Stem growth phenology, not canopy greening constrains deciduous tree growth

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Canopy phenology is not a predictor of annual stem growth

Abstract

Canopy phenology is a widely used proxy for deciduous forest growth with various applications in terrestrial ecosystem modeling. Its use relies on common assumptions that canopy greening and stem growth are tightly coordinated processes, enabling predictions on the timing and the quantity of annual tree growth.

Here, we present parallel observations of canopy and stem growth phenology and annual stem increment in around 90 deciduous forest trees with diffuse-porous (*Fagus sylvatica, Acer pseudoplatanus*, *Carpinus betulus*) or ring-porous (*Quercus robur x petraea*) wood anatomy. These data were collected in a mixed temperate forest at the Swiss-Canopy-Crane II site, in four years with strongly contrasting weather conditions.

We found that stem growth resumption lagged several weeks behind spring canopy greening in diffuse-porous but not in ring-porous trees. Canopy greening and stem growth resumption showed no or only weak signs of temporal coordination across the observation years. Within the assessed species, the seasonal timing of stem growth varied strongly among individuals, as trees with high annual increments resumed growth earlier and also completed their main growth earlier. The length of main growth activity had no influence on annual increments.

Our findings do not only challenge tight temporal coordination of canopy and stem growth phenology but also demonstrate that longer main growth activity does not translate into higher annual increments. This may compromise approaches modelling tree growth and forest productivity with canopy phenology and growth length.

Key words
Angiosperms
Bud break
Wood formation
Growing season
Annual increment

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Introduction

Observing canopy phenology is a popular approach to study the seasonal dynamic of temperate deciduous forests and infer further information on annual tree growth and ecosystem carbon cycles at local to global scales (*White et al 1999, Richardson et al. 2010*). Related to this are important questions such as how changing phenological cycles may influence feedbacks of terrestrial ecosystems to the climate system through changes in the seasonal patterns of photosynthetic carbon uptake. Much effort has been devoted to assessing the phenological shifts in boreal and temperate forest growth that result from recent climate warming (*Vitasse et al. 2022*). Observations of earlier leaf out and later leaf senescence were taken as evidence that increasing global temperature has already led to a significant extension of the growing season length and it was speculated, that this might ultimately result in higher annual forest growth and carbon sequestration (*Menzel and Fabian 1999, Rossi et al. 2014, Rossi et al. 2013, Gao et al. 2022*).

Knowledge of the processes that control the start and length of the growing season is key to any approach modeling terrestrial carbon fluxes and forest growth. Still, there is potential confusion how the widely used term "growing season" is defined (*White et al. 2003*). In ecological modeling, it is often meant to describe the period between spring canopy greening and autumnal leaf senescence in deciduous trees (e.g. *Richardson et al. 2010, Richardson et al. 2018, Piao et al. 2019, Lian et al. 2022*), assuming that the time a tree keeps a green canopy equals the time a tree can allocate the assimilated carbon to growth. In dendroecology, however, the term growing season is more strictly defined as the period a tree actually grows. This period does not necessarily cover the same time a tree retains a green canopy as shown by several wood-anatomical studies on deciduous species which found earlier or later times for bud burst compared to wood growth resumption (*Suzuki et al. 1996, Klein et al. 2016, Perez-de-Lis et al. 2016, Lavrič et al. 2017, Gričar et al. 2022*).

Despite the different interpretation of phenological terminology in ecological modeling and dendroecology, canopy greening is considered as the key phenological event that marks the seasonal transition of a tree from dormancy to a physiologically active state, with new photosynthesizing foliage providing carbon for growth (*Savage and Chuine 2021*). Based on this, several attempts have been undertaken to predict the annual rate of tree growth with the seasonal onset and duration of canopy photosynthesis, but many of those ecosystem studies failed to show a clear interdependency of the two processes or provided controversial results (rev. in *Delpierre et al. 2016a*). This uncertainty is not surprising as canopy photosynthesis and

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carbon availability must not necessarily been seen as growth-limiting factors in boreal and temperate trees (*Muller et al. 2011*, *Körner 2015*). However, phenological studies in which the timing of canopy greening and stem growth were assessed simultaneously are relatively rare and do not provide a consistent picture on the interplay of the two processes (*Suzuki et al. 1996*, *Čufar et al. 2008, Antonucci et al. 2015, Klein et al. 2016, Perez-de-Lis et al. 2015, Gričar et al. 2022*). Further controversy may arise from recent global dendroecological studies, either supporting or rejecting the view that the annual rate of tree growth depends on its seasonal timing and duration (*Gao et al.* 2022, *Dow et al. 2022*).

Although it is still unclear how closely canopy greening and stem growth resumption are linked by internal fluxes of assimilated carbon or other physiological cues, they are generally thought to exhibit a high degree of temporal coordination throughout the season. (critically reviewed in *Delpierre et al. 2016b, Savage and Chuine 2021*). At first glance this seems reasonable, as the mechanisms controlling canopy greening and stem growth resumption are both driven by seasonal fluctuations in temperature and light; and timely coordination of seasonal organ activity is critical to the physiology of the whole tree. Seasonality of tree activity is therefore an important element in forest growth and carbon flux models, which often include simplified assumptions about the temporal coordination of canopy phenology with annual tree growth (*Rötzer et al. 2004, Krinner et al. 2005, Deckmyn et al. 2006, Deckmyn et al. 2008, Medvigy et al. 2009*). However, it can be problematic to use canopy phenology data as driving variables in tree growth models because the principles linking canopy phenology to stem growth are not fully understood. Some progress has been made in boreal conifers, enabling statistical description of annual wood production as function of canopy phenology and cambium activity (*Huang et al. 2014*). So far, similar attempts are lacking for temperate deciduous tree species.

Here, we report the results of a phenological study combining field observations of spring canopy greening with observations of annual stem growth in four major European, broad-leafed tree species with diffuse-porous (*Fagus sylvatica*, *Acer pseudoplatanus*, *Carpinus betulus*) or ring-porous wood anatomy (*Quercus robur x petraea*). This work was carried out at the Swiss-Canopy-Crane II site, a semi-natural, temperate forest area with a high diversity of European tree species. Using a dataset collected in about 90 trees over four climatically contrasting years, we were able to test temporal coordination of canopy greening in spring with the timing and rate of seasonal stem growth. Specifically, we aimed to explore the suitability of phenological observations of tree canopies as predictors of tree growth and forest productivity.

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Material and Methods

Research site and study trees

This study was conducted at the Swiss-Canopy-Crane II (SCCII) research site close to Hölstein/BL, Switzerland (47°26′17″N, 7°46′37″E; 550 m a.s.l.). The site is situated in a semi-natural, uneven-aged forest stand, with *Fagus sylvatica* L. and *Picea abies* L. as dominant tree species and admixed trees of *Acer pseudoplatanus*, *Carpinus betulus*, *Quercus robur x petraea* and other species. The average climate conditions are 9°C annual temperature and 1,009 mm annual precipitation (data taken from a nearby climate station operated by the Swiss meteorological service; detailed description in *Arend et al. 2021*). A canopy crane is installed in the center of the site, enabling access to canopies within a radius of 50 m. In early spring 2018, 54 individuals of *F. sylvatica*, 16 trees of *Q. robur x petraea*, 11 trees of *C. betulus* and 10 trees of *A. pseudoplatanus* were selected for this study. The breast height diameter of the selected trees ranged from 16.7 to 61.0 cm for *F. sylvatica*, from 31.9 to 65.1 cm for *Q. robur x petraea*, from 19.0 to 37.4 cm for *C. betulus* and from 26.4 to 65.0 cm for *A. pseudoplatanus*.

Study period and weather conditions

All observations and measurements of this study were carried out in the years 2018 to 2021. Weather data for this period and the corresponding long-term trend (norm period 1990-2020) for comparison were collected from a nearby climate station operated by the Swiss meteorological service (station Rüneberg), located 7.5 km from the Swiss-Canopy-Crane II research site (47°26′04″N, 7°52′45″E; 611 m a.s.l.; Tab. 1). From the collected data, deviations of monthly temperature from the norm period were derived for the spring months April and May. The monthly climatic water balance (sum of monthly precipitation and potential evaporation) was used as a drought index and averaged over the main vegetation period from June to October.

The observation period 2018 to 2021 included years with strongly contrasting weather conditions as the exceptional year 2018. It was characterized by very warm April and May temperatures exceeding the values of the meteorological norm period by 4.9 and 2.0 K, respectively, as well as a severe summer to autumn drought with a strongly negative climatic water balance of -35 mm during the main vegetation season from June to October. Another exceptional year was 2021 with April and May temperatures -0.8 and -2.5 K below the values of the meteorological norm period as well as a wet summer with a strongly positive climatic water balance of 43 mm.

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Canopy observations

The phenological status of the canopies was assessed from the ground in approx. weekly intervals from end of March to end of May. In a few cases where canopies were not assessable from the ground, the canopy crane was used for phenological observations. The onset of spring canopy greening was defined as the week of observation (woy) when ≥10% of the buds within a given canopy were open. Buds were considered to be open when the bud scales were clearly separated from each other or partly lost and the green - but still folded - leaf tissue became visible (Fig. S1). Autumnal leaf senescence could not be assessed due to the spatially and temporally very heterogenous progression of leaf yellowing and shedding in the observed canopies.

Stem growth assessment

Dendrometer bands (D1 tree girth band, UMS GmbH München, Germany) were mounted at breast height on the stems after cleaning the stem surface from mosses and climber vegetation and removing loose or uneven parts of the outer bark. The dendrometer readings were preferentially conducted in the late morning hours, in approx. weekly intervals throughout the four observation years. The time series obtained from weekly dendrometer readings were used as unprocessed data (except correction of very few erroneous signals) to approach the timing of stem growth as close as possible. Diurnal stem diameter variations due to transpirational water loss were assumed to have little influence on the dendrometer readings as the magnitude of the weekly collected signals is larger than that of daily stem diameter fluctuations (*Delpierre et al. 2016b*). Additional tests in the field did not show any fluctuations of the dendrometer readings throughout the morning to afternoon hours (data not shown).

The time of spring stem growth resumption was determined as the week of observation when the dendrometer readings exceeded the value of the previous week by at least 0.2 mm and the subsequent readings showed further increases. This threshold was used to avoid misinterpretation of potential reading errors at the 0.1 mm resolution limit of the dendrometer bands. In a few trees, stem growth started very slowly, with weekly increments matching the 0.1 mm detection limit. To account for potential reading errors associated with such small increments in those trees, the dendrometer reading in the second week of the spring period of continuous stem diameter increase was considered as the week of growth resumption.

To obtain further information on the duration of main stem growth activity, we adopted an approach that has been previously used by *Delpierre et al.* (2016b). In brief, we determined the

week of observation when the dendrometer readings exceeded 90% of the total diameter increase from beginning of April to beginning of January the following year ($SDI_{90\%}$; Fig. S2). The beginning of January was chosen as end point in our analysis as the dendrometer readings remained almost stable in the following time from January to March. The relative $SDI_{90\%}$ threshold was applied (1) to account for common difficulties in defining a distinct date of growth stop in the gradually flattening dendrometer trends, (2) minimize the influence of small growth-independent diameter fluctuations or reading uncertainties at the end of season, and (3) normalize the data to make low and high increment trees better comparable. Since the $SDI_{90\%}$ excludes some late-season growth, it was only considered as a time estimate for the completion of the main part of stem growth activity.

Statistical analysis

All data were analyzed with IBM SPSS Statistics, Version 28.0.1.1 (IBM Incorp., USA). The GLM function was used with a repeated measure design to analyze general effects of the study years on species means of phenological metrics and stem growth. Linear regression models were employed to characterize relationships between phenological metrics and stem growth among and within populations. Spearman's Rank Order correlation was used to test associations between variation patterns within a given population in different years. Data are reported as means ± SD and results are considered to be statistically significant when $P < 0.05$.

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Results

In this study, we assessed the canopy and stem growth phenology of four temperate deciduous tree species over the course of four years with strongly contrasting weather conditions. The observation period included the exceptional year 2018 which was characterized by an unusually warm spring and a very dry summer as well as the year 2021 with an unusual cold spring and a wet summer (Tab. 1). In the three diffuse-porous species (*F. sylvatica*, *A. pseudoplatanus*, *C. betulus*), we found that the average onset of spring canopy greening preceded the average resumption of stem growth in all observation years (Fig. 1; Tab. 2). In *F. sylvatica* and *A. pseudoplatanus*, the delay of stem growth resumption was up to five or six weeks, respectively. In *C. betulus,* the delay of stem growth resumption was particularly remarkable, as stem growth started on average eight to ten weeks after the onset of canopy greening. A contrasting pattern was observed in the ring-porous species (*Q. robur x petraea*), where the average timing of stem growth resumption mostly matched the onset of canopy greening (Fig. 1; Tab. 2). One exception was the unusually warm spring 2018, in which *Q. robur x petraea* resumed stem growth on average three weeks after the onset of canopy greening. In all species, we found that the average onset of canopy greening and the resumption of stem growth varied strongly across the four observation years (Tab. S1), but regression models did not provide significant evidence for temporally synchronized co-variation (Fig. 1). Only in *A. pseudoplatanus* we found a positive, but non-significant trend of co-variation across the four years.

Within the four species, we found in all years a very high intra-specific variability in the seasonal timing of stem growth resumption, while the onset of canopy greening varied much less. In *F. sylvatica*, for instance, the onset of canopy greening differed by two weeks among the trees assessed in 2018 compared to seven weeks for growth resumption in the same trees and the same year. The high intra-specific variability in the timing of stem growth resumption was attributable to early stem growth resumption in trees with high annual increment and late stem growth resumption in trees with low annual increment (Fig. 2). The onset of canopy greening, in contrast, did not show any relationship with annual increment in the four species and four observation years. Notably, the pattern of intra-specific variability of growth resumption and annual stem increment was mostly preserved across the four observation years, i.e., trees which grew much and early in one year did so in the next year (Tab. S2). This is well illustrated in *F. sylvatica*, where the large number of assessed trees could be clearly separated in early versus late growing individuals over the course of the four observation years (Fig. 3a). The social position of an individual tree, as indicated by its stem size, had no influence on the

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intra-specific variation of stem growth resumption. In fact, our observations in *F. sylvatica*, which included individuals of very different size classes (breast height diameter 10 to 60 cm), did not reveal any significant trend of canopy and stem growth phenology with the size of the trees (Tab. S3).

To capture the full sequence of stem growth phenology, we also derived estimates for the cessation of main growth activity from the dendrometer readings. As a general pattern, we found that stem growth gradually declined towards the end of the summer but continued at low level throughout the autumn season before an almost stable stem diameter was reached in late autumn to early winter (Fig. S2). To account for the uncertainty associated with the analysis of slowly diminishing late-season growth, we excluded data at the very end of the flattening dendrometer trend and determined the time when a tree reached 90% of its annual stem diameter increment (SDI_{90}) as an estimate for the cessation of main growth activity. In general, the SDI_{90} value was reached throughout the late summer to early autumn period, with strong variation across species and years (Tab. 2; Tab. S1). A remarkable exception was the severe drought year 2018, when the average SDI_{90} value in *C. betulus* was reached much later (woy 47) than in the other three years (woy 42). Among the four species, the SDI_{90} was generally latest reached in the ring-porous species *Q. robur x petraea* while it occurred earliest in the diffuse-porous species *A. pseudoplatanus* (Tab. 2).

Within the four species, we found a very high intra-specific variability in the seasonal timing of the SDI_{90} value, spanning a maximum range from mid-summer to late autumn across all assessed trees and observation years. Like spring growth resumption, the high intra-specific variability was mainly attributable to a distinct pattern of earlier SDI_{90} in trees with high annual stem increments compared to trees with low annual stem increments (Fig. 2). Remarkably, the temporal spread of SDI_{90} was generally larger than that of spring growth resumption. Consequently, trees with a low annual stem increment needed longer time to complete the main growth of their stems than trees with high annual stem increment. One exception was the relatively cold and wet summer 2021, in which the patterns of annual stem increment with spring growth resumption and the timing of SDI_{90} were almost similar in the four tested tree species. As already observed for stem growth resumption, the pattern how the SDI_{90} value varied among individual trees was mostly preserved across the observation years, i.e., trees which grew much and ceased their main growth early in one year did so in the next year (Tab. S2). This is well illustrated in *F. sylvatica*, where the large number of assessed trees could be

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clearly separated in individuals with high increment and early growth stop versus individuals with low increment and late growth stop (Fig. 3b,c).

Our phenological study did not only include years with cold or warm spring conditions but also the exceptional drought year 2018 (Tab. 1). Against our expectation, however, the severe summer to early autumn drought that the trees experienced in 2018 did not lead to an earlier growth stop and thus shorter main growth period. In *F. sylvatica* and *C. betulus*, we even found that the period of main growth activity was at least two weeks longer in 2018 compared to the other three years, which was mainly a result of prolonged late-season growth as indicated by the late SDI_{90} values (Tab. 2, Fig. 4). Notably, however, late-season growth contributed little to the total amount of annual stem increment, as growth rates declined gradually towards the end of the summer and the remaining growth activity was very low (Fig. S2). Accordingly, we did not find evidence that a longer period of main growth activity translates into larger annual stem increment (Fig. 4, Tab. S1). Neither *F. sylvatica* or *C. betulus* - where annual increment was even lowest in the year with the longest duration of main growth activity - nor *A. pseudoplatanus* showed clear trends. In *Q. robur x petraea*, the only ring-porous species, we found a slightly positive trend of the duration of main growth with annual stem increment, but the relationship was not significant. *Q. robur x petraea* was also the species that showed the longest duration of main growth when compared to the other three species.

Discussion

The use of phenological data in forest ecosystem modeling often relies on the assumption that the time a tree keeps a green canopy equals the time of carbon fixation and growth. While the physiological significance of spring canopy greening for photosynthetic carbon assimilation can hardly be questioned, temporal coordination with down-stream growth processes has not been systematically proven. In line with previous studies (*Suzuki et al. 1996, Sass-Klaassen et al. 2011, Michelot et al. 2012, Klein et al. 2016*), we show that canopy greening precedes stem growth resumption in diffuse-porous but not in ring-porous trees. With up to five or six weeks in *F. sylvatica* and *A. pseudoplatanus*, respectively, and up to ten weeks in *C. betulus*, the delay of stem growth resumption was remarkable. This, and non-synchronous variation of the two metrics across climatically contrasting years, contradicts the theory that the re-greening canopy triggers stem growth resumption through hormonal signaling or other physiological cues (*Aloni 1991, Larson 1994, Aloni 2013, Sorce et al. 2013, Bhalerao and Fischer 2017*). Noteworthy, winter heating has shown to stimulate growth in dormant stems independently of the canopy's phenological stage, compromising tight coupling of canopy and stem growth phenology (*Begum et al. 2007, Begum et al. 2013, Gričar et al. 2006*). In ring-porous trees, on the other hand, wood cell formation may even start before canopy greening (see Fig. 1, 2; *Suzuki et al. 1996, Sass-Klaassen et al. 2011, Michelot et al. 2012*), further questioning canopy control over the timing of stem growth resumption.

Our findings and previous reports demonstrate that observations of spring canopy greening should be interpreted with care, as their use as proxy for stem growth may lead to wrong conclusions. This is impressively demonstrated in *C. betulus* where stem growth resumption lagged up to ten weeks behind the onset of canopy greening. It also implies that the seasonal duration of stem growth cannot be deduced from observations of canopy phenology if the onset of growth remains uncertain. We therefore compared the timing of spring growth resumption with the time when the trees had completed their main growth activity. Since the analysis of diminishing late-season growth is subject to some uncertainty, we have used the SDI_{90} estimate as a reliable indicator for the end of main growth activity. Based on this, we further tested whether the seasonal duration of main growth activity relates to annual stem increment. Although the duration of main growth activity varied considerably across the climatically contrasting years, we did not find evidence that longer growth translates into larger annual stem increment as recently suggested by analysis of tree-ring chronologies or annual wood growth (*Lempereur et al. 2015, Gao et al. 2022, Chen et al. 2022*). Yet, our finding is consistent with

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recent reports showing that annual growth increment is more closely linked to favorable conditions within the season than to season length (*Etzold et al. 2021, de Sauvage et al. 2022*) and that earlier growth onset in warm springs does not necessarily translate into larger annual stem increments (*Čufar* et al. 2015, *Dow et al. 2022*).

An unexpected pattern that was common in our data may further challenge the intuitive belief that longer growth must be associated with higher annual increment. Instead, we found that trees with early growth resumption and short main growth activity had higher annual stem increments than trees with late growth resumption and long main growth activity. This may simply reflect the fact that reduced late-season growth contributes relatively more to seasonally accumulated wood formation in trees with low annual increments than in trees with high annual increments, thus shifting the relative SDI_{90} estimate for main growth cessation towards the end of the year. Nevertheless, we show that the main proportion of seasonal stem increment - as defined by the date of growth resumption and the timing of SDI_{90} - is completed earlier and in shorter time in trees with high annual increment. This must not necessarily be seen as physiological contradiction, as early-season growth is much more dynamic than late-season growth and thus contributes relatively more to the annual stem increment (*van der Werf et al. 2007, Čufar et al. 2011, Michelot et al. 2012*).

Notably, we observed in our study that a few trees showed an unusually long main growth activity, as their stem diameter continued to increase at very low rate until the end of the year. It seemingly conflicts general knowledge that temperate tree growth stops with the transition to the autumn season. However, most studies dealing with intra-annual growth dynamics do not cover the late autumn months or do not pay attention to occurrences of diminished late-season growth. The very few studies which do so suggest that temperate deciduous trees may keep some low stem growth activity throughout the autumn season (*Delpierre et al. 2016a*), particularly when they suffered from previous summer drought (*van der Werf et al. 2007*). Similarly, we found in our study, that *C. betulus* - and partly *F. sylvatica* - showed prolonged late-season growth after the exceptionally severe drought in 2018. We cannot exclude that water-dependent stem swelling after drought release has mimicked some growth in 2018. However, stem swelling is a fast process that occurs shortly after rewetting (e.g., *Ehrenberger et al. 2012*, *Zweifel et al. 2016*), and is thus not likely to explain the gradual diameter increase we observed throughout the wet autumn weeks. It is also noteworthy that the severe 2018 drought was not associated with a pronounced reduction of annual stem increments, a finding that was also reported in other studies (*Salomon et al. 2022*).

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Our observations of larger annual stem increments in trees with earlier and shorter main growth activity resemble strikingly the recently discovered "grow fast - live shortly" phenomenon in woody plants (*Büntgen et al. 2019*, *Brienen et al. 2020*). Although assessed at shorter, seasonal time scale, our observations are likely to reflect a similar phenomenon, linking high annual stem increments with early growth start and a short main growth activity. Importantly, we can exclude that this phenomenon simply reflects an effect of higher social position of larger, dominating trees, as it was independent of tree size. Similarly, previous attempts to explain the large intra-specific variability of spring canopy phenology by differences in tree size provided only very weak evidence for a tree size effect. (*Marchand et al. 2020*). More likely, trees with seasonally advanced growth may benefit disproportionally from humid conditions in spring and early summer while late-starting trees are more constrained by exhausted soil water reserves and increasing drought towards the end of the season (*Buermann et al. 2013, Buermann et al. 2018, Lian et al. 2020*). Also, genetic factors controlling stem growth might play a particular role, as the pattern of seasonally advanced but shorter main growth was mostly preserved in individual trees across the observation years. The conservation of phenological ranks across tree individuals and years has also been reported in other studies (*Delpierre et al. 2017*, *Charlet de Sauvage et al. 2022*).

The following conclusions can be drawn from this study. First, the onset of canopy greening is not a useful predictor of stem growth phenology, as particularly demonstrated in diffuse-porous species where growth resumption lagged several weeks behind canopy greening. This and non-synchronous variation of canopy greening and stem growth resumption across warm and cold years supports the assumption that the two metrics respond differently to environmental cues (*Antonucci et al. 2015, Gričar et al. 2022*). Lagged stem growth resumption also calls for rethinking phenological terminology defining the growing season length as time a tree keeps a green canopy. As far as growth modeling is concerned, it supports the view that canopy duration alone has little predictive power (*White et al. 2003*). Second, individual trees may follow contrasting seasonal growth strategies in that earlier/shorter main growth activity is associated with higher annual growth rates and later/longer main growth activity with lower annual growth rates. Although this phenomenon needs further physiological explanation it must not be ignored as it represents a strong source of intra-specific variation that compromises any approach modeling tree growth with phenology. Thus, deeper understanding how stem growth phenology codetermines the annual growth rate in individual trees may help reduce existing uncertainties in forest productivity predictions.

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Data and Materials Availability

All study data are included in the article and/or supplement. Raw data are available upon request.

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Author contributions

M.A. designed the study, organized the field work and analyzed the data; M.A. wrote the manuscript with contributions from G.H. and A.K.

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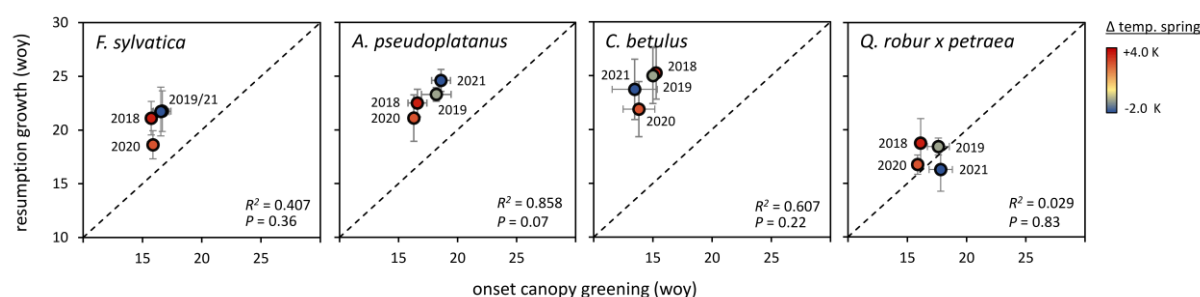
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Fig. 1. Onset of spring canopy greening in relation to the resumption of stem growth in the three diffuse-porous species *F. sylvatica*, *A. pseudoplatanus* and *C. betulus* and the ring-porous species *Q. robur x petraea* in the four climatically different observation years. Deviations from the dashed 1:1 line indicate temporal differences between the two phenological metrics. Color codes indicate the deviation of average spring temperature in April and May (Δ temp.) from the norm period 1991-2020. (all data mean ± SD; woy = week of observation; R^2 values with corresponding P values are given for linear regression of "onset canopy greening" on "resumption growth")
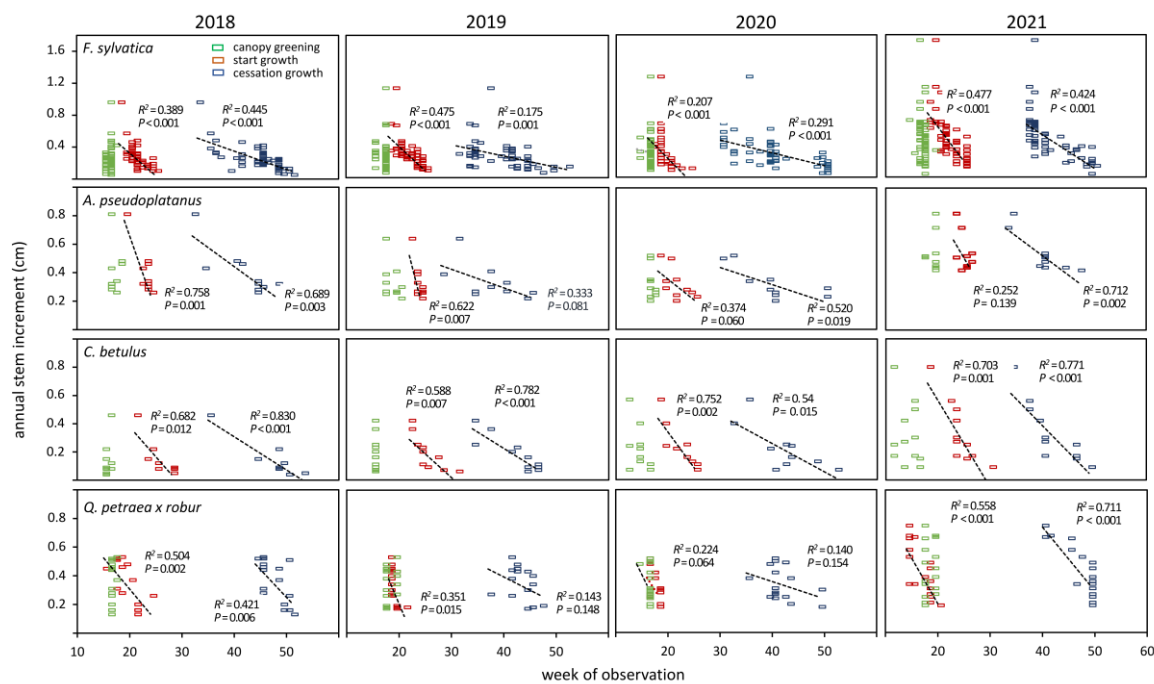
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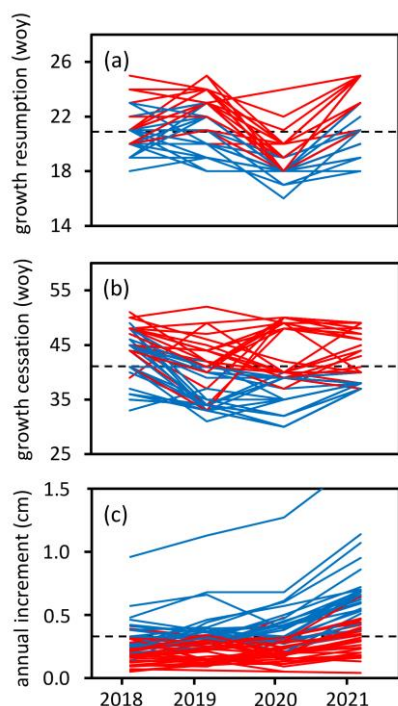
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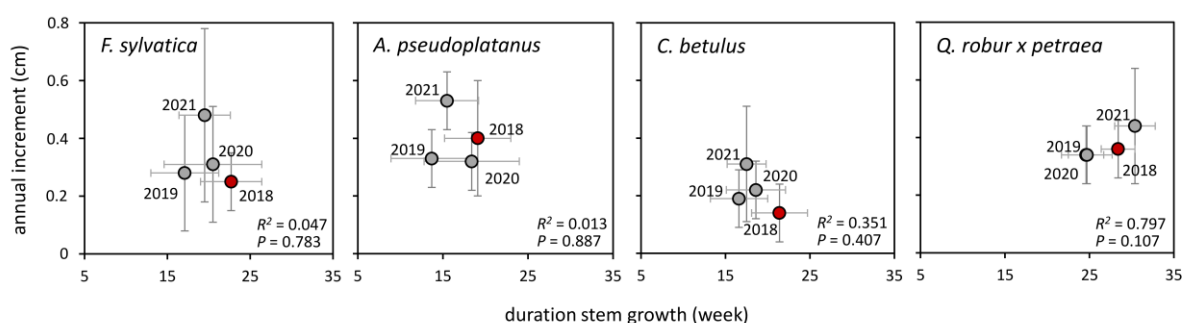

Fig. 4. Seasonal length of main growth activity derived from growth resumption and cessation (SDI$_{90}$) in relation to annual stem increment in *F. sylvatica*, *A. pseudoplatanus*, *C. betulus* and *Q. robur x petraea* in the four study years. (duration: weeks $\pm$ SD; increment: cm $\pm$ SD; R^2 values with corresponding P values are given for linear regression of "duration" on "increment")

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Tables

Tab. 1. Weather conditions in the four observation years 2018 to 2021. Monthly temperature in April and May and deviation of monthly temperatures in April and May from the norm period 1990-2020 (Δ temp in K; norm temperature April 8.2°C, norm temperature May 12,6°C) and average climatic water balance in the summer and early autumn months June to October (sum of potential evapotranspiration and precipitation in mm). All data were taken from the nearby climate station *Rünenberg*, operated by the Swiss Meteorological Service *SwissMeteo*.

	temp Apr	Δ temp April (K)	temp May	Δ temp May (K)	water balance (mm)
2018	13.1	4.9	14.6	2.0	-35.3
2019	8.6	0.4	10.2	-2.4	-22.0
2020	12.9	4.7	13.2	0.6	-1.8
2021	7.4	-0.8	10.1	-2.5	43.0

Tab. 2. Average species values for spring canopy greening, stem growth resumption and cessation of main growth activity (SDI_{90}) in *F. sylvatica*, *A. pseudoplatanus*, *C. betulus* and *Q. robur x petraea* in the four study years. (weeks $\pm$ SD; asterisks indicate significant "study year effects" with *$P<0.05$, **$P<0.01$, ***$P<0.001$)

	F. sylvatica			*C. betulus*			*A. pseudoplatanus*			*Quercus robur x petraea*		
	canopy greening ***	growth start ***	growth cessation ***	canopy greening **	growth start ***	growth cessation ***	canopy greening ***	growth start ***	growth cessation *	canopy greening ***	growth start ***	growth cessation ***
2018	15.7 (±0.5)	21.1 (±1.6)	44.1 (±4.3)	15.3 (±0.4)	25.3 (±2.4)	47.0 (±4.8)	16.6 (±0.8)	22.5 (±1.3)	41.6 (±4.8)	16.1 (±0.3)	18.8 (±2.3)	47.1 (±2.4)
2019	16.7 (±0.7)	21.8 (±1.9)	39.3 (±5.0)	15.0 (±0.0)	25.0 (±2.6)	41.6 (±4.4)	18.2 (±1.2)	23.3 (±5.2)	37.0 (±5.2)	17.6 (±0.9)	18.4 (±0.8)	43.1 (±2.3)
2020	15.9 (±0.5)	18.6 (±1.3)	39.7 (±6.5)	13.8 (±1.3)	21.9 (±2.6)	41.6 (±5.5)	16.3 (±0.5)	21.1 (±2.2)	39.5 (±6.2)	15.9 (±0.5)	16.8 (±0.9)	41.4 (±3.4)
2021	16.5 (±0.7)	21.7 (±2.3)	41.4 (±4.4)	13.5 (±1.9)	23.7 (±2.8)	41.9 (±4.8)	18.6 (±0.8)	24.6 (±1.0)	39.7 (±3.9)	17.8 (±1.0)	16.3 (±2.0)	46.7 (±3.3)

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