1 + \exp^{-\kappa_1(t-M_1)}} + \frac{C-B}{1 + \exp^{-\kappa_2(t-M_2)}} \quad (2)$$

where A is the lower asymptote describing the initial stem size in spring, B is the middle asymptote, representing the accumulated growth (in μm) until the end of the first half of the growing season or until a temporary growth depression, C is the upper asymptote, denoting the final tree-ring width (in μm), t is the point in time, κ_1 is the rate of change parameter and M_1 is the time of the maximum growth rate during the first phase of the growing period, and κ_2 and M_2 during the second phase of the growing season, respectively. The parameters of the model were estimated for all trees and years using the *nlsLM* function of the *minpack.lm* package (Elzhov et al. 2015).

As the complexity of the DSF model bears the risk of overfitting, we applied the four parametric Gompertz model as presented by Duchesne et al. (2012) for model comparison. The Akaike information criterion (AIC) was used to choose the model that represented a better trade-off between number of parameters and goodness of fit (Burnham and Anderson 2010, Cury et al. 2013). The DSF considerably outperformed the Gompertz model as indicated by significantly lower (i.e., better) average AIC values (133,899 vs 147,556) and only in 2% of all cases was the Gompertz model found to be more adequate. Consequently, we decided to exclusively apply the DSF within the framework of this study.

For model validation, we calculated for each set of parameter estimates the modeling efficiency (EF), which is a relative measure of the goodness of fit for the class of non-linear regression models:

$$\text{EF} = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (3)$$

where y_i represents the observed value, \hat{y}_i represents the respective simulated value and \bar{y} denotes the mean of n observed values. EF values of close to 1 represent almost optimal fits, whereas values of zero or less indicate low predictive power of the model (Mayer and Butler 1993, Cury et al. 2013). With a minimum EF of 0.871, a mean EF of 0.996 and 75% of the EF values being above 0.997, the DSF demonstrated its capability to provide very close overall fits to the raw data of our dendrometer time series.

With the parameter estimates of the *nlsLM* function (see Eq. (2)), we predicted the daily growth rate from the 1 May until the 30 September based on the first derivative of the double sigmoid function DSF', which is expressed as follows:

$$y'(t) = \frac{B\kappa_1 \exp^{M_1\kappa_1 - \kappa_1 t}}{(\exp^{M_1\kappa_1 - \kappa_1 t} + 1)^2} + \frac{(C-B)\kappa_2 \exp^{M_2\kappa_2 - \kappa_2 t}}{(\exp^{M_2\kappa_2 - \kappa_2 t} + 1)^2} \quad (4)$$

The DSF' was used to determine the seasonal maximum daily radial growth rate (r_{max}) and its corresponding DOY (t_{max}) as well as to compute the average daily growth rate for each month (mt) between May and September (r_{mt}). By dividing the tree-ring width (TRW) measured on the increment cores by the number of days of growth, i.e., the growth duration ($\Delta t = t_{\text{ce}} - t_{\text{on}}$), the average daily growth rate ($r_{\Delta t}$) between growth onset and growth cessation was determined. Not all monitored growing seasons included the full count of days between 1 May and 30 September. As the initial and final stem size in spring and late summer was indicated by a plateau in the SRD data, the DSF' had the capability to provide reasonable predictions for the non-available days of year. In the cases of the response variables t_{on} , Δt , $r_{\Delta t}$ and r_{May} , the outputs of the statistical models are therefore less robust and must be interpreted more carefully.

Growth response of yellow birch and sugar maple to inter-annual climate variability was analyzed with linear mixed models accounting for repeated measurements of individual trees. The mixed effects models were implemented with the *lmer* function of the *lme4* package (Bates et al. 2015) and formulated as follows:

$$y_{ijkl} = \mu + C_i + S_j + (C \times S)_{ij} + yr(C)_{ik} + t_l + e_{ijkl} \quad (5)$$

where y_{ijkl} denotes the values of the response variable, μ is the overall experimental mean, C is the fixed effect of the climate i (classified into 'spring heat wave 2010', 'summer drought 2012' and 'reference' year(s) as described above), S is the fixed effect of the tree species j (yellow birch or sugar maple), $(C \times S)_{ij}$ represents the climate by tree species interaction, $yr(C)_{ik}$ is the random effect of year k within the climate class i , t_l is the random effect of the individual tree l and e_{ijkl} is the residual error term.

Post hoc tests were performed within each tree species and between the factor levels of the climate effect based on Tukey's procedure for pairwise comparisons using the *lsmeans* function of the package *lsmeans* (Lenth and Hervé 2015).

To study temporal growth dynamics, we compared the annual variability of the response variables t_{on} , t_{ce} , Δt , t_{max} , r_{max} , $r_{\Delta t}$ and TRW between the two tree species and computed a chronology with annual estimates derived from a mixed effects model with a tree species by year interaction $(S \times yr)_{jk}$ as fixed effect and t_l as random effect. ANOVA tables with P -values and F -statistics were compiled with

support of the *ImerTest* package (Kuznetsova et al. 2016). Based on this model, we also performed direct comparisons to test for significant differences between the two tree species within each year of the observation period.

Results

Year to year variability of growth phenology and productivity

During the period between 2005 and 2010, the tree species followed a synchronous pattern of growth onset (t_{on}) (Figure 2a). However in 2011, the year after the leaf drop event, sugar maple showed a distinctly delayed growth onset (DOY 150) compared with yellow birch (DOY 140) ($P < 0.001$). Also in the following years, growth onset of sugar maple remained delayed, but only in 2014 the difference was again significant ($P < 0.01$).

Growth cessation (t_{ce}) was, for most of the studied years, rather synchronous and not significantly different between tree species (Figure 2b). Only in 2010, where the leaf drop event occurred in spring, growth cessation of sugar maple (DOY 195) occurred significantly earlier in comparison with yellow birch (DOY 214) ($P < 0.01$). Similarly, the duration of growth (Δt) was different between the tree species only in 2010 ($P < 0.05$) (chronology not illustrated). No significant differences between the tree species in terms of growth cessation or growth duration could be detected in the year with the summer drought 2012.

The similar overall pattern of both tree species regarding the DOY where the maximum growth rate occurred (t_{max}) was interrupted between 2010 and 2012 (Figure 2c). In 2010, sugar maple (DOY 147) showed maximum growth rates around 10 days earlier than yellow birch (DOY 157) ($P < 0.05$). In sharp contrast, in 2011 maximum growth rate occurred in sugar maple 12 days later compared with yellow birch (DOY 188 vs DOY 176, $P < 0.01$). In 2012, sugar maple (DOY 158) achieved maximum growth rate 17 days earlier than yellow birch (DOY 175) with the difference between the tree species being highly significant ($P < 0.001$). The daily maximum growth rate (r_{max}) of yellow birch was generally higher than r_{max} of sugar maple, but the differences were not significant in any year (Figure 2d). The average daily growth rate between growth onset and growth cessation ($r_{\Delta t}$) was mostly higher in yellow birch than in sugar maple, but only in 2010 was the difference significant ($36 \mu\text{m day}^{-1}$ vs $18 \mu\text{m day}^{-1}$, $P < 0.001$) (chronology not shown).

Between 2006 and 2010, TRW of yellow birch was wider compared with sugar maple ($P < 0.01$ in 2006, 2007, 2009 and $P < 0.05$ in 2008) (Figure 2e). In 2010, where the spring heat wave occurred, sugar maple produced an average TRW of only 0.81 mm, which was 1.86 mm lower than yellow birch ($P < 0.001$). Although between 2011 and 2014 average TRW of yellow birch also remained at higher levels compared with sugar maple, only in 2013 could significant differences ($P < 0.05$) be detected.

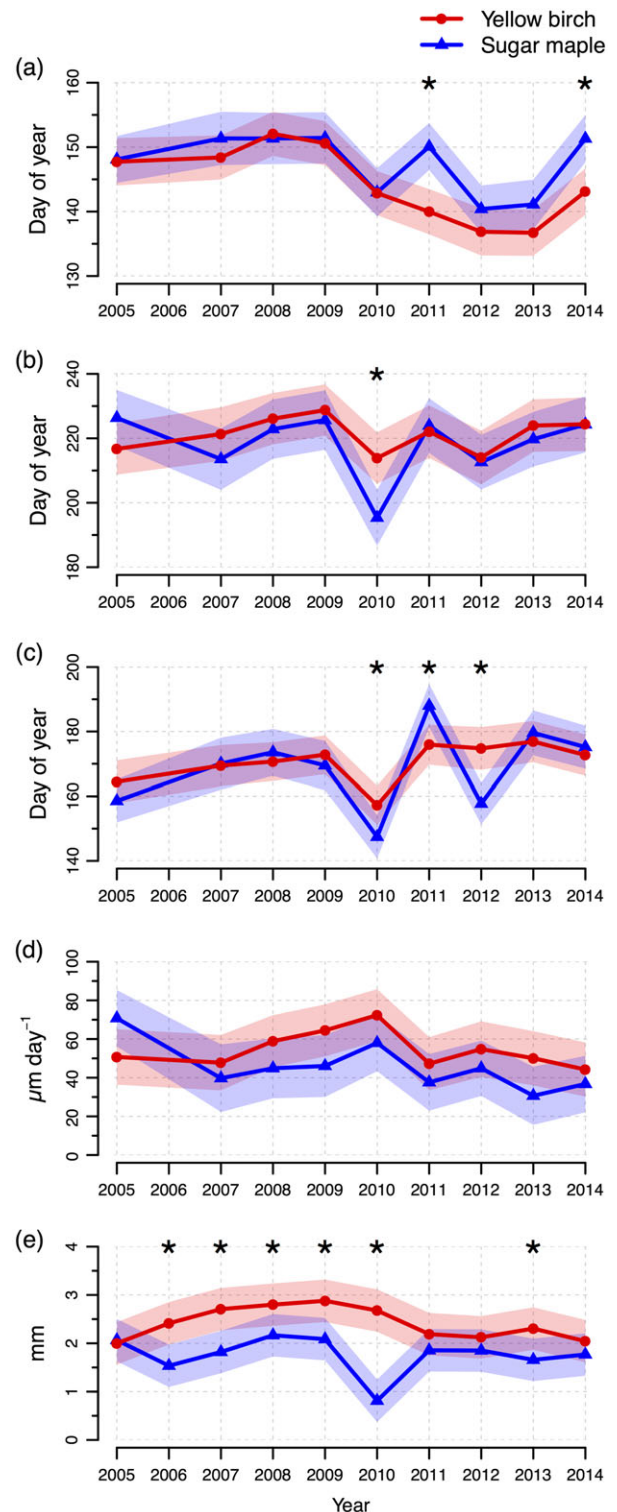


Figure 2. Year to year variability of growth onset (t_{on}), growth cessation (t_{ce}), day and extent of maximum daily growth rate (t_{max} and r_{max}) and tree-ring width (TRW) of yellow birch and sugar maple during the study period. Transparent ribbons indicate 95% confidence intervals of the mean and stars denote significant differences between tree species ($P < 0.05$). (a) Onset of radial growth, (b) cessation of radial growth, (c) time of maximum growth rate, (d) maximum growth rate and (e) tree-ring width.

Table 2. ANOVA table for the mixed effects models with tree species and year as fixed effects, compiled for all investigated response variables.

	Species		Year		Species x Year	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Onset (t_{on})	3.428	0.074	22.093	<0.001	3.441	0.001
Cessation (t_{ce})	0.483	0.493	10.036	<0.001	2.973	0.004
Duration (Δt)	0.484	0.492	3.485	0.001	1.698	0.102
Day of max. growth rate (t_{max})	0.500	0.485	17.714	<0.001	4.025	<0.001
Max. growth rate (r_{max})	1.512	0.230	5.576	<0.001	2.284	0.024
Average growth rate ($r_{\Delta t}$)	2.256	0.145	1.857	0.069	2.768	0.007
Tree-ring width (TRW)	6.291	0.015	6.965	<0.001	8.150	<0.001

P-values <0.05 are highlighted in bold type.

Over the whole observation period, a significant difference between tree species was only detected in TRW as yellow birch showed on average considerably higher annual growth rates (Table 2). Except for growth duration (Δt), significant interaction effects of tree species and year were detected for all response variables, underlining the distinctly different growth dynamics of yellow birch and sugar maple during parts of the observation period.

Seasonal growth dynamics in response to contrasting climates

In 2010 cumulative SRD of yellow birch remained permanently higher than in 2012 and was not surpassed by the mean curve of the reference years before the beginning of August (Figure 3a). The occurrence of the leaf drop event on sugar maple in 2010 was accompanied by a subsequent stagnation of SRD and the average curve of the reference years already rapidly surpasses the 2010 curve in the middle of June (Figure 3b). The heat wave disturbance also caused a significant deviation of the typical sigmoid growth pattern found in the reference years. During the drought conditions of late July and August 2012, large daily oscillations of SRD were detected on both tree species, accompanied by a seasonal stagnation and even negative rates of SRD during the second half of August. In sugar maple, the inhibiting effect of the drought conditions on SRD dynamics and the depletion of stem internal water reserves appeared to be more pronounced.

In contrast to the reference years, the rate of radial growth of yellow birch and sugar maple in 2010 already peaked before the beginning of June, resulting in right-skewed intra-annual growth patterns of both tree species (Figure 3c and d). However, the drastic decline that followed closely after the temperature peak on the 26 May 2010 was more extreme and permanent in sugar maple. Declining growth rates for both tree species were also detected during the drought of July 2012. In 2012 the daily rate of radial growth of sugar maple fell below the respective level of the reference years around 2 weeks earlier than was the case for yellow birch.

Growth phenology and productivity under contrasting climates

In response to the 2010 heat wave and 2012 summer drought, yellow birch showed less variation in growth phenology, the timing and extent of the maximum growth rate or in TRW than sugar maple (Figure 4). In contrast, sugar maple showed considerable variation in the assessed response variables. Although no significant differences in growth onset could be detected, the average timing of growth cessation was significantly earlier in the spring heat wave year 2010 (DOY 195) compared with the summer drought year 2012 (DOY 213, $P < 0.05$) and reference years (DOY 223, $P < 0.001$). Consequently, the only 53 days of radial growth duration in 2010 was significantly shorter than the 72 days in 2012 ($P < 0.05$) and the average of 74 days of the reference period ($P < 0.01$) (data not illustrated in Figure 4). The day of the maximum daily growth rate occurred in the year 2010 significantly earlier in comparison with the reference years (DOY 147 vs DOY 174, $P < 0.05$). With only 0.81 mm, the TRW in the heat wave and leaf mortality year 2010 was very low and differences were almost highly significant in comparison with the reference years (1.91 mm, $P < 0.0102$) and almost significant in comparison with the drought year 2012 (1.85 mm, $P < 0.053$).

With $18 \mu\text{m day}^{-1}$, the average daily growth rate of yellow birch in May 2010 was significantly higher ($P < 0.05$) compared with the average of $7 \mu\text{m day}^{-1}$ during the reference period (Figure 5). Also in sugar maple, average growth rates in May 2010 ($18 \mu\text{m day}^{-1}$, $P < 0.01$) and 2012 ($15 \mu\text{m day}^{-1}$, $P < 0.05$) were at distinctly higher levels compared with the reference period with $6 \mu\text{m day}^{-1}$. For yellow birch, no further significant differences in monthly (r_{mt}) or seasonal average growth rates ($r_{\Delta t}$) could be found. In contrast, sugar maple showed in June 2010, the month that directly followed the leaf drop event, already significantly lower radial growth rates ($12 \mu\text{m day}^{-1}$ compared with $30 \mu\text{m day}^{-1}$ during the reference years, $P < 0.05$). The difference between the heat wave year 2010 and the reference period was even more pronounced in July ($4 \mu\text{m day}^{-1}$ vs $27 \mu\text{m day}^{-1}$, $P < 0.001$). In the summer drought year 2012, the average daily growth rate in July ($15 \mu\text{m day}^{-1}$)

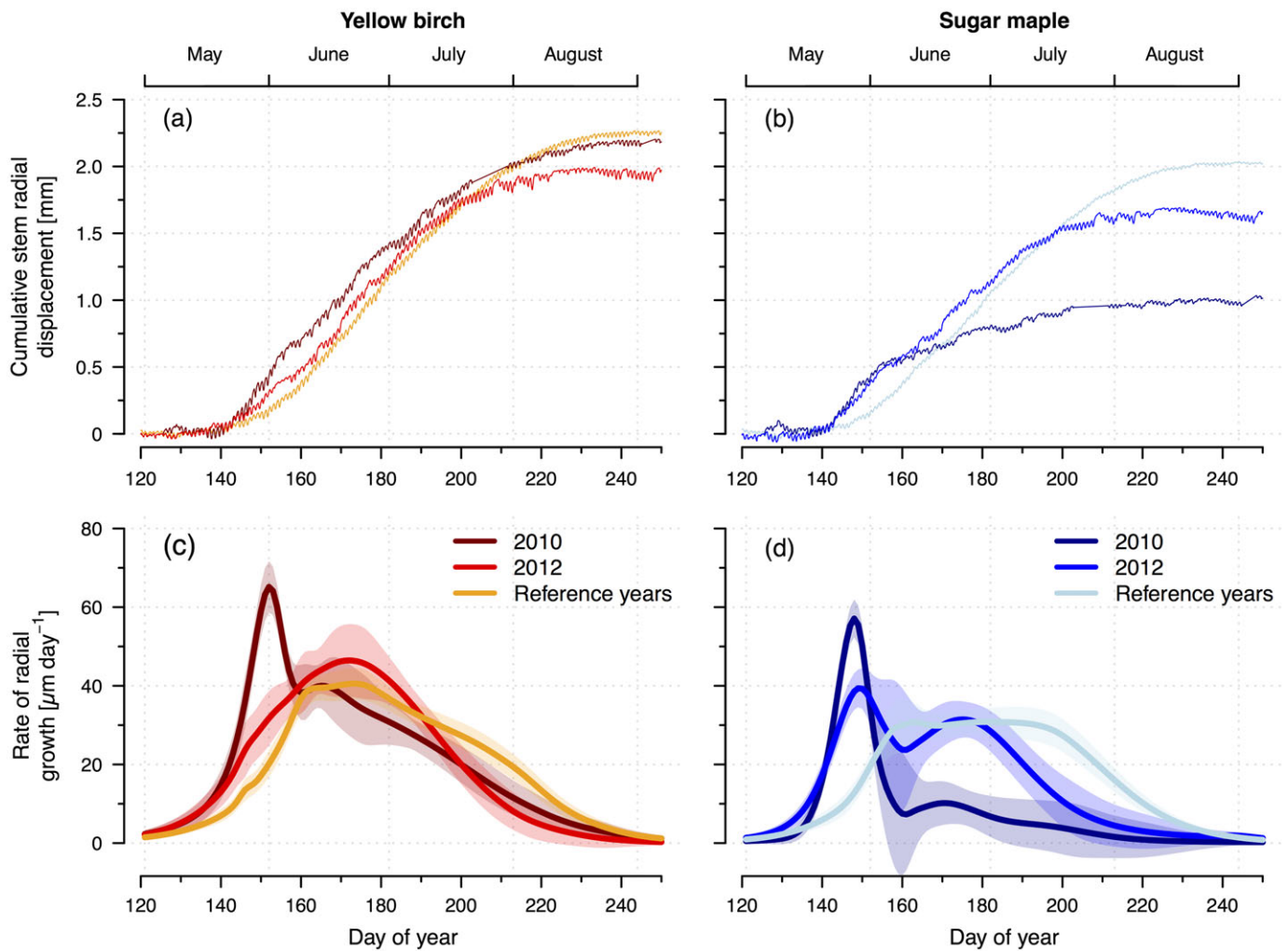


Figure 3. Seasonal dynamics of cumulative SRD as well as daily rates of radial growth during the heat wave year 2010, the summer drought year 2012 and reference years for yellow birch (a, c) and sugar maple (b, d). Transparent ribbons indicate standard errors of the estimates.

of sugar maple also showed a distinct reduction compared with the reference years ($P < 0.01$). No differences could be found in August or when comparing daily average growth rates for the period of growth.

Discussion

Critical evaluation of the applied algorithms

In this study, we used a new set of algorithms to provide estimates for growth onset (t_{on}), growth cessation (t_{ce}), growth duration (Δt) and average daily growth rate for the period of growth ($r_{\Delta t}$) based on dendrometer measurements. For the determination of growth onset and growth cessation, we refused to apply relative threshold values, such as 5% and 95% of the seasonal radial increment (Hauser 2003, Mäkinen et al. 2008, Swidrak et al. 2013), as these are a function of final TRW and would have produced biased results, due to highly variable growth patterns in the uneven-aged stand. Determining growth onset by use of the SNR has the advantage of taking the variability of the

tree water status before growth onset into account (Turcotte et al. 2009). Although dendrometer monitoring was reactivated within the time window after snow melt and before leaf expansion and our measurements were affected rarely by frost-induced bark shrinkages (Zweifel and Häsler 2000), we would expect more precise and comparable growth onset estimates if time series had not been interrupted during the winter period. As the algorithms to estimate growth onset and growth cessation were based on subjectively defined threshold values, future dendrometer research should focus on calibrated algorithms with support of complementary approaches for studying intra-annual wood formation processes, such as the micro-coring method or the pinning technique (Rossi et al. 2006, Seo et al. 2007).

Growth response to warm spring conditions in 2010 and 2012

Higher than average spring temperatures have been identified to be responsible for earlier growth onset and modification of the

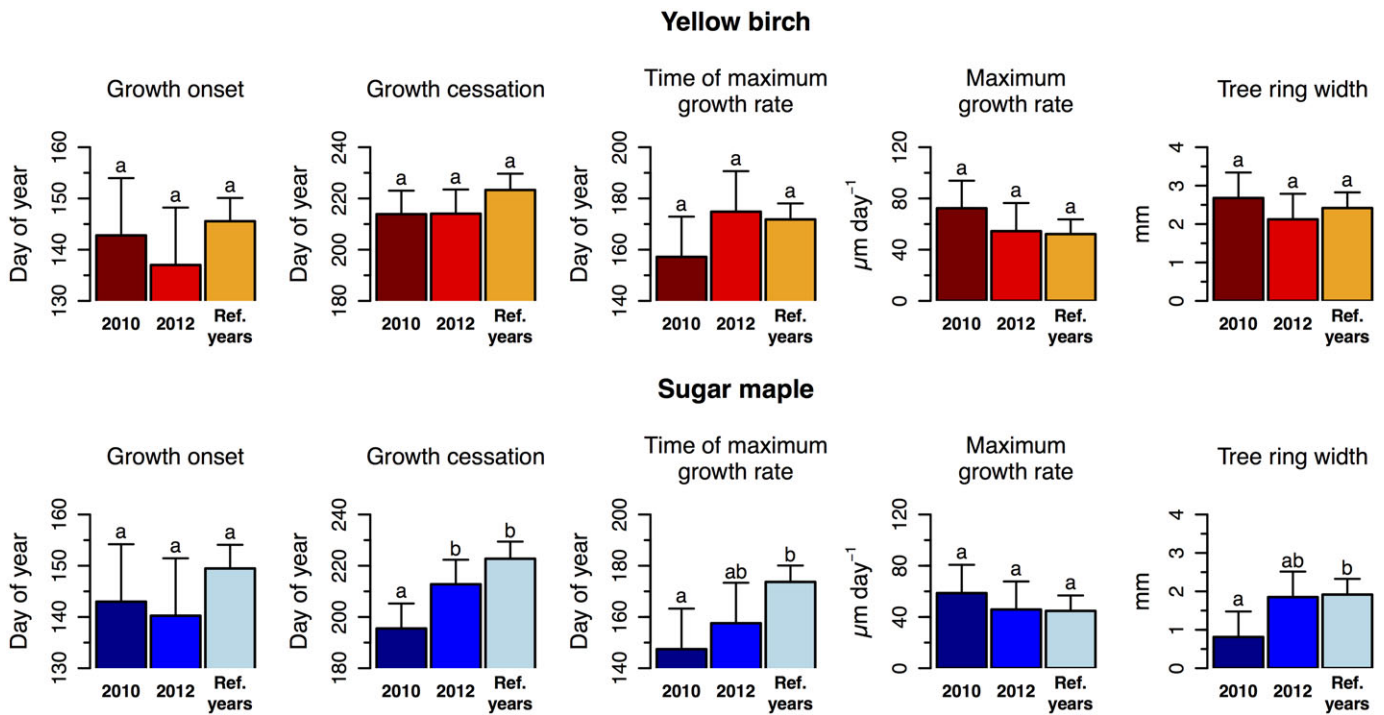


Figure 4. Sample means of growth onset (t_{on}), growth cessation (t_{ce}), day and extent of maximum daily growth rate (t_{max} and r_{max}) and tree-ring width (TRW) of yellow birch and sugar maple for the heat wave year 2010, the summer drought year 2012 and the reference years. Error bars indicate 95% confidence intervals. Identical lowercase letters above the error bars indicate P -values of the pairwise comparisons being higher than the 0.05 α -level.

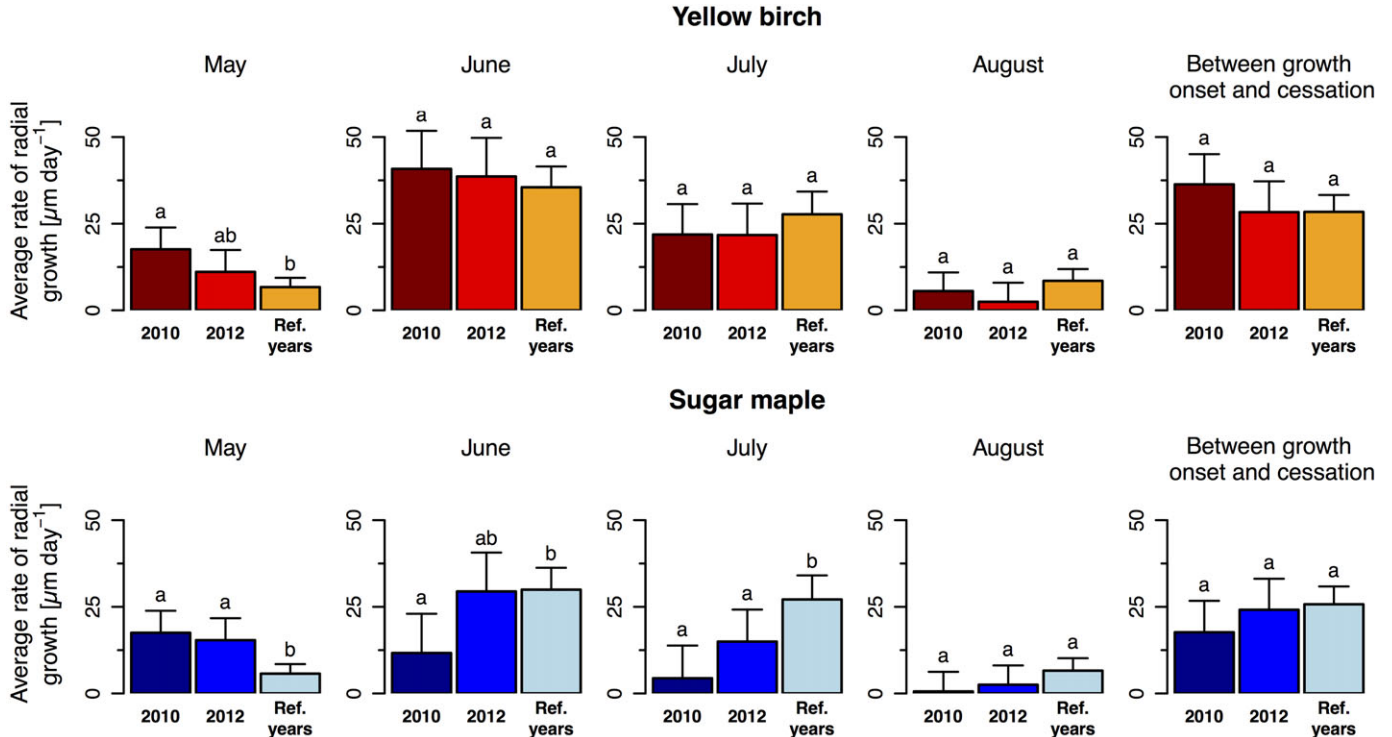


Figure 5. Average daily radial growth rates per month (r_{mt} , May to August) and for the period of growth ($r_{\Delta t}$) of yellow birch and sugar maple during selected years (heat wave year 2010, summer drought year 2012 and reference years). Error bars indicate 95% confidence intervals. Identical lowercase letters above the error bars indicate P -values of the pairwise comparisons being higher than the 0.05 α -level.

total duration of xylogenesis in several studies (Gričar et al. 2006, Deslauriers et al. 2008, Lugo et al. 2012). Our hypothesis that warm spring conditions would cause earlier growth onset of both tree species was not confirmed. However, the warm spring conditions in May 2010 and 2012 were accompanied by above average growth rates of both tree species, with differences being more pronounced in sugar maple. The earlier occurrence of the maximum daily radial growth rate of sugar maple in both years also suggests a more positive effect of spring temperature in comparison with yellow birch. Under cool climates and particularly in boreal or mountainous forest regions, temperature is generally accepted as the major limiting factor controlling growth processes and productivity rates (Rossi et al. 2007, Kirilyanov et al. 2008, Babst et al. 2013). As the duration of mitosis increases exponentially below a temperature threshold of 10 °C, the investment of carbon into meristematic activities and cell differentiation might still have been inhibited to a large extent during the lower May temperatures of the reference years (Körner 2003).

Drought response in seasonal growth dynamics

During periods of drought stress and high evaporative demand, isohydric tree species such as sugar maple and yellow birch minimize water loss and risk of xylem cavitation via stomatal regulation, leading to possible carbon starvation, as well as prioritizing plant available carbon reserves for respiration rather than for cell production (Davies and Kozlowski 1977, Catovsky and Bazzaz 1999, Allen et al. 2010). Thus, summer drought and heat waves during late summer and early autumn can act as driving factors that determine the end of seasonal radial growth processes (Kahle 2006, van der Maaten 2013). Although both tree species did not show a significantly earlier growth cessation in 2012, drought sensitivity of sugar maple was clearly demonstrated by low daily growth rates in July and a seasonal growth pattern that fell below the reference levels around 2 weeks earlier than was the case for yellow birch. Our results therefore confirm previous findings that summer precipitation is a dominant factor that controls the variability of radial growth of sugar maple (Tardif et al. 2001, He et al. 2005). In contrast, TRW of both tree species was not significantly reduced by the summer drought in 2012. The reason for the small reduction of TRW in 2012 was evidently the higher daily growth rates during May 2012 that compensated the subsequent productivity losses in July. Also, the temporary depletion of stem internal water reserves during the second half of August can be interpreted as a period of prolonged water stress (Zweifel et al. 2005, Koecher et al. 2013). However, distinct lag effects of the summer drought 2012 on growth dynamics of yellow birch and sugar maple in 2013 were not detected.

Impacts of the spring heat wave of May 2010

In response to the spring heat wave, another study conducted ~7 km northwest of our research plot found that

sugar maple shed its expanding leaves, whereas yellow birch remained largely unaffected (Filewod and Thomas 2014). The leaf loss phenomenon was interpreted as a possible physiological response of the trees to minimize water deficits and to avoid xylem embolism due to increased transpiration rates caused by the heat wave. Other observations of trees shedding their fully expanded leaves during a summer heat wave, as occurred in July 2012, are not documented in our study area within the time frame of our monitoring period. Leaves of C₃ and C₄ plants also rely on transpirational cooling (Taiz and Zeiger 2008). Stomatal conductance is controlled by the guard cells in the leaf epidermis and this cooling mechanism as well as other protective layers against heat such as the cuticle or trichomes might still have been partly dysfunctional in leaves undergoing differentiation processes in May (Kalve et al. 2014).

Due to the contrasting response of yellow birch and sugar maple to the spring heat wave, we expected that growth cessation and intra-annual growth dynamics in 2010 would vary between the tree species and would show considerable deviation of the general trend. The highly anomalous, right-skewed intra-annual growth pattern of sugar maple, characterized by low productivity levels throughout the growing season, followed by unusual early growth cessations, can be interpreted as direct consequences of the leaf drop event. Primary growth processes and metabolic activities in spring largely depend on starch reserves stored in the parenchyma rays of the xylem during previous years (Wong et al. 2003). With the carbon pools already exhausted by the first flush of leaves and accumulated new xylem cells, the sink strength of the expanding second flush of leaves in sugar maple might have resulted in a reduced allocation of available non-structural carbohydrates to secondary growth processes. The low growth rates monitored by the dendrometers directly synchronize with the reduced photosynthetic capacities of the second flush of neo-formed leaves in early summer as detected by Filewod and Thomas (2014). In addition, autotrophic respiration losses at the leaf and tree level are largely increased under high temperatures and might therefore have contributed to the growth reduction (Teskey et al. 2015). Although photosynthetic rates recovered to normal levels in late July and August, no bimodal growth patterns could be detected that were triggered by a second peak of the radial growth rate during late summer. In contrast, we detected highly significant time lags of growth onset and day of maximum growth rate between yellow birch and sugar maple in 2011. The reduced carbon uptake during summer 2010 could have caused sugar maple to enter the subsequent dormancy period and next growing season with depleted pools of non-structural carbohydrates, resulting in highly asynchronous growth dynamics of the two tree species in the following spring. Pools of non-structural carbohydrates are highly dynamic and time lags between carbon fixation during previous growing seasons and biomass increment during the following years have also been suggested by previous studies (Rocha et al. 2006, Richardson et al. 2013).

Two hypotheses for the contrasting response of the two investigated tree species have been stated by Filewod and Thomas (2014): compared with co-occurring hardwood tree species such as red maple and American beech, sugar maple is known to expand its leaves relatively early during spring. This is supported by a canopy phenology study on sugar maple, American beech and yellow birch, which also found that sugar maple was the first species to flush its leaves during spring (Richardson et al. 2006). However, it is also suggested that the observed differences could be explained by the fact that leaf mortality in 2010 was mainly observed on shade-tolerant tree species, which are considered to be more sensitive to extreme temperatures peaks (Dreyer et al. 2001, Filewod and Thomas 2014). Furthermore, late frosts that were monitored in early May might have predisposed the sugar maple trees to become more vulnerable to the effect of the spring heat wave (Filewod and Thomas 2014). Despite the multitude of negative impacts of the spring heat wave on the seasonal growth patterns of sugar maple in 2010 with lagged effects on growth onset being visible in 2011, a remarkable growth resilience of sugar maple was demonstrated by TRWs that returned to normal levels already in the growing season 2011.

Our results are also in accordance with records from an eddy covariance flux station, located in a comparable hardwood stand ~4.5 km northeast of our research plot that identified 2010 as a year in which the forest stands acted as a significant carbon source in comparison with 2011 and 2012 (Geddes et al. 2014). The carbon source signal from the flux tower installation suggests that the dendrometer measurements of this study apply beyond the individual stand that we selected. Our findings may therefore also have implications for growth response of sugar maple and yellow birch under climate change. According to IPCC (2014), a higher frequency of heat waves is expected under warming climate and our study has shown that sugar maple, a species that dominates northern temperate hardwood forests, might be relatively vulnerable to such extreme events.

Supplementary Data

Supplementary data for this article are available at *Tree Physiology* Online.

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Author Contributions

D.F.S. wrote the manuscript with support of A.H., H.P.K. and H.S. The main concept and ideas of this study were developed by H. S. in collaboration with the manager of HFWR. Sampling of increment cores in the field was conducted by D.F.S. and H.S. Tree ring measurements and crossdating was performed by D.F.S. Data was analyzed by D.F.S. with support of A.H. and with advice from H.P.K. and H.S.

Conflict of interest

The authors declare no conflict of interest.

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