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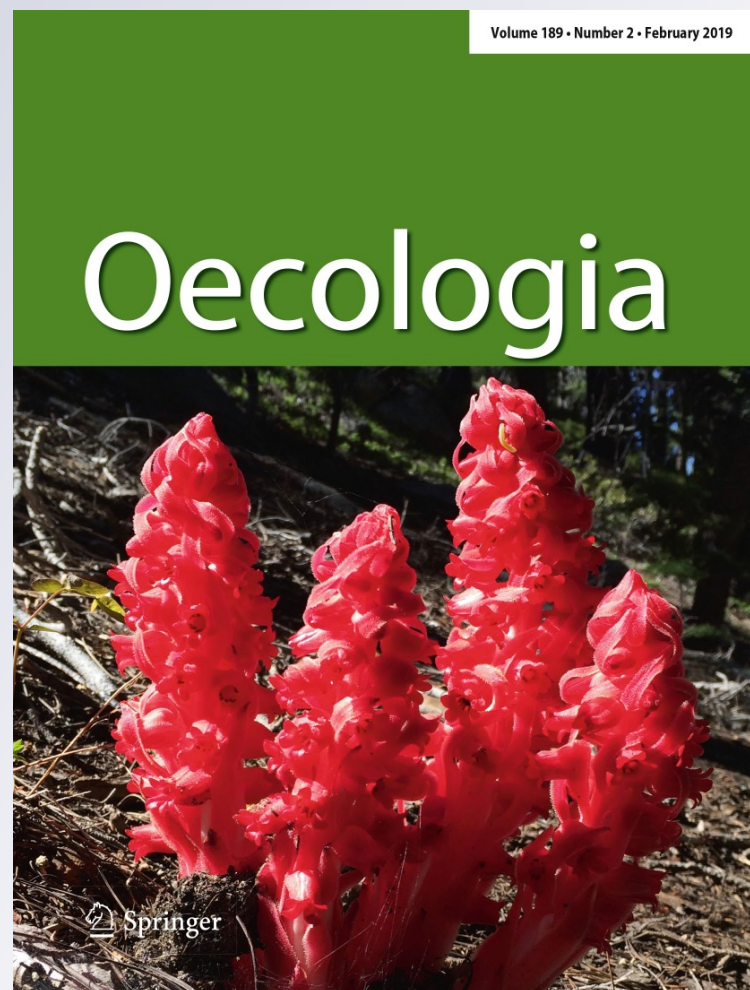
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Ongoing seasonally uneven climate warming leads to earlier autumn growth cessation in deciduous trees

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Abstract

Ongoing global warming is causing phenological shifts that affect photosynthesis and growth rates in temperate woody species. However, the effects of seasonally uneven climate warming—as is occurring in much of Europe, where the winter/spring months are warming twice as fast than the summer/autumn months—on autumn growth cessation (completion of overwintering buds) and leaf senescence, and possible carry-over effects between phenophases, remain under-investigated. We conducted experiments in which we exposed saplings of canopy and understory species to 4 °C warming in winter/spring, summer/autumn, or all year to disentangle how the timing of bud break, bud set completion, and leaf senescence is affected by seasonally uneven warming. All-year warming led to significantly delayed leaf senescence, but advanced bud set completion; summer/autumn warming only delayed leaf senescence; and winter/spring warming advanced both bud set and senescence. The non-parallel effects of warming on bud completion and leaf senescence show that leaf senescence alone is an inadequate proxy for autumn growth cessation in trees and counterintuitively suggest that continued uneven seasonal warming will advance cessation of primary growth in autumn, even when leaf senescence is delayed. Phenological responses to warming treatments (earlier spring onset, later autumn senescence) were more than twice as high in understory species than in canopy species, which can partly be explained by the absence of carry-over effects among phenophases in the former group. This underscores the need to consider differences among plant functional types when forecasting the future behaviour of ecosystems.

Keywords Global Change Ecology · Plant–climate interactions · Phenology · Climate change · Vegetation period · Leaf-out · Bud set · Senescence · Chlorophyll · Climate warming experiment

Introduction

The seasonal rhythm of temperate deciduous species is characterized by a photosynthetically active period and a dormancy period during the unfavourable time of the year. The

length of the vegetation period influences biogeochemical cycles (Richardson et al. 2013), competitive and mutualistic interactions (Thackeray et al. 2016), and species geographic ranges (Chuine 2010). Climate warming may allow species to extend their photosynthetically active period, leading to increased productivity and altered carbon balances (Penuelas and Filella 2001). However, because the environmental cues and genetic mechanisms determining the onset and end of dormancy in woody species (with long generation times) are still poorly understood, it remains unclear to what extent additional warmth at the start and end of a season translates into increased tree growth. Dormancy can broadly be classified into three phases: During paradormancy (summer to autumn), bud set is completed and leaf senescence occurs; during endodormancy (autumn to winter), bud cell growth is internally inhibited by blocked cell–cell communication (Tylewicz et al. 2018); and during ecodormancy (mid-winter to spring), bud cell growth is externally inhibited by low

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temperatures (Lang et al. 1987; Delpierre et al. 2016). In many species, shortening day length is required to initiate paradormancy (Heide 1974; Rohde et al. 2011; Cooke et al. 2012), while endodormancy release is triggered by chilling accumulation and/or increasing day length (Heide 1993a, b; Laube et al. 2014; Zohner et al. 2016).

To forecast forest productivity under extended vegetation periods, studies have either used community-scale phenological observations (derived from remote sensing data) or species-level observations (derived from in situ monitoring) and have then correlated leaf-out and leaf senescence with relevant environmental parameters (Menzel et al. 2006; Jeong et al. 2011; Keenan et al. 2014). Uncertainty in the prediction of photosynthetically active periods under climate warming arises from species-specific phenological strategies (differences in day-length, chilling, and forcing requirements), which are the result of long-term evolutionary adaptation to environmental (climatic) conditions (Zohner and Renner 2014; Körner et al. 2016; Zohner et al. 2016, 2017, Zohner and Renner 2017). These adaptive strategies involve correlated traits, such as plant architecture (branching mode; polycyclic or monocyclic growth), height, successional status, and wood anatomy (Lechowicz 1984; Panchen et al. 2014; Laube et al. 2014). Internal constraints may connect phenophases, for example, spring leaf-out and autumn senescence in the same or successive years, additionally complicating predictions of tree seasonality under warmer climates (Heide 2003; Hänninen and Tanino 2011; Liu et al. 2016; Fu et al. 2014; Keenan and Richardson 2015). Six canopy species, three from North America monitored over 20 years and three from Europe exposed to experimental warming, have been investigated in this regard (Fu et al. 2014; Keenan and Richardson 2015). Both studies found that autumn leaf senescence (defined as the date when 50% or 95% of leaves had changed colour) advances with the advance of the preceding spring leaf unfolding. Such internal developmental constraints seem to be especially pronounced in species with determinate shoot growth that put out a single flush of leaves per year, such as *Fagus sylvatica* and *Quercus robur*, but not in species that form new leaves throughout the year (e.g., *Betula pendula*) (Fu et al. 2014). These studies lacked direct data on autumn growth cessation, but the importance of bud set as an indicator of primary growth cessation and a landmark in the dormancy cycle has long been clear. Nevertheless, a direct link between bud set and leaf senescence has never been shown (Tanino et al. 2010; Rohde et al. 2011; Cooke et al. 2012; Strømme et al. 2015; Signarbieux et al. 2017).

That visual proxies, such as leaf colour turning, which is often used to measure leaf senescence, can be decoupled from internal (invisible) developmental processes was shown by Bauerle et al. 2012 who demonstrated that cessation of photosynthetic activity is determined largely by day-length,

whereas leaf senescence may be determined more by temperature. A remote sensing study that compared the widely used NDVI (describing the presence/absence of chlorophyll) with solar-induced chlorophyll fluorescence (SIF; theoretically describing photosynthetic activity) found that there is “a large-scale seasonal decoupling of physiological activity and changes in greenness in the fall” (Jeong et al. 2017, p. 178). Thus, while the NDVI linearly responded to temperature, SIF did not, pinpointing the importance of focusing on an alternative phenophases, such as bud set, to infer the end of aboveground primary growth and productivity.

Finding out the extent to which leaf-out, bud set, and leaf senescence are coupled is relevant because climate warming in the Northern Hemisphere is not happening uniformly throughout the year—at least in Central Europe, the winter and spring months are warming faster than the summer and autumn months (Fig. 1 in Renner and Zohner 2018;

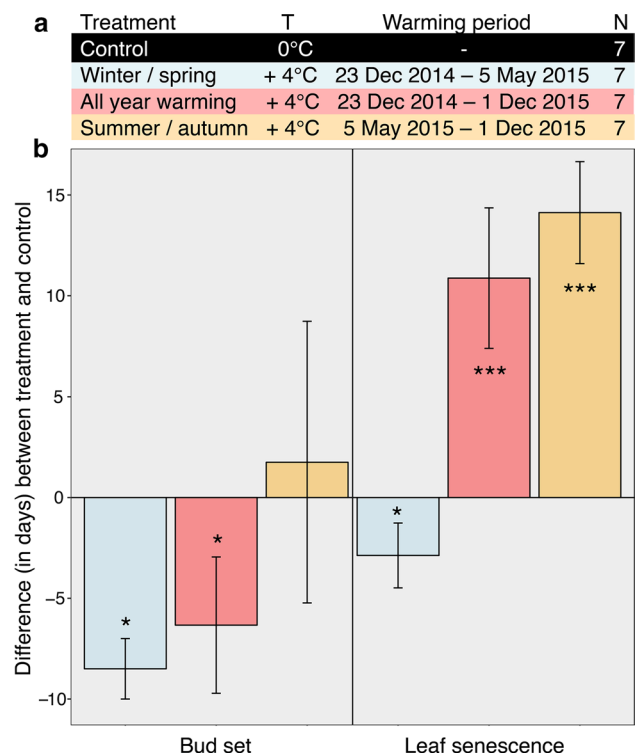


Fig. 1 **a** Experimental design. *T* is the temperature difference compared to field conditions. *Warming period* indicates the times during which warming treatments were applied. *N* indicates the number of replicates used per species and treatment. **b** Contrasting responses of autumn bud set and leaf senescence in eight (senescence) or four (bud set) woody species to experimental warming treatments. Bars show the mean difference in days between treatment and control (\pm standard error). Asterisks within bars indicate whether treatments differed from the control according to a mixed effects model including species as a random effect (* $P < 0.05$, *** $P < 0.001$). *P* values for leaf senescence were the same when including only the four species with data on bud set (Fig. S3). The figure is available in colour in the online version of the journal

Fig. 2 in Vitasse et al. 2018; our Supplementary Fig. 1 for Munich: average winter/spring warming = 0.37 °C/decade; average summer/autumn warming = 0.19 °C/decade). Thus, to predict the future phenology and productivity (growth) of temperate plants, experiments are needed to detect the effects of warming in different seasons on leaf-out, bud set, and leaf senescence. And since understory shrubs or trees have different phenological strategies than canopy trees (Augsburger et al. 2005; Panchen et al. 2014), such experiments should include these two functional types of deciduous woody species.

We, therefore, carried out a biannual warming experiment on saplings of eight species, four of them canopy trees, the other four understory shrubs or small trees. Specifically, we tested (i) if leaf unfolding, bud set, and leaf senescence (chlorophyll breakdown) are affected differently by raised temperatures, (ii) if leaf-out phenology in spring affects the timing of bud set and leaf senescence, (iii) whether phenological responses to raised temperatures are more pronounced in understory than canopy species, and (iv) the extent to which experimental spring, autumn, or all-year warming translates into overall growth. Our study presents the first experimental approach to test for the separate effects of seasonal warming on the timing of bud set and leaf senescence and to our knowledge provides the first direct links between phenology and growth parameters such as plant height and bud length.

Materials and methods

Species selection

We selected eight deciduous woody species covering different life forms (understory and canopy growth), growth strategies (polycyclic and monocyclic growth) and a range of phenological strategies relating to winter chilling and day length sensitivity (Zohner et al. 2016, 2017). See Table 1 for species selection and relevant traits.

Experiment

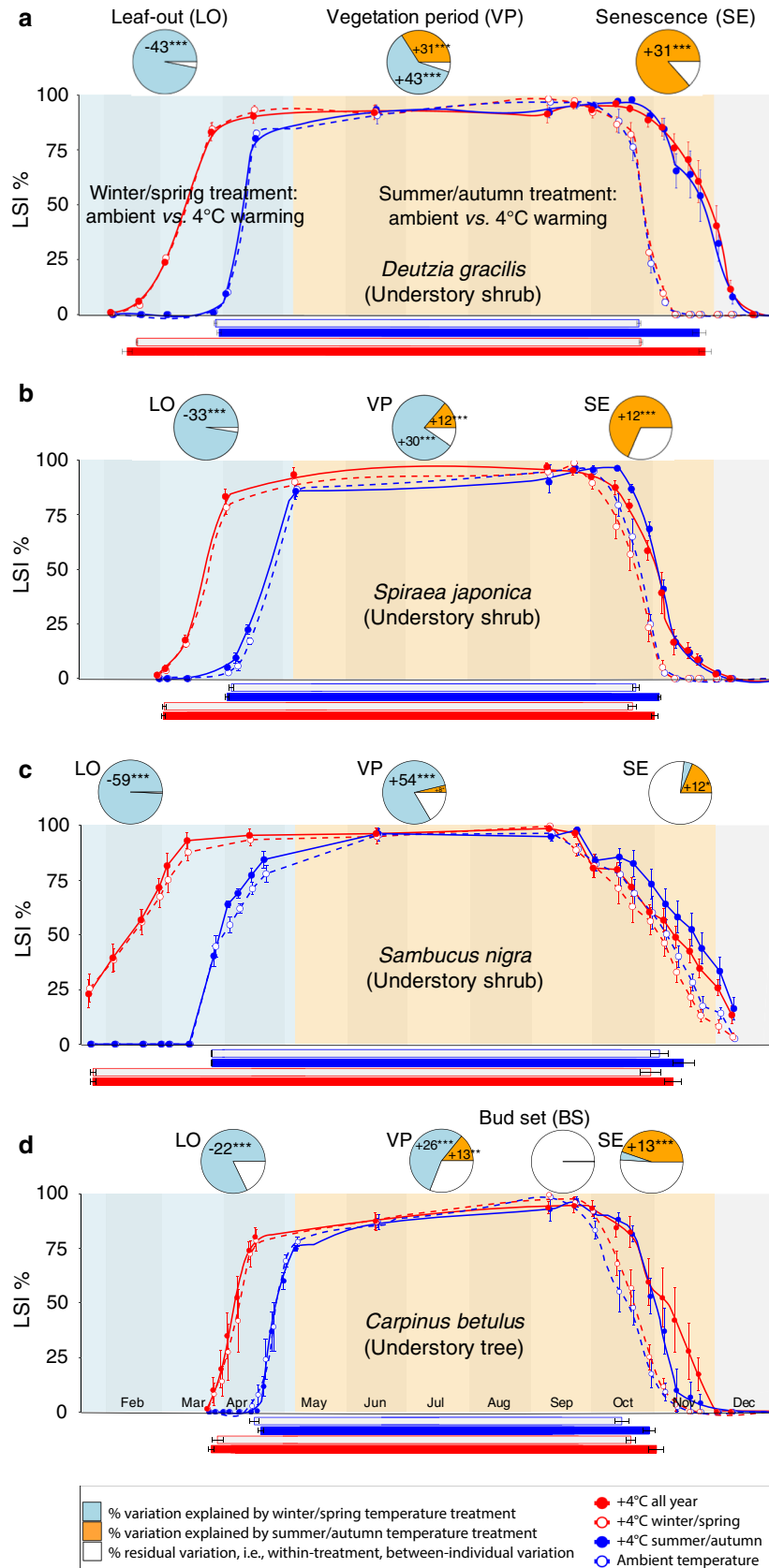
The experiment was conducted in the Munich Botanical Garden (48°09'N, 11°30' E; 501 m a.s.l.) between December 2014 and December 2016. Three-year-old plants were obtained from a local nursery in October 2014, transferred to plastic pots (30 × 30 cm) with sandy soil, and kept outdoors under uniform conditions until the start of the experiment (21 December 2014). Seven individuals per species and treatment were exposed to warming treatments and the effects on phenology then followed until autumn 2016. Throughout the experiment, pots were watered once or twice a week to keep soil moisture constant. Three treatments were

Table 1 Species selection, phenological characterization, and growth parameters

Species	Life form	Growth strategy	Chilling	Day length	Carry-over bud set	Carry-over senescence	S _T	A _T (Yearly)	A _T (autumn)	Bud length		Height	
										WS	SA	WS	SA
<i>Deutzia gracilis</i>	Understory	Poly	None	None	None	None	10.5	8.3	7.5	None	None	None	7.7
<i>Spiraea japonica</i>	Understory	Poly	None	None	None	None	8.1	2.3	3	None	None	None	None
<i>Sambucus nigra</i>	Understory	Poly	None	None	None	None	14.8	1.8	3	None	None	None	None
<i>Carpinus betulus</i>	Understory	Poly	Yes	None	None	None	5.5	4.3	3.5	None	1.9	13.3	26.6
<i>Acer campestre</i>	Canopy	Poly	Yes	None	0.8	None	4.6	1.8	3.3	0.4	None	None	None
<i>Fagus sylvatica</i>	Canopy	Mono	Yes	High	0.7	0.4	3.4	1.3	1.8	1.2	1.8	None	None
<i>Sorbus aucuparia</i>	Canopy	Mono	Yes	None	0.3	0.3	4.5	1.5	4.3	None	None	None	17.5
<i>Quercus robur</i>	Canopy	Mono	Yes	Low	0.3	0.3	5.3	0.8	2	None	None	None	23.5

Life form, growing mainly as understory or canopy plant; *Growth strategy*, monocyclic (a single shoot flush in spring) or polycyclic (two or more successive flushes per season); *Chilling*, phenological sensitivity to winter chilling inferred in Zohner et al. (2017); *Day length*, phenological sensitivity to day length increase in spring inferred in Zohner et al. (2016); *Carry-over bud set*, advance in the timing of bud set (in days) caused by a 1 day advance in spring leaf unfolding if significant ($P < 0.05$, see Fig. 4); *Carry-over senescence*, advance in the timing of leaf senescence (in days) caused by a 1 day advance in spring leaf unfolding if significant ($P < 0.05$, see Fig. 4); *S_T*, Temperature sensitivity of spring leaf unfolding (days advance of leaf unfolding per one °C warming) as inferred from the experimental warming treatment; *A_T*, Temperature sensitivity of autumn leaf senescence (days delay of leaf unfolding as inferred from the whole-year warming treatment (control vs. 4 °C warming from winter to autumn) or from the summer/autumn warming treatment (in brackets) (control vs. 4 °C warming in summer/autumn); *Bud length*, mean increase in autumn bud length (in mm) under winter/spring warming (WS) and summer/autumn warming (SA) if significant. *Height*, mean increase in plant height (in cm) under winter/spring warming (WS) and summer/autumn warming (SA) if significant. Empty cells: parameter not measured in the respective species

Fig. 2 Relative leaf-spectral index (LSI) [mean \pm standard error of the mean (SEM)] in 2015 for four understory woody species, **a** *Deutzia gracilis*, **b** *Spiraea japonica*, **c** *Sambucus nigra*, and **d** *Carpinus betulus*, under ambient temperature (open blue circles and dashed blue lines), 4 °C warming in summer/autumn 2015 (filled blue circles and solid blue lines), 4 °C warming in winter/spring 2014/2015 (open red circles and dashed red lines), and 4 °C warming in all year (winter 2014/2015 to autumn 2015; filled red circles and solid red lines). Bars below graphs show the length of the vegetation period, based on means (\pm SEM) for the date of spring leaf-out and autumn senescence (50% decrease in LSI relative to peak LSI) for the four treatments. Pie charts above graphs show the percentage of variation (derived from the sums of squares) for each phenological parameter (leaf-out (LO); length of vegetation period (VP); leaf senescence (SE)) that can be attributed to winter/spring treatment (light blue), summer/autumn treatment (orange), or the remaining residuals, i.e., within-treatment variation (white). For *Carpinus betulus* we also show a pie chart for bud set (BS). The figure is available in colour in the online version of the journal (color figure online)



applied: 4 °C warming conditions in winter/spring, summer/autumn, or during the whole year in a climate-controlled glasshouse with an openable top (actual warming was within $\pm 20\%$ of the prescribed value). The control consisted of individuals kept at ambient conditions (± 0 °C) outdoors. Winter/spring warming was applied from 21 December 2014 (winter solstice) until all individuals had leafed out (5 May 2015). Summer/autumn warming was applied from 5 May 2015 until the leaves of all individuals had senesced 100% (1 December 2015). Whole-year warming was applied from 21 December 2014 until 1 December 2015 (see Fig. 1a for details on treatment conditions). Because we did not want to test the effect of extreme heat on plants, we did not allow temperatures in the glasshouse to exceed 35 °C (maximum temperature measured in the field). Thus, during summer, the average temperature difference between the warming and the ambient treatment was < 4 °C (July: 3.4 °C difference, August: 3.2 °C). Day length, light intensity and wavelength spectra in the glasshouse did not differ from outdoor conditions (see Fig. S2). After the end of all experimental warming (1 December 2015), individuals were kept outdoors, arranged randomly in rows with 50 cm between rows.

Phenological observations and measurements of growth traits

Observations and trait measurements involved all 28 individuals for each of the eight species. Leaf-out observations were conducted twice a week in winter/spring 2015 and 2016. A bud was considered as leafed out when its leaves had unfolded and pushed out all the way to the petiole (BBCH 11). The day when three branches on a plant had leafed out was considered that individuals' leaf-out date (Denny et al. 2014; Zohner and Renner 2014; IPG 2016). We also recorded the percentage of leaf-out, defined as the number of leafed-out buds divided by the number of total buds of an individual.

In 2015 and 2016, we measured the leaf spectral index (LSI, a proxy for chlorophyll concentration and nitrogen content) at, on average, 1-week intervals during spring and autumn and 2-week intervals during summer (see Figs. 2 and 3) with an SPAD-502 Plus (Soil Plant Analysis Development, Minolta Camera Co., Ltd, Tokyo, Japan). Per individual, LSI readings from 10 leaves selected at random were averaged. To infer seasonal changes in LSI, we relativized individual means by their maximum LSI reading for the respective season (values between 0% and 100%). To calculate relative LSIs per individual, we additionally included the percentage of opened buds in spring and leaf abscission in autumn for each individual, allowing us to calculate whole-individual LSIs (rather than leaf-level LSIs) relative to maximum LSI (when individuals are fully leaved); e.g., an individual with 50% of buds still closed in spring and a

relative LSI of 50% for the already flushed leaves has a total relative LSI of only 25% because the still closed buds are assigned a relative LSI of 0%. Similarly, an individual that has already lost 50% of its leaves in autumn, with a relative LSI of 50% for the remaining leaves has a total relative LSI of only 25% because the already dropped leaves have a relative LSI of 0%. We defined leaf senescence as the date when relative LSI had decreased by 50%, and the length of the vegetation period as the period between leaf-out and leaf senescence (BBCH 95).

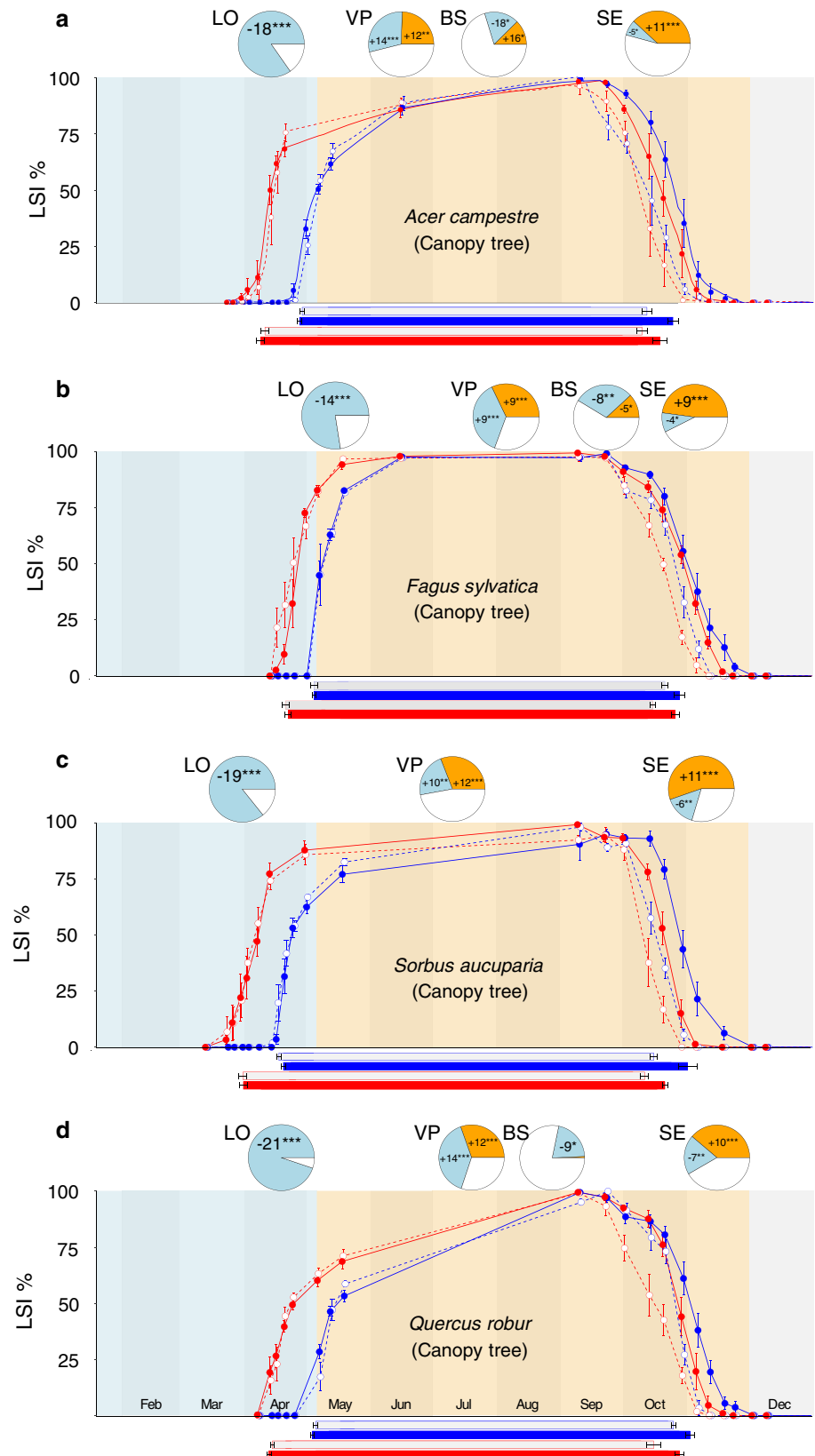
The length of overwintering leaf buds was recorded from 15 July 2015 until 4 November 2015 in three canopy and one understory species (bud length was not measured in *Deutzia gracilis*, *Sambucus nigra*, *Spiraea japonica*, and *Sorbus aucuparia* where minute buds were set late in the season). Ten terminal buds per individual were recorded. Completion of bud set (hereafter referred to as *bud set*) was defined as the date when the buds of an individual had reached $> 90\%$ of their final length. At this stage, elongation growth has already ceased and bud maturation (which is often used as an indicator of bud set, e.g., transition from small green to large brown buds in *F. sylvatica*; see Signarbieux et al. 2017) is completed. Hence, bud set can reasonably be considered an indicator of aboveground primary growth cessation. Total bud numbers were counted in February 2015 and 2016 in five species, viz. *A. campestre*, *C. betulus*, *F. sylvatica*, *Q. robur*, and *S. aucuparia*. For *Deutzia gracilis*, *Sambucus nigra*, and *Spiraea japonica* the bud number was too large to be counted.

Height (in cm) was measured in December 2015 as the length from the ground (soil) until the uppermost twig of an individual. For *Sa. nigra*, we did not measure height nor chlorophyll content in 2016 because plants outgrew their pots; for *Sp. japonica*, we did not measure height because plants were spreading sideways.

Data analysis

We applied two-way ANOVAs to test for an effect of winter/spring and summer–autumn temperature treatment on phenology and growth parameters. Based on the ANOVA sums of squares for each phenological stage (leaf-out, LO; bud set, BS; senescence, SE; length of vegetative period, VP), we calculated the percentage of variation that could be attributed to winter/spring treatment (light blue in the pie charts, see Figs. 2 and 3) and summer/autumn treatment (orange) [the remaining residuals, i.e., between-individual variation within treatment, are shown in white in the pie charts]. A post hoc Tukey–Kramer test was conducted to detect which treatments (ambient temperature, 4 °C winter/spring warming, 4 °C summer/autumn warming, 4 °C whole-year warming) separately affected phenology and growth parameters (Table S1). To test for effects of the warming treatments on

Fig. 3 Relative leaf-spectral index (LSI) (mean \pm standard error of the mean) in 2015 for four canopy tree species, **a** *Acer campestre*, **b** *Fagus sylvatica*, **c** *Sorbus aucuparia*, and **d** *Quercus robur*. See legend of Fig. 2 for further details. Note that a pie chart for bud set (BS) is missing for *Sorbus aucuparia* because BS was not monitored in this species. The figure is available in colour in the online version of the journal (color figure online)



the timing of leaf-out, bud set, and leaf senescence, while controlling for between-species variation, we applied mixed effects models including species as a random effect.

To test for correlations among the phenological stages in 2015 and for their possible effects on leaf-out phenology in 2016 and growth (bud length and plant height), we applied partial correlation analyses to remove the covariate effects of winter/spring or summer/autumn treatment. Thus, when testing for an effect of 2015 leaf-out on the remaining parameters, we controlled for 2015 summer/autumn treatment; when testing for an effect of 2015 senescence on the remaining parameters, we controlled for 2014/2015 winter/spring treatment.

All statistical analyses were conducted in R (R core Team 2019).

Results

Independent timing of bud set and leaf senescence

On average, across all four species for which there were data on both the timing of bud set completion and leaf senescence, winter/spring warming significantly advanced both the timing of bud set (by 8.5 days or 2.1 days/°C) and senescence (by 3.3 days or 0.8 days/°C); all-year warming significantly advanced bud set by 6.4 days (or 1.6 days/°C) but delayed senescence by 8 days (or 2.0 days/°C); and summer/autumn warming had no effect on bud set and delayed leaf senescence by 10.5 days (2.6 days/°C) [Figs. 1b and S3]. Note that the calculations for leaf senescence in Fig. 1 are based on data for all eight study species, whereas Supplementary Fig. S3 includes only those four species for which there were data on bud set. Whether four or eight species were included, however, did not affect the average responses of leaf senescence to experimental warming treatments (compare Figs. 1b and S3).

When focusing on individual species, in *C. betulus*, *F. sylvatica*, and *Q. robur*, there was no significant correlation between the timing of bud set and leaf senescence (Fig. 4, $P > 0.05$), and summer/autumn warming had idiosyncratic and partly opposite effects on bud set and senescence: It delayed senescence by 13, 9, or 10 days, respectively, while it did not affect bud set in *C. betulus* and *Q. robur* and advanced bud set by 5 days in *F. sylvatica* (Figs. 2 and 3; Table S1). In *A. campestre*, summer/autumn warming delayed bud set and senescence by 16 and 11 days, respectively (Fig. 3). In all three canopy species, winter/spring warming advanced bud set (by 18, 8, and 9 days, respectively) and senescence (by 5, 4, and 7 days; Fig. 3). In *C. betulus*, winter/spring warming had no effect on bud set and senescence.

The effect of leaf-out phenology on the timing of bud set and leaf senescence

Bud set and/or leaf senescence in 2015 were affected by the preceding winter/spring temperatures (Figs. 1b, 2, and 3, Tables 1 and S1). All other conditions being equal, an advance of 1 day in spring leaf-out resulted in 0.4-, 0.3-, and 0.3-day earlier leaf senescence (*F. sylvatica*, *S. aucuparia*, *Q. robur*, respectively) and in 0.8-, 0.7-, and 0.3-day earlier bud set (*A. campestre*, *F. sylvatica*, *Q. robur*; $P < 0.05$; see positive correlations in Fig. 4 and Table 1). In *F. sylvatica* and *S. aucuparia*, we also detected an effect of autumn senescence on next year's leaf-out times, with each day later senescence in 2015 resulting in 0.2 and 0.5 days later leaf-out in 2016 ($P < 0.05$; Fig. 4). Such phenological carry-over effects were absent in the understory species (Fig. 4 and Table 1), in which the timing of autumn senescence was determined only by summer/autumn temperature (Fig. 2).

Temperature sensitivity of spring leaf-out (S_T), autumn senescence (A_T), and the length of the vegetation period differs between understory and canopy species

Comparison of the winter/spring warming treatment to the ambient control showed that a one-degree increase in air temperature advanced leaf-out by, on average (\pm SEM), 7.1 ± 1.4 days (Fig. 5a). Understory species were more than twice as sensitive to spring temperature than canopy trees [S_T (days advance of leaf unfolding per one °C warming) of 9.8 ± 2.0 days/°C vs. 4.5 ± 0.4 days/°C].

A one-degree increase in summer/autumn delayed senescence by an average of 3.5 ± 0.6 days (Fig. 5a, all eight species). Understory species again were more sensitive than canopy trees [A_T (days delay of leaf senescence per one °C warming) of 4.2 ± 1.1 days/°C vs. 2.8 ± 0.5 days/°C]. When individuals were exposed to experimental warming throughout the year (winter to autumn), A_T in canopy trees decreased to 1.3 ± 0.2 days/°C, whereas in understory species it remained unchanged (A_T of 4.2 ± 1.5 days/°C); average across all species = 2.8 ± 0.8 days/°C.

Whole-year warming had a 2.4 times greater effect on the length of the vegetation period in understory species than in canopy trees (lengthening of, on average, 14.1 days/°C vs. 5.8 days/°C; Fig. 5b). In the understory species, winter/spring warming had a 2.3 times greater effect than did summer/autumn warming: Winter/spring warming led to a lengthening of the vegetation period by 38 days (or 9.5 days/°C), while summer/autumn warming lengthened it by only 17 days (4.3 days/°C). In canopy trees, the vegetation period was equally affected by winter/spring and summer/autumn warming: Winter/spring warming led to a

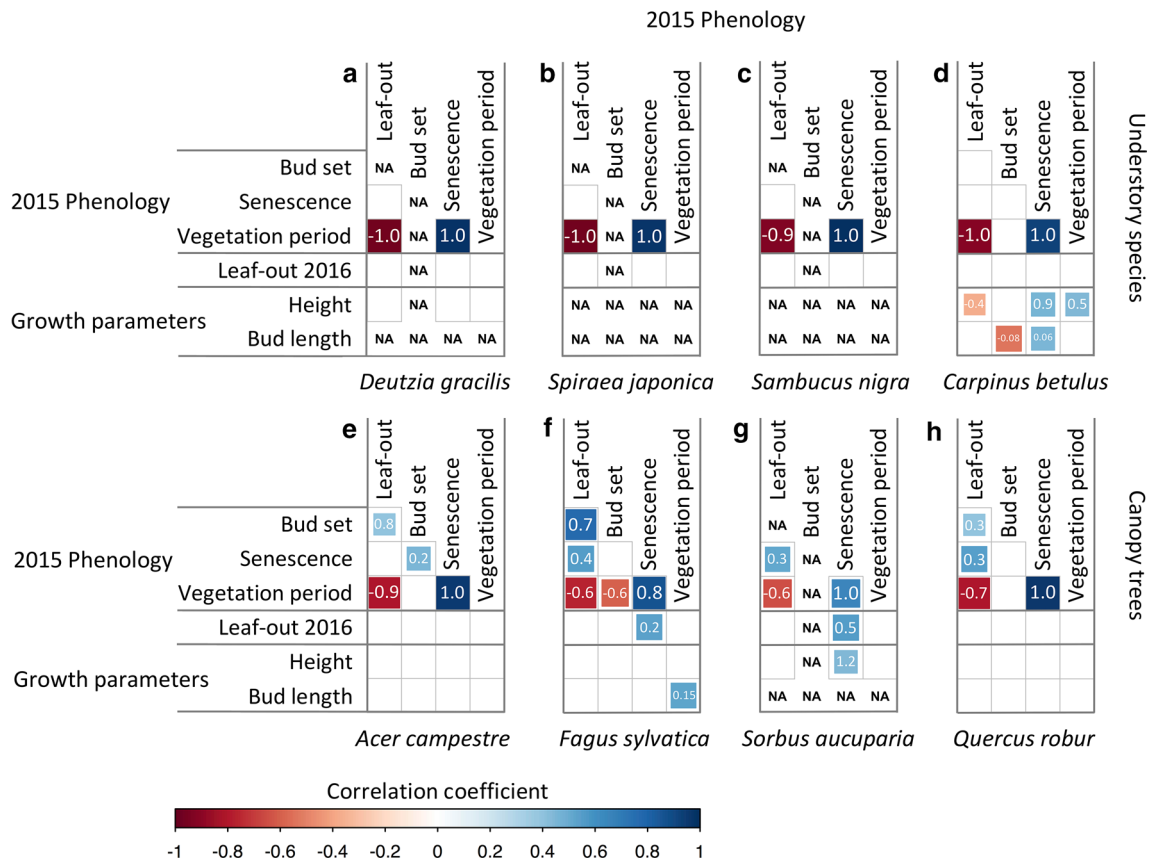


Fig. 4 Effects of 2015 phenology (leaf-out, bud set, and leaf senescence dates and length of vegetation period) on subsequent phenological stages in 2015 and 2016, and growth parameters in eight species, **a** *Deutzia gracilis*, **b** *Spiraea japonica*, **c** *Sambucus nigra*, **d** *Carpinus betulus*, **e** *Acer campestre*, **f** *Fagus sylvatica*, **g** *Sorbus aucuparia*, and **h** *Quercus robur*. Colours indicate (partial) correlation coefficients ($N=28$ individuals per species; white boxes if $P>0.05$). Numbers show the slopes (regression coefficients) of 2015 phenology against the respective vertical (left) parameter modelled with (partial) regres-

sion (slope units: days/day, correlations among phenological parameters; cm/day, effect of phenological parameters on height; mm/day, effect of phenological parameters on bud length), e.g., -1.0 in panel **a** (*Deutzia gracilis*) indicates that, on average, vegetation period in 2015 was extended by 1.0 days for each day advance in 2015 leaf-out. Growth parameters were measured at the end of the experiments, in autumn 2015. The figure is available in colour in the online version of the journal

lengthening of 12 days (3.0 days/ °C) and summer/autumn warming to a lengthening of 11 days (2.8 days/ °C).

The effect of warming on bud length and plant height

The lengths of mature buds were significantly positively correlated with summer/autumn temperature: under 4 °C warming conditions, buds (at the end of the season) were 1.9 mm and 1.8 mm longer than the controls in *C. betulus* and *F. sylvatica* (Figs. 6a, c, and S3; Table 1). In *F. sylvatica*, bud length was also affected by winter/spring treatment, with individuals exposed to this treatment having 1.2 mm longer buds at the end of the season (Fig. 6c, and S3; Table 1). In *F. sylvatica*, a one-day increase in length of the vegetation period led to 0.15 mm longer buds ($R^2=0.29$, $P<0.01$, Fig. 4).

We additionally measured the weight of the primordial leaf tissue, and the number of primordial leaves in 30 buds from 4 individuals of *F. sylvatica* and found a strong positive relationship between bud length and leaf primordial weight ($R^2=0.95$, $P<0.001$) and bud length and the number of primordial leaves ($R^2=0.81$, $P<0.001$, inset Fig. 6c). This relationship predicts that buds of *F. sylvatica*, on average, contain 0.11 more leaves per additional day of vegetation period ($R^2=0.27$, $P<0.01$) or translated into degree Celsius: per each degree increase in air temperature, buds contain 0.54 more leaves.

In most species, summer/autumn warming had a significantly positive effect on individual plant height (Table 1 and Fig. S4). In *C. betulus*, winter/spring warming also significantly affected height, with a one-day advance in spring leaf-out leading to an increase in height of 0.4 cm (Fig. 4).

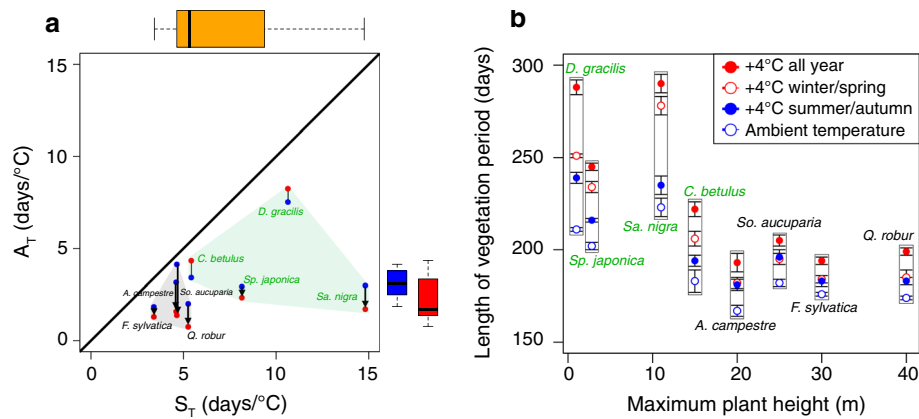


Fig. 5 **a** Temperature sensitivity (days per degree °C) of spring leaf-out (S_T) and autumn leaf senescence (A_T) for eight temperate woody species as inferred from the warming treatments. Red dots (and red boxplot) show A_T when the warming treatment was applied all year (ambient vs. 4 °C warming from 21 Dec 2014 to 1 Dec 2015); blue dots (and blue boxplot) show A_T when the warming treatment was only applied during summer and autumn (ambient vs. 4 °C warming from 5 May 2015 to 1 Dec 2015). The orange boxplot shows the S_T of the eight species. The $x=y$ line (black) indicates where points

would be located if species showed similar temperature sensitivities in spring and autumn. Values of canopy trees (black names) included in grey convex envelope; values of understory species (green names) included in light-green convex envelope. **b** Maximum plant height and 2015 length of vegetation period (mean \pm SEM in days) in the studied species under ambient temperature, 4 °C summer/autumn warming, 4 °C winter/spring warming, and 4 °C all-year warming. The figure is available in colour in the online version of the journal (color figure online)

Discussion

Do bud set and leaf senescence show similar responses to climate warming?

Few studies have focused on bud set (but see Strømme et al. 2015; Signarbieux et al. 2017) although bud set completion may be the best visual proxy for cessation of aboveground primary growth (Signarbieux et al. 2017) and may scale to growth and carbon gain (McKown et al. 2016). The present study for the first time quantifies the extent to which individual bud set and leaf senescence in a year are uncoupled from each other (Figs. 1, 4, and S3): Leaf senescence and bud set showed opposite reactions to the experimental whole-year warming treatment, with an average advance in bud set of 1.6 days/°C, and a delay in leaf senescence of 2.0 days/°C (Figs. 1b and S3). The timing of bud set and leaf senescence, therefore, appears driven by different physiological mechanisms and environmental cues. That all-year warming caused earlier bud set indicates that temperature-driven development predicts autumn growth cessation, supporting the idea that primary growth ceases once plants have stored a maximum of carbohydrates (Fatichi et al. 2013; Keenan and Richardson 2015). By contrast, that leaf senescence was delayed by warmer summer/autumn conditions (Fig. 1b) indicates that low temperatures modulate leaf senescence.

In *A. campestre*, *F. sylvatica*, and *Q. robur* bud set advanced by 18, 8, and 9 days, respectively (Figs. 1b, 2, and 3). These strong advances of primary growth cessation under winter/

spring warming are especially relevant given that that climate warming is not happening uniformly throughout the year. Instead, the months January to May, on average, are warming twice as much as the summer and autumn months (see our Fig. S1 for Munich 1960–2014; also Renner and Zohner 2018, Fig. 1 for all of Germany). Based on our experimental results for the species for which we have data for both traits (Table 1), this uneven seasonal warming predicts an advance in at least some European tree species in bud set dates of ~ 1.9 days and a delay in leaf senescence of ~ 0.5 days per each degree increase in mean annual temperature (assuming that temperature responses will lie somewhere in the middle of the responses inferred from the whole-year warming and the winter/spring-only warming treatments). For Central Europe, current climate warming thus should lead to earlier growth cessation, but later leaf senescence, and therefore lengthen the period between both events. Such increased time-lag between growth cessation and cessation of carbon fixation might allow plants to accumulate more non-structural carbohydrates in autumn. Future studies, however, will have to test if photosynthetic activity also ceases earlier today than in the past, leading to increased transpiration/photosynthesis ratios in autumn (Piao et al. 2008).

Temperature sensitivity of understory vs. canopy trees and its ecological implications

Previous studies showed that understory plants have lower winter-chilling requirements and leaf out earlier than canopy

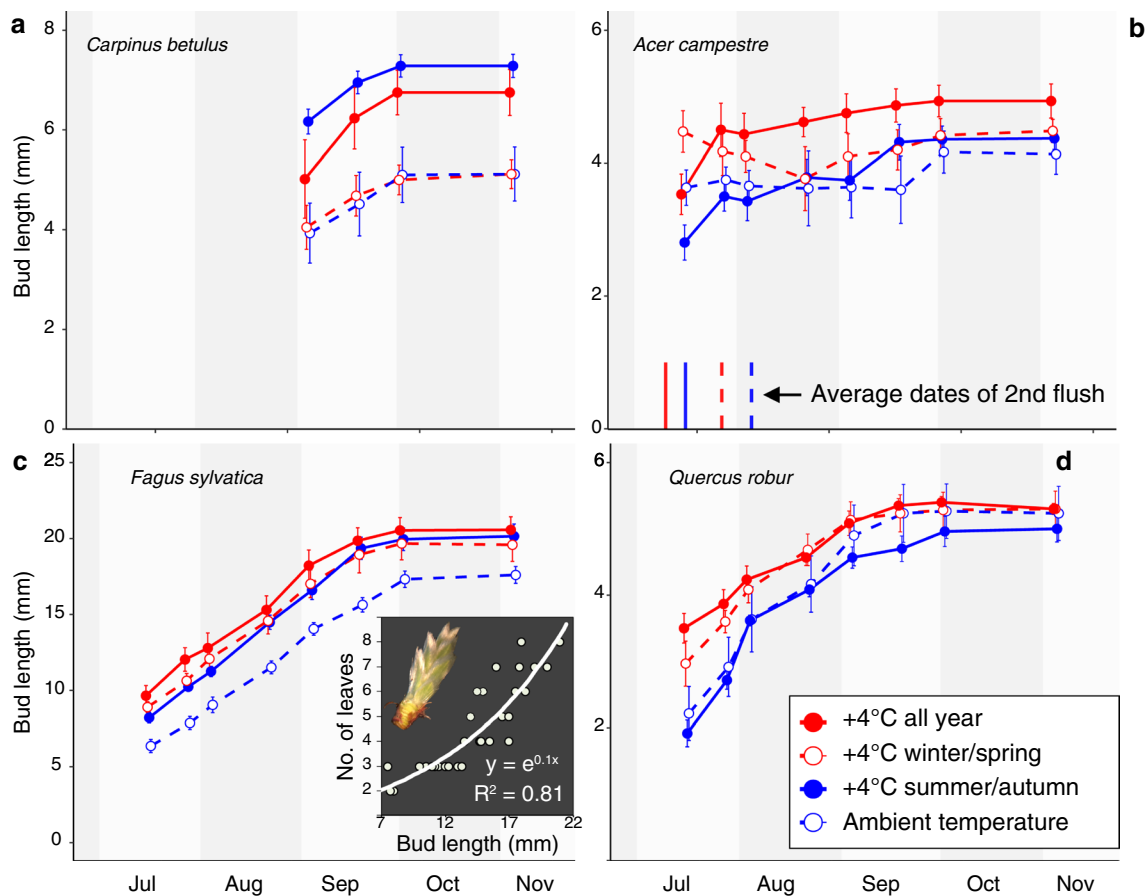


Fig. 6 Average bud length (in mm) \pm SEM between July and November 2015 for *Carpinus betulus* (a), *Acer campestre* (b), *Fagus sylvatica* (c), and *Quercus robur* (d) under the temperature treatments shown in the inset. For *F. sylvatica*, the additional graph shows the relationship between bud length (in winter) and the number of pri-

mordial leaves inside the respective bud ($N=30$ buds). The photograph shows the primordial leaves of a dormant *F. sylvatica* bud in winter after removing the bud scales. The figure is available in colour in the online version of the journal

trees (Augspurger and Bartlett 2003; Vitasse 2013; Laube et al. 2014; Panchen et al. 2014; Polgar et al. 2014), suggesting that understory species generally exhibit more opportunistic phenological behaviour. We, therefore, expected stronger phenological responses to elevated temperatures in the understory species. Despite our small sample of four understory and four canopy species, this expectation was met: Under year-long warming, the temperature sensitivity of the understory species was two to three times higher than that of the canopy tree species ($S_T=9.8$ days/°C vs. 4.5 days/°C; $A_T=4.2$ days/°C vs. 1.3 days/°C; Fig. 5a). In addition, winter/spring warming had a 2.3 times greater effect on overall vegetation period than summer/autumn warming (lengthening of 9.5 days/°C vs. 4.3 days/°C, respectively). In the canopy tree species, by contrast, the effect of winter/spring warming on the length of the vegetation period was comparably small and of similar magnitude as that of summer/autumn warming (lengthening of ~ 3 days/°C). This can be partly explained by

spring-to-autumn carry-over effects, which exist in long-lived canopy trees, but not understory species: In the canopy trees *F. sylvatica*, *S. aucuparia*, and *Q. robur*, the relationship between the timing of spring leaf-out and autumn leaf senescence was about 3:1, i.e., 1 day earlier leaf unfolding caused 0.3–0.4 day earlier leaf senescence (see numbers in Fig. 4 which show the regression coefficients between leaf-out and leaf senescence; $P < 0.05$). Thus, any extension of the vegetation period resulting from advances in leaf unfolding was offset (by up to 40%) by earlier leaf senescence, i.e., a 1 day advance in spring leaf unfolding caused a lengthening of only 0.6–0.7 days (Fig. 4). The timing of primary growth cessation (bud set) was even more strongly affected by leaf-out date, and thus in the canopy species *A. campestre*, *F. sylvatica*, and *Q. robur*, each day earlier leaf unfolding caused an advance in bud set of 0.3–0.8 days (Fig. 4, $P < 0.05$). Similarly, in a 20-year (1992–2012) long-term study on the North American *Fagus grandifolia*, *Acer saccharum*, and *Betula alleghaniensis*, Keenan and Richardson

(2015) found that 1 day earlier leaf-out leads to 0.66 days earlier leaf senescence.

In combination, these findings predict that continued climate warming will have stronger effects on the growth phenology of understory than canopy species, such that the growth period before canopy closure (or after canopy leaf fall) in understory plants will be extended. This likely will have consequences for the performance of understory species and may alter productivity, nutrient composition and trophic-level interactions at the forest floor (Fridley 2012). That the period before canopy closure is critical for growth and survival of understory species has been shown in a forest in Illinois, USA (Augspurger et al. 2005, Augspurger 2008): earlier leaf unfolding of the understory shrubs led to an estimated annual irradiance gain of 36–98%, whereas experimental shading before canopy closure in spring led to significantly decreased growth and survival rates.

The proximate reasons for the carry-over effects in trees, but not understory shrubs may have to do with their different growth strategies [monocyclic (a single shoot flush in spring) vs. polycyclic shoot growth (multiple successive flushes per season); Table 1]. In this study, only for the three species with monocyclic shoot growth, did we find a significant effect of leaf-out date on autumn leaf senescence (Table 1 and Fig. 4), which might be the result of constraints on leaf longevity (Reich et al. 1992; Lam 2004). By contrast, in species with several successive leaf flushes (within the same vegetation period), young leaves might still be functioning optimally late in the season. However, that leaf-out date had an even stronger effect on the timing of primary growth cessation (bud set) than on the timing of leaf senescence (Fig. 4) demonstrates that constraints on leaf longevity are not sufficient to fully explain spring-to-autumn carry-over effects. Fu et al. (2014) observed a larger starch content in autumn in individuals exhibiting earlier leaf unfolding in spring, which might indicate that autumn phenology is linked to plants' carbohydrate storage capacity (Herold 1980; Fatichi et al. 2013).

How phenology shifts translate into growth

This study quantifies how earlier leaf unfolding and longer vegetation periods due to increased temperatures translate into increased growth. In the polycyclic species *C. betulus*, an advance of 1 day in spring leaf-out led to an increase in height of 0.4 cm (Fig. 4). In *F. sylvatica*, we did not detect an effect of warming treatments on height because seasonal shoot length is determined by the amount of leaf primordial tissue formed in the preceding year's buds. Thus, in this species, bud development has to be monitored to quantify the effects of climate on seasonal aboveground primary growth. This is underscored by the strong positive relationship between bud length and the number of primordial leaves

within the respective bud (inset Fig. 6c). Four degree warming in summer and autumn led to buds that were 1.8 mm longer than controls, and the same amount of warming in winter and spring led to buds that were 1.2 mm longer (Figs. 6c and S3; Table 1). This predicts increased biomass accumulation in *F. sylvatica*, with a one °C increase in air temperature resulting in buds containing 0.54 more primordial leaves due to advanced leaf-out and accelerated bud growth. This for the first time provides experimental data on how earlier leaf presentation contributes to primary growth.

Summer and autumn warming led to significantly increased growth height in four (namely *Deutzia gracilis*, *Carpinus betulus*, *Sorbus aucuparia*, and *Quercus robur*) of the six species studied in this regard (Table 1 and Supplementary Fig. 4). However, since the warming treatments led to earlier not later cessation of primary growth (Fig. 1) this effect can be attributed to increased growth throughout the season, not prolonged autumn growth.

Conclusions

The present experimental results from four canopy and four understory species reveal partly opposing effects of experimental temperature warming in different seasons and carry-over effects between a year's spring and autumn phenophases in the canopy, but not in the understory species. Shortcomings of our study are its duration of only 2 years and the use of saplings, which may show a more opportunistic phenology than adult trees (Vitasse et al. 2013). Nevertheless, the data demonstrate that the timing of leaf senescence and growth cessation is uncoupled. This cautions against overreliance on leaf senescence (usually measured through remote spectral reflectance) for predicting the autumn productivity of woody species. That the effects of elevated temperature on phenology and growth strongly differed among seasons, with winter/spring warming leading to earlier leaf senescence, but summer/autumn warming leading to delayed senescence, underscores the need to consider seasonal climate projections rather than trends in annual mean temperatures when we are to model the future behaviour of temperate woody plants. Our results further imply that the time lags in spring and autumn phenology between understory and canopy plants are currently increasing, likely benefitting the performance of understory species and altering productivity, nutrient composition and trophic-level interactions at the forest floor.

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Author contribution statement CMZ designed the study and conducted the experiments and analyses. CMZ and SSR wrote the manuscript.

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