RESEARCH ARTICLE

How changes in spring and autumn phenology translate into growth-experimental evidence of asymmetric effects

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Abstract

1. Earlier leaf-out and later autumn leaf senescence under climate warming have been linked to increases in plant productivity and ecosystem carbon uptake. Yet, despite the potential implications of shifting phenology for plant carbon uptake, the degree to which phenological changes affect overall plant growth and the partitioning between above- and below-ground biomass remains unclear.

2. Here we use a 3-year experiment to quantify changes in root and shoot growth of three woody plant species (two common European tree species, *Fagus sylvatica* and *Quercus robur*, and one shrub *Lonicera xylosteum*) under spring and autumn warming.

3. In both tree species, the magnitude—and in *Quercus* even the direction—of the effects of growing-season length on growth depends on whether the warming happened in spring or in autumn. Each day earlier leaf-out in response to warming resulted in total biomass increases of 0.8%–2.5%, whereas delayed senescence led to reductions of 0.2%–2.1%. Advances in leaf-out also led to increased root-to-shoot biomass ratios because root growth was proportionally more stimulated than shoot growth. In the shrub species, earlier leaf-out had no effect, while delayed senescence led to increases in root, but not shoot, biomass.

4. *Synthesis*. The strong asymmetry between growth responses to spring versus autumn phenology demonstrates that growing-season length per se is a weak indicator of individual-level tree productivity. The results further imply that phenological shifts are reshaping the functional balance between above- and below-ground growth, which is critical for quantifying forest carbon dynamics under climate change.

KEYWORDS
carbon cycle, climate change, leaf-out, phenology, plant growth, senescence, warming experiment

1 | INTRODUCTION

Plant phenology is a fundamental determinant of seasonal vegetation activity in temperate and boreal regions (Cleland et al., 2012; Polgar & Primack, 2011; Zohner et al., 2020). Shifts in the phenological cycles of trees affect ecosystem carbon, water and nutrient balances, and feedback to the climate system by modulating carbon fluxes, surface energy budgets and the albedo effect (Keenan et al., 2014; Richardson et al., 2013). Climate warming is currently reshaping the growing seasons of trees, with each degree increase in spring

temperature causing an advance in spring leaf-out of 2–7 days (Fu et al., 2015; Zohner et al., 2020; Zohner & Renner, 2014). Similarly, autumn warming is delaying senescence dates—by up to 8 days per each degree increase in autumn temperature in some species (Fu et al., 2018)—although warmer springs and summers strongly counteract these delays (Zani et al., 2020). The relationships between plant phenology and growth have been experimentally investigated in arctic and montane ecosystems (Choi et al., 2019; Cleland et al., 2012; Livensperger et al., 2016; Natali et al., 2012), but the extent to which phenological changes affect growth in temperate woody plants remains largely unknown. If we are to quantify the consequences of climate change for plant growth, above- and below-ground biomass allocation and terrestrial carbon balance, quantification of the link between phenology and growth is critical.

To date, our knowledge about the effects of phenological shifts on forest productivity mostly stems from ecosystem-level studies based on CO_2 flux observations or global carbon cycle models (Chen et al., 2016; Keenan et al., 2014; Zohner et al., 2020). While most studies suggest strong increases in both plant photosynthesis and whole-ecosystem carbon uptake as a result of advanced spring leaf-out, there is mixed evidence about the effects of delayed autumn phenology on photosynthesis and growth. Using a combination of flux tower data and phenological observations, Keenan et al. (2014) predicted that each day advance in spring leaf-out would increase ecosystem net carbon uptake by 45 kg carbon per hectare forest and each day delay in autumn senescence would translate into an increase of 98 kg/ha. In contrast, despite longer growing seasons, Piao et al. (2008) found carbon losses in autumn across northern ecosystems, offsetting 90% of the increased spring CO_2 uptake. While the carbon loss might be largely driven by increases in soil respiration, there is also evidence from studies of tree growth that delayed leaf senescence will not necessarily translate to elevated plant productivity (Bauerle et al., 2012; Zohner & Renner, 2019). In fact, warmer springs and summers can lead to earlier growth cessation (Zohner & Renner, 2019; Zohner et al., 2019).

The physiological mechanisms linking plant phenology and overall growth may differ between spring leaf emergence and autumn senescence. Spring leaf-out coincides with the start of photosynthesis and is thus directly related to plant productivity (Polgar & Primack, 2011; Richardson et al., 2010, 2013). Autumn senescence and productivity are less clearly linked because visible changes do not necessarily reflect physiological progression (Zhang et al., 2020), and cessation of gross primary productivity and growth can be decoupled from leaf senescence (Dox et al., 2020; Zhang et al., 2020; Zohner & Renner, 2019). Warming-induced delays in autumn senescence therefore do not necessarily translate to increased tree growth. In response to declining day length, leaves gradually reduce photosynthetic capacity after the summer solstice, despite retaining their green colour (Bauerle et al., 2012), and declining radiation during autumn may further enhance the limitation on autumn photosynthesis (Zhang et al., 2020). In addition, plant photosynthesis is not only limited by external environmental drivers, such as day length, but feedbacks between sink (growth) and source activity (photosynthesis) govern the carbon uptake capacity of plants (Körner, 2003; Paul & Foyer, 2001; Zani et al., 2020).

Autumn productivity therefore appears to be limited by plant's carbon sink strength (e.g. nutrient limitation), despite warmer conditions (Fu et al., 2014, 2019; Keenan & Richardson, 2015; Lim et al., 2007; Woo et al., 2019; Zani et al., 2020; Zohner et al., 2019). Because the magnitude of these effects on overall autumn growth is not well-understood, experimental studies disentangling the relative roles of phenology and climate during the growing season are needed.

Another important question is how phenological shifts may alter biomass allocation and turnover in different organs. If phenological shifts alter the allocation of biomass between above- and below-ground components, this changes resource acquisition and ecosystem carbon storage, driving feedbacks between climate and the terrestrial carbon cycle (Luo, 2007). For example, due to large variations in the longevity of different plant tissues, increased below-ground growth could lead to faster carbon turnover as a result of increased fine root biomass. Ecosystem-wide changes in root biomass allocation and root turnover rates will thus be important determinants of future soil carbon pools (Matamala et al., 2003). To match the demand and supply of resources, plants show considerable plasticity in their biomass distribution patterns, and variations thereof are linked to the relative availability of nutrients, water, CO_2 and light (Bardgett et al., 2014; Hermans et al., 2006; Poorter et al., 2012; Reich, 2002; Reich et al., 2014). With respect to phenology, one might expect that longer growing seasons and associated increases in photosynthesis would lead to increased water and nutrient demand, potentially increasing plants' investment into below-ground resources. Yet, to our knowledge, this possibility remains unexplored.

Here, we present the results of a 3-year experiment on two broad-ranged European tree species and one shrub, in which we tested the direct effects of changes in the timing of spring leaf-out and autumn senescence on seasonal biomass increment. To isolate the effects of growing-season length, that is, the timing of spring leaf-out and autumn senescence, from growing-season temperature, plants were exposed to experimental warming in spring, autumn or autumn-to-spring, but not during summer (May–August). Because photosynthetic activity at the end of the season is constrained by light (day length and radiation) and sink capacity (Bauerle et al., 2012; Zani et al., 2020; Zhang et al., 2020), we expected that warming-driven advances in spring leaf-out would have a proportionally larger effect on growth than would warming-driven delays in autumn leaf senescence. We also expected that a longer growing season might increase the relative allocation of biomass to roots.

2 | MATERIALS AND METHODS

2.1 | Experimental setup

The experiment was conducted in the Munich Botanical Garden (48°09′N, 11°30′E; 501 m a.s.l.) between January 2017 and December 2019. Three-year old individuals (40 per species) of *Fagus sylvatica*, *Quercus robur* and *Lonicera xylosteum* were exposed to warming conditions in spring or autumn, and the effects on phenology and

growth then followed from spring 2017 until December 2019. Plants were obtained from a local nursery in winter 2016/2017, transferred to 40-l plastic pots with uniform soil from a nearby patch and kept outdoors under uniform conditions until the start of the experiment (15 January 2017). Throughout the experiment, pots were watered once or twice a week to keep soil moisture constant. Every spring, each plant was treated with 50 g NPK fertilizer (DCM ECO-XTRA 1) and 0.6 g micronutrients (DCM MICRO-MIX).

The experiment consisted of four treatments, each with 10 individuals per species (ambient control treatment and +5°C warming in spring, autumn or autumn-to-spring in climate-controlled glasshouse chambers with an openable top; Zohner et al., 2019). Each year, spring warming was applied from 1 January until 15 May (date when all individuals had leafed out). Autumn warming was applied from 1

September until 31 December, and autumn-to-spring warming was applied from 1 September until 15 May (see Figure 1a for details on treatment conditions). The glasshouse provided a stable warming treatment, and the median of daily warming (Δ temperature treatment vs. control) was 4.71°C during spring and 4.67°C during autumn (see Figure 1b,c for a comparison of daily temperatures between treatments and the control during the 3 study years). Day length and light intensity in the glasshouse did not differ from outdoor conditions (see fig S2 in Zohner & Renner, 2019). Individuals were distributed evenly between two chambers, that is, five individuals of each treatment and species were randomly placed in each chamber. During summer (15 May–1 September), all individuals were kept outdoors under the same conditions and arranged in a randomized block design; each block consisted of one individual from each of the four treatments.
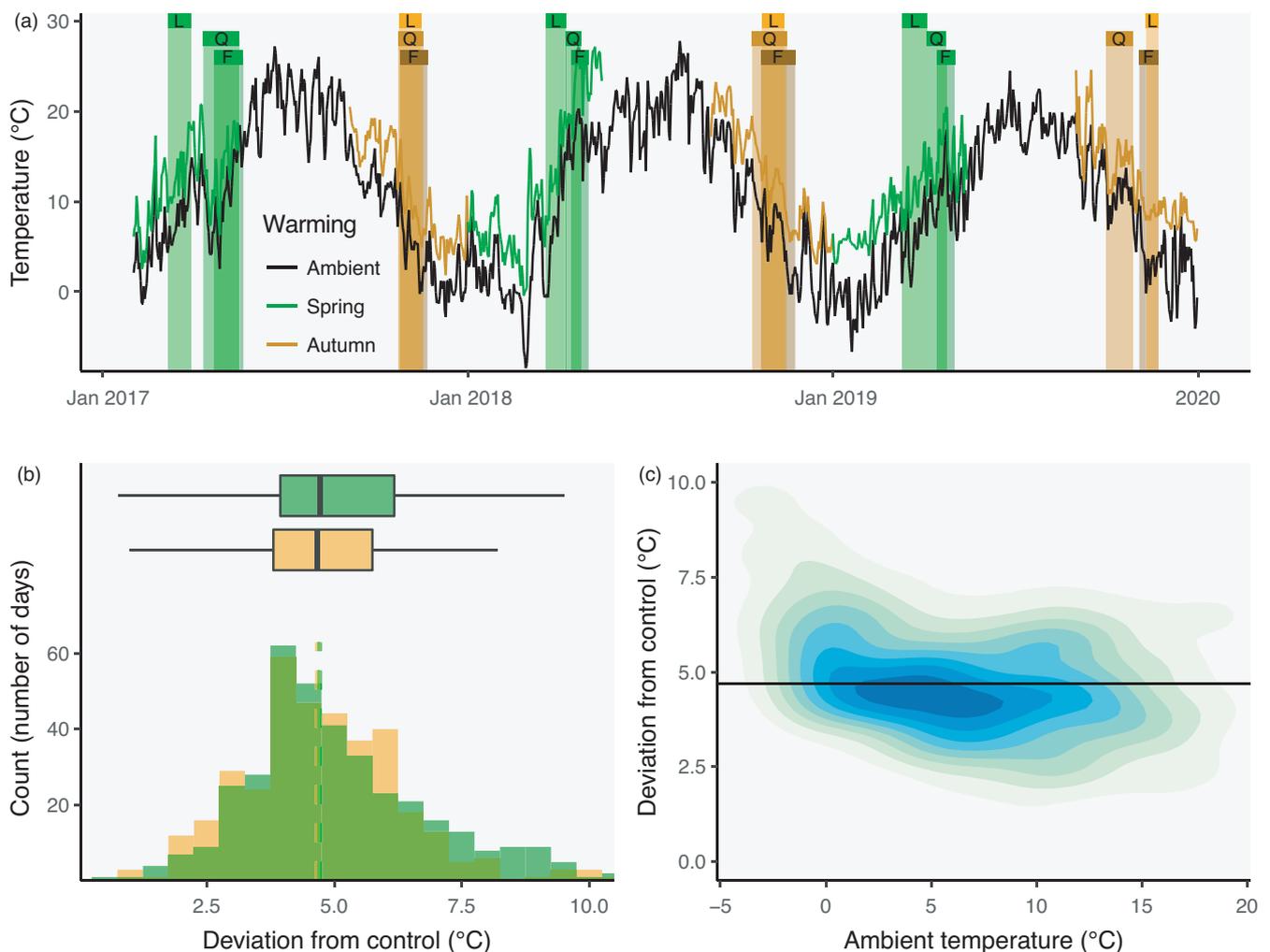

FIGURE 1 Temperature regimes and phenological timing during the three study years. (a) Mean daily temperatures from January 2017 until December 2019 under ambient conditions (black lines) and for the spring (green lines) and autumn warming treatments (orange lines). Green and orange areas represent the mean ± SD of leaf-out (green) and senescence dates (orange) for the studied *Lonicera* (L), *Quercus* (Q) and *Fagus* (F) individuals respectively. (b) Mean daily temperature deviation of the spring warming (green) or autumn warming treatment (orange) from the control. The histogram shows the full distribution across all days, the boxplots and the dashed lines indicate the median deviation of 4.72°C for the spring warming treatment and 4.67°C for the autumn warming treatment. (c), Density plot showing the temperature deviation of the warming treatments from the control in response to the respective daily temperature of the control. The colour gradient represents the number of observations within a particular area, with high observation densities towards dark blue areas; the black line indicates the median deviation

2.2 | Phenological observations

Observations and trait measurements involved all individuals for each of the three species. Spring leaf-out was observed twice a week, and autumn leaf senescence was observed at weekly intervals. Leaf-out was defined as the day when three branches on a plant had leaves pushed out all the way to the petiole and unfolded (BBCH code 11). Leaf senescence was defined as the day when ~50% of leaves on a plant had turned yellow or dropped (BBCH code 94). Growing-season length was defined as the period between leaf-out and leaf senescence (Zohner & Renner, 2017).

2.3 | Climate data

Accumulated warming required to leaf-out was calculated as the sum of daily degree-days from 1 January until the date of leaf-out in the respective individual. Degree-days were calculated from mean daily temperatures with a base temperature of +5°C.

To characterize the temperatures that the young leaves of each individual experienced in spring, we calculated the mean of daily temperatures during the 4 weeks after leaf-out (post-leaf-out temperature). Similarly, we calculated pre-senescence temperatures as the temperature each individual experienced during the 4 weeks before leaf senescence.

Chill days were calculated as days with an average temperature below 11°C. Baumgarten et al. (2021) show that for both beech and oak, all temperatures between −2°C and +11°C effectively induce dormancy release, and we therefore chose 11°C as the threshold chilling temperature above which dormancy is not released anymore. For each year, we then calculated the total number of winter chill days in the warming treatments and the control as the chill days from 1 October to 1 April.

Vapour pressure deficit was calculated based on hourly measurements of relative air humidity and air temperature, using the 'RHtoVPD' function of the R package PLANTECOPHYS (Duursma, 2015). Air pressure was fixed to 101 kPa. To test for potential effects of vapour pressure deficit on daytime stomatal conductance, that might ultimately affect transpiration and photosynthesis rates, we obtained daytime vapour pressure deficit by calculating the average vapour pressure deficit during daytime hours, that is, from sunrise to sunset. As a result of slightly decreased air humidity and increased temperature in the glasshouse, vapour pressure deficit was higher in the spring and autumn warming treatments compared to the control (Figure S1). However, in the autumn warming treatment, vapour pressure deficit was consistently below 0.6 kPa, suggesting that the slight increases in vapour pressure deficit did not affect transpiration and photosynthetic rates. For both *F. sylvatica* and *Q. robur*, stomatal conductance can be expected to decline at vapour pressure deficits >0.6 kPa and complete stomatal closure is expected for values >3 kPa (Kerstiens, 1995; Morecroft & Roberts, 1999; White et al., 2000).

2.4 | Measurements of annual growth and plant biomass

Plant biomass was measured after the end of the experiment in May 2020, after air-drying plants for 5 months (December–May) in a 25°C room. Plants were cleansed with water before drying to remove all soil from the roots. Plants were in full dormancy (inactive) at the start of the drying procedure, preventing respiratory carbon losses that could otherwise have affected the measurements. For all individuals, we weighed roots and shoots separately to quantify total biomass, shoot biomass, root biomass and the ratio between root and shoot biomass (root–shoot ratio).

Each December (from 2016 to 2019), we measured the stem apical diameter, the stem basal diameter at 3 cm from the ground and the stem length for each individual of *F. sylvatica* and *Q. robur*. In addition, diameter and length of the longest branch were measured. For the shrub *L. xylosteum*, we measured diameter and length of the three longest branches. All diameter measurements were made with a digital caliper (Mitutoyo IP67 ABS, accuracy 0.01 mm), stem length was measured with a tape (accuracy 0.1 cm). We calculated the volume of the stem assuming a truncated cone shape (Signarbieux et al., 2017):

$$V_i = \frac{1}{3} \times \pi \times L \times (R^2 + r^2 + R + r) \text{ mm}^3,$$

where V is the volume of the stem or branch i, R is the basal diameter of the stem, r is the apical diameter of the stem and L is the length of the stem.

2.5 | Data analysis

The experiment followed a two-factor full-factorial design with repeated measurements, resulting in four treatments: control treatment, spring warming, autumn warming and autumn–spring warming. The experimental and observational unit was a pot with a single individual. To obtain individual-level phenology anomalies, for each individual and year, we calculated the deviation in leaf-out date, senescence date and growing-season length from the mean of all individuals of the respective species and then averaged annual anomalies across the last two study years (2018 and 2019; phenological observations of the year 2017 were not included because carry-over effects of preceding phenological stages could not have been present during that first spring). A few individuals showed signs of disease, and we removed them from the analysis to make sure pathogen attacks did not affect our results (final sample sizes per treatment and species are shown in Table 1).

To test for the relative effects of spring and autumn warming on phenology and growth, we ran multivariate linear models, including spring and autumn warming as binary variables of whether the individual was warmed in spring or not and autumn or not. We additionally included interaction terms to test if spring warming or autumn warming effects depended on the other treatment. We conducted

T-tests to check for significant differences in phenology and growth between treatments and the variable mean of the control group. We used linear models to study the relative effects of individual-level leaf-out dates, senescence dates and growing-season length on biomass, and tested the regression assumptions, such as linearity of the data, normality of residuals, homogeneity of residuals variance and independence of residuals error terms, by visually inspecting diagnostic plots. Additionally, we ran a Shapiro–Wilk test to confirm the normality of residuals.

All analyses were performed in R 3.6.2 (R Core Team, 2019).

3 | RESULTS

3.1 | Phenological differences among treatments

In all three species, warmer spring conditions led to earlier leaf-out, and warmer autumns led to delayed leaf-out. Specifically, spring warming advanced leaf-out dates by, on average, 16, 14 and 22 days in *Quercus*, *Fagus* and *Lonicera* respectively (Figure 2a,d,g; Figure S2). Autumn warming delayed leaf-out by 2, 7 and 4 days. In *Lonicera*, but not the other species, there was a significant interaction between autumn and spring warming, with autumn warming

TABLE 1 Sample sizes (number of individuals) per species and treatment included in the final analysis

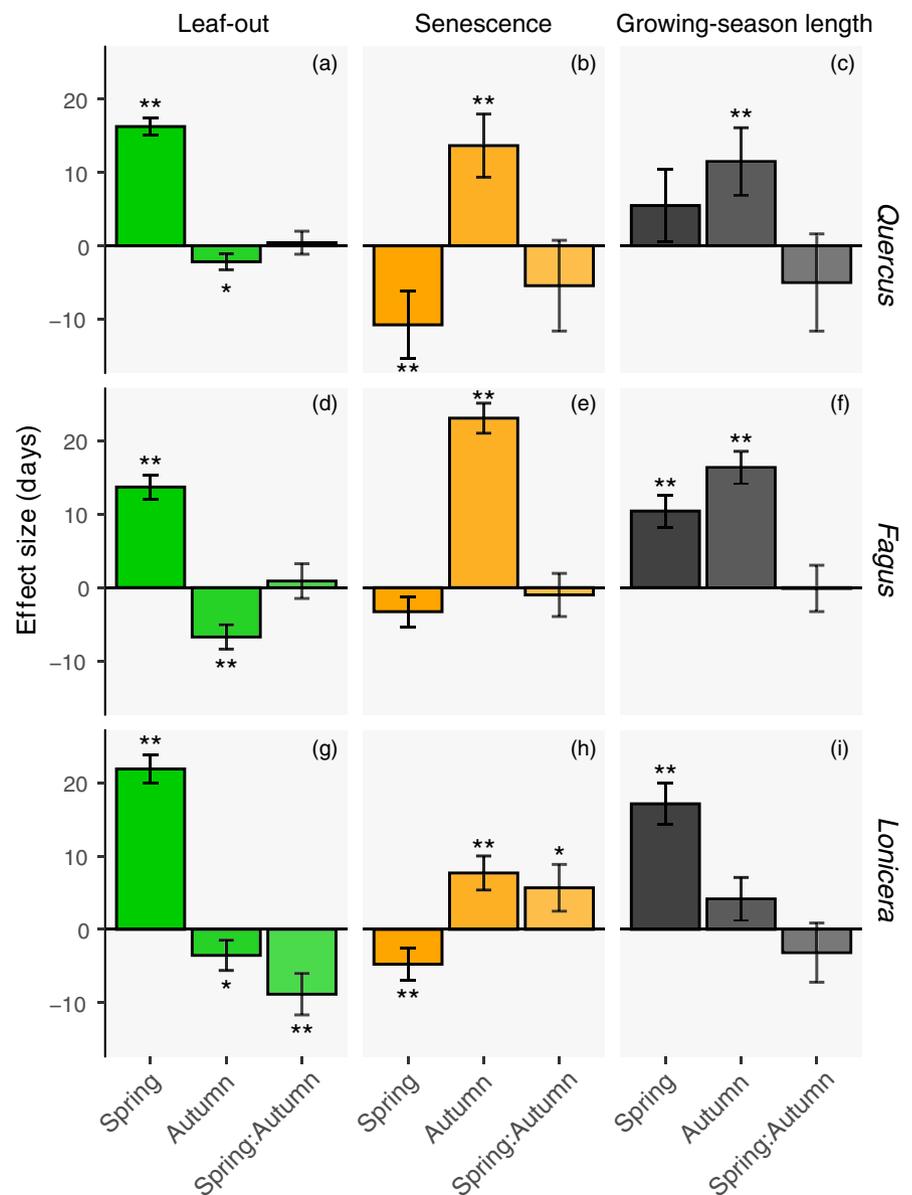|	Quercus robur	Fagus sylvatica	Lonicera xylosteum
Control	9	10	9
Spring warming	8	9	10
Autumn warming	10	9	8
Autumn–spring warming	10	9	9

FIGURE 2 Phenological responses of *Quercus robur* (a–c), *Fagus sylvatica* (d–f) and *Lonicera xylosteum* (g–i) to +5°C warming in spring or autumn across 2 years (2018–2019) as inferred from multivariate linear regression models. Bars show the mean ± SE effect (in days) of spring warming, autumn warming and the interaction between spring and autumn warming on spring leaf-out (a, d, g), autumn senescence (b, e, h) and overall growing-season length (c, f, i). Positive effect sizes represent a lengthening of the growing season, that is, advances in leaf-out (left panels), delays in senescence (middle panels) or increases in overall growing-season length (right panels). *p < 0.1, **p < 0.05

reducing the effect of spring warming by 9 days (Figure 2g). Across all species and years, warming (degree-day) requirements to leaf-out were highest in the autumn–spring warming treatment, followed by the spring warming and autumn warming treatments, and lowest in the ambient control (Figure S3). Winter chilling was slightly reduced in the warming treatments compared with the control, with an average reduction in chill days in the spring warming treatment of 10% across all years, a reduction of 13% in the autumn warming treatment and a reduction of 23% in the autumn–spring warming treatment.

Autumn warming generally delayed senescence by, on average, 14, 23 and 8 days in *Quercus*, *Fagus* and *Lonicera* respectively. By contrast, warmer springs consistently led to advances in autumn senescence of 11, 3 and 5 days (Figure 2b,e,h).

In combination, these effects led to variable implications for total growing-season length. In *Quercus* and *Fagus*, spring warming led to a growing season extension of 6 and 10 days and autumn warming to an extension of 12 and 16 days (Figure 2c,f). In *Lonicera*, spring warming had the largest effect on growing-season length, with an extension of 17 days, while autumn warming led to a growing season extension of only 4 days (Figure 2i).

3.2 | Post-leaf-out and pre-senescence temperatures

To test whether acclimation of individual leaves to warming conditions in spring or autumn could have affected the overall growth responses, we determined the temperatures that individual trees experienced during the 4 weeks after leaf-out (post-leaf-out temperature) and before leaf senescence (pre-senescence temperature) respectively. Leaves of individuals in the spring-only warming treatment, on average, experienced 1.9, 1.9 and 0.7°C warmer 'post-leaf-out' conditions relative to the control for *Quercus*, *Fagus* and *Lonicera* respectively (Figure S4). The leaves of individuals in the autumn-only warming treatment, on average, experienced 2.3 and 1.9°C warmer 'pre-senescence' conditions relative to the control for *Lonicera* and *Quercus* or 0.5°C colder conditions for *Fagus*.

3.3 | Growth differences among treatments

In *Quercus* and *Fagus*, spring warming had a strong positive effect on tree growth, leading to an increase in total plant biomass of 36% and 21% respectively (Figures 3 and 4a,e). In both species, spring warming had a greater effect on root growth than shoot growth (52% and 35% vs. 17% and 10% respectively), resulting in an increase of root–shoot biomass ratios by 27% and 23% (Figure 4d,h).

Autumn warming reduced total tree growth in *Quercus* by 41% and slightly increased growth in *Fagus* (+11%). The autumn effect was of similar magnitude for root and shoot growth, resulting in no significant change in root–shoot ratios. In *Fagus*, there was a significant interaction between autumn and spring warming, with autumn-to-spring warming exhibiting an even smaller effect on growth than autumn-only warming (Figure 4g; Figure S5).

In *Lonicera*, autumn warming led to increases in root biomass of 16% but had no effect on shoot biomass, resulting in an increased root–shoot ratio of 21%. Although spring warming had no significant effects on root and shoot growth, there was a tendency for an increased root–shoot ratio (+14%, $p = 0.14$).

3.4 | Direct link between phenology and growth

The relationship between growing-season length and total plant growth also varied among species. In *Quercus* and *Fagus*, earlier spring leaf-out had a positive effect on growth, with each day advance in leaf-out resulting in a total biomass increase of 2.5% and 0.8% respectively (Figure 5a,d). In *Lonicera*, earlier spring leaf-out barely affected growth (Figure 5g). In the two tree species, the effect of spring phenology differed between above- and below-ground growth: While shoot biomass only increased by 1.8% and 0.4%, root biomass increased by 3.0% and 1.2% for each day advance in leaf-out respectively (Figure 5a,d). In *Lonicera* there was hardly any difference in allocation (Figure 5g).

Delays in autumn senescence negatively affected total (root and shoot) growth in *Quercus* (−2.1% per day delay in senescence; Figure 5b), led to slightly reduced root growth in *Fagus* (−0.5% per
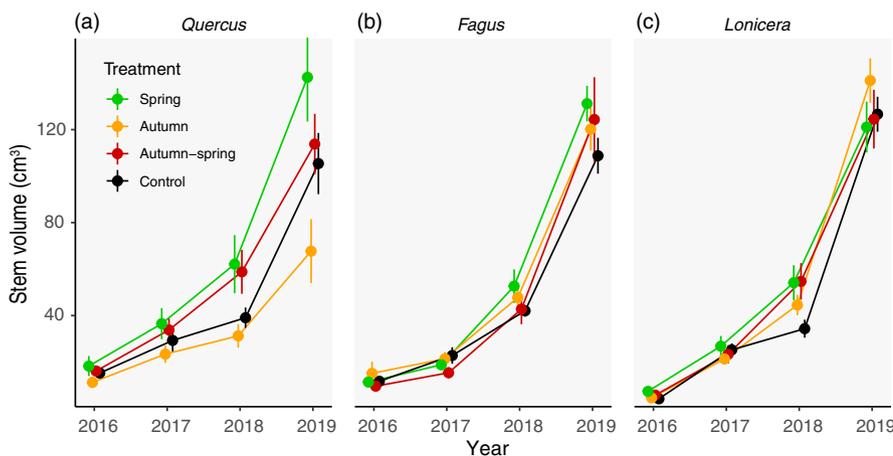

FIGURE 3 Above-ground growth responses of *Quercus robur* (a), *Fagus sylvatica* (b) and *Lonicera xylosteum* (c) to 3-year (2017–2019) exposure to +5°C warming in spring (green), autumn (orange), autumn-to-spring (red) and ambient temperatures (black). Points show the mean (±*SE*) stem volume measured each December for all studied individuals (see Section 2)

FIGURE 4 Changes in biomass of *Quercus robur* (a–d), *Fagus sylvatica* (e–h) and *Lonicera xylosteum* (i–l) in response to 3-year (2017–2019) exposure to +5°C warming in spring or autumn as inferred from multivariate linear regression models. Bars show the mean ± *SE* effect (in percent) of spring warming, autumn warming and the interaction between spring and autumn warming on total biomass (a, e, i), shoot biomass (b, f, j), root biomass (c, g, k) and root–shoot biomass ratio (d, h, l). *$p < 0.1$, **$p < 0.05$
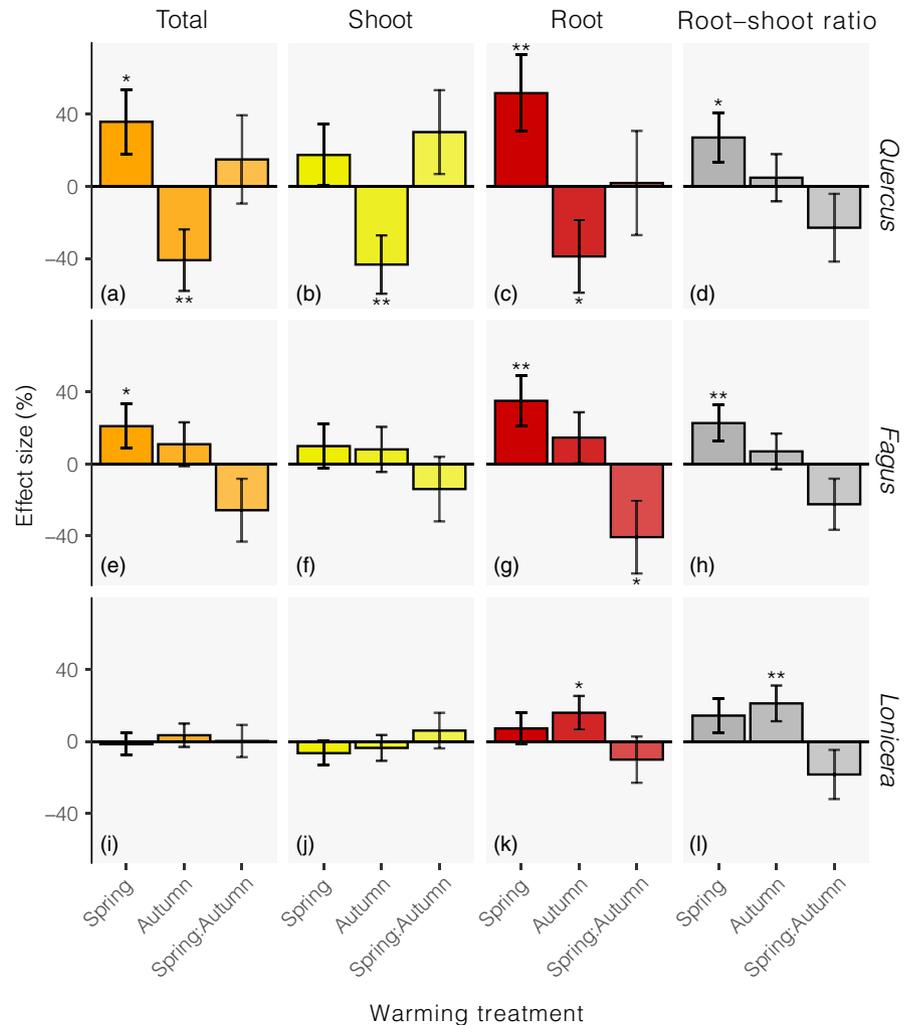
day^{-1}, Figure 5e), and increased root growth in *Lonicera* (+0.9% day^{-1}; Figure 5h). Overall, increased growing-season length had a negative effect on root and shoot growth in *Quercus*, with a total biomass decrease of 1.3% per each day increase in growing-season length (Fig. 5c), a slightly positive effect on growth in *Fagus* (+0.3% day^{-1}, Figure 5f), and no effect in *Lonicera* (Figure 5i).

4 | DISCUSSION

The experiment we report here allowed us to directly test the relationship between warming-induced phenological changes and growth in temperate woody plants. We expected that spring phenological changes would have a larger impact on growth than would changes in autumn because day length and sink limitation impose strong constraints on photosynthesis in autumn, but not in spring (Bauerle et al., 2012; Zani et al., 2020; Zohner et al., 2016). In addition, we expected that growing-season extensions might lead to proportionally larger increases in root than shoot biomass because below-ground resources (water and nutrients) might become limiting. Both expectations were partially met.

4.1 | Asymmetric effects of spring and autumn phenology on tree growth

In both tree species, earlier leaf-out in response to 5°C warming in spring led to an increase in total biomass (36% in *Quercus* and 21% in *Fagus*; Figure 4a,e). This strong control of net primary productivity by leaf-out timing underscores the importance of phenological forecasts for future projections of terrestrial carbon balances (Zohner et al., 2020). In contrast, warmer autumns and delays in leaf senescence had a much smaller effect on growth for *Fagus* or even led to decreased growth in *Quercus*. The lack of a positive association between autumn warming and plant growth at the tree level is in agreement with recent studies suggesting that light and sink limitation represent important constraints on autumn productivity (Bauerle et al., 2012; Zani et al., 2020; Zhang et al., 2020).

Photosynthesis declines predictably with shortening day length and decreasing radiation after the summer solstice, even if leaf chlorophyll content remains at constant levels until autumn (Bauerle et al., 2012). Warming-driven senescence delays might therefore increase the vegetation period without increasing photosynthesis levels. This might even cause decreases in tree net carbon uptake if the respiration/photosynthesis ratio increases during autumn (Piao et al., 2008).
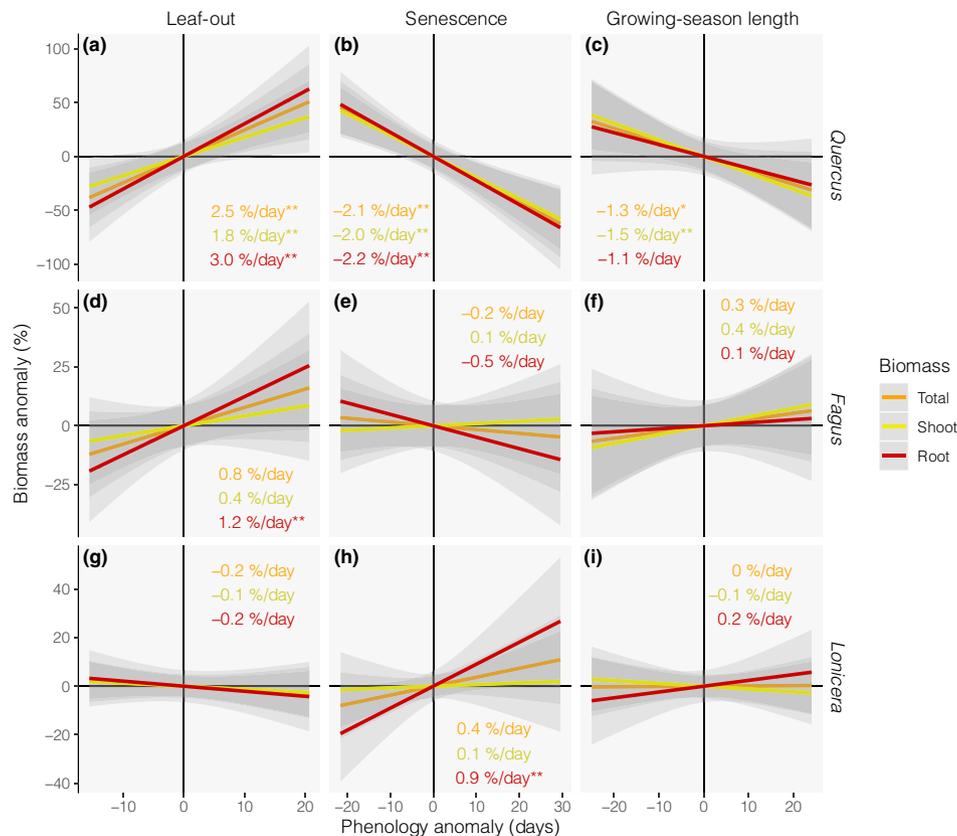
FIGURE 5 Changes in biomass of *Quercus robur* (a–c), *Fagus sylvatica* (d–f) and *Lonicera xylosteum* individuals (g–i) in response to leaf-out timing, senescence timing and overall growing-season length. Lines show the linear effect (in percent biomass increase per day ±*SE*) of spring leaf-out (a, d, g), autumn senescence (b, e, h) and growing-season length (c, f, i) on plant biomass (orange line = total biomass, yellow = shoot biomass, red = root biomass) across 3 years (2017–2019). Growth and phenology are shown as anomalies, that is, shown as deviation from the mean biomass or phenology observed across all individuals of the respective species. Positive phenology values represent the lengthening of the growing season, that is, advances in leaf-out, delays in senescence or increases in overall growing-season length. *$p < 0.1$, **$p < 0.05$. [Correction added on 6 June 2021, after first online publication: Figure 5 has been corrected to remove the lower part.]

Apart from day-length effects, physiological constraints resulting from sink limitation also lead to a downregulation of photosynthesis in autumn (Kumar et al., 2019). Because the seasonal sink capacity of plants is limited, for instance by nutrient supply (Y. H. Fu et al., 2019), sink strength is gradually decreasing towards autumn as the demand for growth is declining (Kuptz et al., 2011). The limiting effect of sink capacity on autumn productivity and phenology has recently been demonstrated by experimental and observational work, showing that increasing spring and summer productivity advance autumn growth cessation and senescence (Fu et al., 2014; Lim et al., 2007; Zani et al., 2020; Zohner & Renner, 2019; Zohner et al., 2019).

While delays in autumn senescence had no significant effect on overall biomass increase in *Fagus* (−0.2% ± 0.4% [mean ± *SE*] biomass per each day delay in autumn senescence, Figure 5e), delayed leaf fall led to reduced growth in *Quercus* (−2.1% ± 0.5% biomass per day, Figure 5b). Interestingly, spring warming had a much stronger negative (advancing) effect on autumn senescence in *Quercus* than in *Fagus* (Figure 2b,e), indicating differences in the extent of sink limitation between the two species, which might be driven by species-level variations in shade tolerance and/or nutrient demand.

In contrast to the tree species, autumn warming had a positive effect on growth in the shrub species, especially on root growth (Figure 4k), while there was no increase in growth in response to elevated spring temperature. Understorey shrubs apparently can make use of the increased light after the canopy trees have shed their leaves (Fridley, 2012), increasing their potential for carbon gain under delayed senescence (Figure 5h).

In addition to the effects of day length and sink limitation, different acclimation of individual leaves to warming conditions in spring or autumn might have affected the overall growth responses we observed. Yet, compared to the controls, the leaves in the spring-only warming treatment experienced only slightly elevated temperatures (0.7–1.9°C) during the 4 weeks after leaf-out (Figure S4). The leaves in the autumn-only warming treatment experienced 0.5°C colder, or 1.9°C and 2.3°C warmer temperatures during the 4 weeks preceding senescence for *Fagus*, *Lonicera* and *Quercus* respectively. Furthermore, all trees were only kept in the glasshouse until late spring (May 15), and thus, while the leaves of the early leafing *Lonicera* might have adapted to some extent to climate chamber conditions, *Fagus* and *Quercus* individuals were moved outside quickly after leaves had unfolded (Figure 1a), preventing any adaptation to

glasshouse conditions. We therefore conclude that metabolic leaf-level adaptation to temperature is unlikely to explain the contrasting effects of spring and autumn phenology on growth.

4.2 | Asymmetric effects of phenology on above- and below-ground biomass production

In all three species, we observed shifts in biomass partitioning between above- and below-ground organs, with stronger increments in root growth compared to shoot growth in response to the warming treatments (Figure 4). In accordance with the finding that spring warming had a larger effect on overall growth than did autumn warming in the trees, while autumn warming had a larger effect in the shrub, root–shoot biomass ratios were most strongly affected by spring warming in the former and by autumn warming in the latter. In general, root growth in trees peaks in early spring before full leaf-out (McCormack et al., 2015; Radville et al., 2016), whereas root production in shrubs tends to peak in late summer when above-ground production already dropped significantly (Steinaker et al., 2010).

Ultimately, such changes may reflect a plants' strategy to maintain functional equilibrium between below- and above-ground organs. Many studies point to the important interrelationship between temperature, CO_2, light, nutrients and water in driving these plastic responses (Poorter et al., 2012; Reich et al., 2014; Way & Oren, 2010). Low-light conditions are expected to cause increased investment into above-ground organs, especially leaves, to compensate for the loss of leaf-level photosynthetic activity. In contrast, water and nutrient limitation should favour biomass allocation to root organs to alleviate limitation of resources acquired below-ground.

Root-to-shoot biomass ratios tend to increase towards colder regions, an effect that is likely driven by decreased soil nutrient availability in cold environments (Reich et al., 2014). Under climate change, nutrient limitation might thus become less pronounced once growing seasons become warmer. Yet, longer growing seasons will also allow for more light capture and photosynthesis, potentially increasing water and nutrient needs. Thus, when controlling for growing-season temperature and nutrient supply—as done in this study—extended growing seasons per se might lead to increased below-ground investment as below-ground resources (water and nutrients) could become proportionally more limited. In all three studied species, this expectation was met, demonstrating, to our knowledge for the first time, that phenological changes can substantially alter biomass distribution patterns within plants.

One caveat that merits consideration is whether increased root-to-shoot biomass ratios under experimental warming reflect true shifts in partitioning or are the result of differences in plant size and thus reflect ontogenetic changes. Above-ground-to-below-ground biomass ratios of plants change during their development (ontogenetic drift), and it has been suggested that differences in biomass distributions among treatments at any one point are not necessarily adaptive and may instead arise from divergent growth rates among

plants (Reich, 2002). The differences in biomass distribution among treatments detected here might thus be a consequence of accelerated ontogenetic development in response to longer growing seasons. However, other work shows that *Fagus* and *Quercus* normally have declining root–shoot ratios as trees grow bigger until a constant ratio of ~0.2 is reached (Genet et al., 2009), which suggests that the observed increasing root–shoot ratios under enhanced growth are, at least to some degree, an adaptive response to altered resource supply under longer growing seasons.

5 | CONCLUSIONS

Our experimental manipulation of spring leaf-out and autumn senescence timing—eliminating confounding factors, such as CO_2 levels, air temperature and soil water availability during the growing season—allowed us to directly assess the direction and magnitude of the relationship between phenology and individual plant growth. While the environmental drivers of woody plant phenology have been studied through observational, experimental and modelling approaches, studies of the link between plant phenology and plant growth are surprisingly scarce. The experiment we report here was conducted on young individuals, and thus its conclusions are especially important with respect to forest recruitment and establishment under continued anthropogenic climate change. Changes in the relative biomass distribution within young plants will have cascading effects on the proportional biomass allocation and turnover rates in adult trees. On the other hand, young individuals might respond more opportunistically than older individuals because in temperate deciduous trees ontogenetic progression is associated with reduced temperature sensitivity (Vitasse, 2013). Nevertheless, the decoupling between shoot and root growth in response to early and late-season warming demonstrates the critical role of below-ground phenology and growth in determining overall plant productivity, emphasizing the importance of whole-plant assessments to quantify the temperature effects on biomass allocation and turnover, nutrient cycling and ecosystem fluxes. In addition, the strong asymmetry in the growth responses to changes in spring and autumn phenology is directly relevant for projections of plant productivity and changes in the terrestrial carbon cycle.

Future efforts should be directed towards assessing the extent to which the short-term (3-year) growth responses we observed may be counteracted by long-term acclimation of trees to newly emerging climate conditions. Furthermore, the absence of a growth stimulation in response to longer growing seasons observed at the individual tree level cannot be expected to hold at the ecosystem level on larger (decadal to centennial) time-scales as species may be replaced by other intraspecific or interspecific genotypes that occupy phenological niches more efficiently. To better understand the roles of day length, stress and sink limitation in mediating the phenology–growth relationship, it will be key to further examine a variety of species from different climatic and phylogenetic backgrounds.

AUTHORS' CONTRIBUTIONS

C.M.Z. conceived and developed the study, conducted the analyses and wrote the paper; C.M.Z. and V.S. performed the experiment; S.S.R. and T.W.C. provided input to the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All code and data are available at https://doi.org/10.5281/zenodo.4727525 (Zohner et al., 2021).

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REFERENCES

Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014, December). Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, *29*(12), 692–699. https://doi.org/10.1016/j.tree.2014.10.006

Bauerle, W. L., Oren, R., Way, D. A., Qian, S. S., Stoy, P. C., Thornton, P. E., Bowden, J. D., Hoffman, F. M., & Reynolds, R. F. (2012). Photoperiodic regulation of the seasonal pattern of photosynthetic capacity and the implications for carbon cycling. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(22), 8612–8617. https://doi.org/10.1073/pnas.1119131109

Baumgarten, F., Zohner, C., Gessler, A., & Vitasse, Y. (2021). Chilled to be forced: The best dose to wake up buds from winter dormancy. *New Phytologist*, *230*(4), 1366–1377. https://doi.org/10.1111/nph.17270

Chen, M., Melaas, E. K., Gray, J. M., Friedl, M. A., & Richardson, A. D. (2016). A new seasonal-deciduous spring phenology submodel in the Community Land Model 4.5: Impacts on carbon and water cycling under future climate scenarios. *Global Change Biology*, *22*(11), 3675–3688. https://doi.org/10.1111/gcb.13326

Choi, R. T., Beard, K. H., Leffler, A. J., Kelsey, K. C., Schmutz, J. A., & Welker, J. M. (2019). Phenological mismatch between season advancement and migration timing alters Arctic plant traits. *Journal of Ecology*, *107*(5), 2503–2518. https://doi.org/10.1111/1365-2745.13191

Cleland, E. E., Allen, J. M., Crimmins, T. M., Dunne, J. A., Pau, S., Travers, S. E., Zavaleta, E. S., & Wolkovich, E. M. (2012). Phenological tracking enables positive species responses to climate change. *Ecology*, *93*(8), 1765–1771. https://doi.org/10.1890/11-1912.1

Dox, I., Gričar, J., Marchand, L. J., Leys, S., Zuccarini, P., Geron, C., Prislan, P., Mariën, B., Fonti, P., Lange, H., Peñuelas, J., Van den Bulcke, J., & Campioli, M. (2020). Timeline of autumn phenology in temperate deciduous trees. *Tree Physiology*, *40*(8), 1001–1013. https://doi.org/10.1093/treephys/tpaa058

Duursma, R. A. (2015). Plantecophys – An R package for analysing and modelling leaf gas exchange data. *PLoS ONE*, *10*(11), e0143346. https://doi.org/10.1371/journal.pone.0143346

Fridley, J. D. (2012). Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature*, *485*(7398), 359–362. https://doi.org/10.1038/nature11056

Fu, Y. S. H., Campioli, M., Vitasse, Y., De Boeck, H. J., Van den Berge, J., AbdElgawad, H., Asard, H., Piao, S., Deckmyn, G., & Janssens, I. A. (2014). Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(20), 7355–7360. https://doi.org/10.1073/pnas.1321727111

Fu, Y. H., Piao, S., Delpierre, N., Hao, F., Hänninen, H., Geng, X., Peñuelas, J., Zhang, X., Janssens, I. A., & Campioli, M. (2019). Nutrient availability alters the correlation between spring leaf-out and autumn leaf senescence dates. *Tree Physiology*, *39*(8), 1277–1284. https://doi.org/10.1093/treephys/tpz041

Fu, Y. H., Piao, S., Delpierre, N., Hao, F., Hänninen, H., Liu, Y., Sun, W., Janssens, I. A., & Campioli, M. (2018). Larger temperature response of autumn leaf senescence than spring leaf-out phenology. *Global Change Biology*, *24*(5), 2159–2168. https://doi.org/10.1111/gcb.14021

Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas, J., Song, Y., Vitasse, Y., Zeng, Z., & Janssens, I. A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, *526*, 104. https://doi.org/10.1038/nature15402

Genet, H., Bréda, N., & Dufrêne, E. (2009). Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiology*, *30*(2), 177–192. https://doi.org/10.1093/treephys/tpp105

Hermans, C., Hammond, J. P., White, P. J., & Verbruggen, N. (2006, December). How do plants respond to nutrient shortage by biomass allocation? *Trends in Plant Science*, *11*(12), 610–617. https://doi.org/10.1016/j.tplants.2006.10.007

Keenan, T. F., Gray, J., Friedl, M. A., Toomey, M., Bohrer, G., Hollinger, D. Y., Munger, J. W., O'Keefe, J., Schmid, H. P., Wing, I. S., Yang, B., & Richardson, A. D. (2014). Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, *4*(7), 598–604. https://doi.org/10.1038/nclimate2253

Keenan, T. F., & Richardson, A. D. (2015). The timing of autumn senescence is affected by the timing of spring phenology: Implications for predictive models. *Global Change Biology*, *21*(7), 2634–2641. https://doi.org/10.1111/gcb.12890

Kerstiens, G. (1995). Cuticular water permeance of European trees and shrubs grown in polluted and unpolluted atmospheres, and its relation to stomatal response to humidity in beech (*Fagus sylvatica* L.). *New Phytologist*, *129*(3), 495–503. https://doi.org/10.1111/j.1469-8137.1995.tb04320.x

Körner, C. (2003). Carbon limitation in trees. *Journal of Ecology*, *91*(1), 4–17. https://doi.org/10.1046/j.1365-2745.2003.00742.x

Kumar, R., Bishop, E., Bridges, W. C., Tharayil, N., & Sekhon, R. S. (2019). Sugar partitioning and source–sink interaction are key determinants of leaf senescence in maize. *Plant, Cell & Environment*, *42*(9), 2597–2611. https://doi.org/10.1111/pce.13599

Kuptz, D., Fleischmann, F., Matyssek, R., & Grams, T. E. E. (2011). Seasonal patterns of carbon allocation to respiratory pools in 60-yr-old deciduous (*Fagus sylvatica*) and evergreen (*Picea abies*) trees assessed via whole-tree stable carbon isotope labeling. *New Phytologist*, *191*(1), 160–172. https://doi.org/10.1111/j.1469-8137.2011.03676.x

Lim, P. O., Kim, H. J., & Gil Nam, H. (2007). Leaf Senescence. *Annual Review of Plant Biology*, *58*(1), 115–136. https://doi.org/10.1146/annurev.arplant.57.032905.105316

Livensperger, C., Steltzer, H., Darrouzet-Nardi, A., Sullivan, P. F., Wallenstein, M., & Weintraub, M. N. (2016). Earlier snowmelt and

warming lead to earlier but not necessarily more plant growth. *AoB Plants*, 8, 1–15. https://doi.org/10.1093/aobpla/plw021

Luo, Y. (2007, December). Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology, Evolution, and Systematics*, 38(1), 683–712. https://doi.org/10.1146/annurev.ecolsys.38.091206.095808

Matamala, R., Gonzàlez-Meler, M. A., Jastrow, J. D., Norby, R. J., & Schlesinger, W. H. (2003). Impacts of fine root turnover on forest NPP and Soil C sequestration potential. *Science*, 302(5649), 1385–1387. https://doi.org/10.1126/science.1089543

McCormack, M. L., Gaines, K. P., Pastore, M., & Eissenstat, D. M. (2015). Early season root production in relation to leaf production among six diverse temperate tree species. *Plant and Soil*, 389(1–2), 121–129. https://doi.org/10.1007/s11104-014-2347-7

Morecroft, M. D., & Roberts, J. M. (1999). Photosynthesis and stomatal conductance of mature canopy Oak (*Quercus robur*) and Sycamore (*Acer pseudoplatanus*) trees throughout the growing season. *Functional Ecology*, 13(3), 332–342. https://doi.org/10.1046/j.1365-2435.1999.00327.x

Natali, S. M., Schuur, E. A. G., & Rubin, R. L. (2012). Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *Journal of Ecology*, 100(2), 488–498. https://doi.org/10.1111/j.1365-2745.2011.01925.x

Paul, M. J., & Foyer, C. H. (2001). Sink regulation of photosynthesis. *Journal of Experimental Botany*, 52(360), 1383–1400. https://doi.org/10.1093/jexbot/52.360.1383

Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., Margolis, H., Fang, J., Barr, A., Chen, A., Grelle, A., Hollinger, D. Y., Laurila, T., Lindroth, A., Richardson, A. D., & Vesala, T. (2008). Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, 451(7174), 49–52. https://doi.org/10.1038/nature06444

Polgar, C. A., & Primack, R. B. (2011). Leaf-out phenology of temperate woody plants: From trees to ecosystems. *New Phytologist*, 191(4), 926–941. https://doi.org/10.1111/j.1469-8137.2011.03803.x

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012, January). Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytologist*, 193(1), 30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Radville, L., McCormack, M. L., Post, E., & Eissenstat, D. M. (2016). Root phenology in a changing climate. *Journal of Experimental Botany*, 67(12), 3617–3628. https://doi.org/10.1093/jxb/erw062

Reich, P. B. (2002). Root-shoot relations: Optimality in acclimation and adaptation or the "Emperor's new clothes"? In *Plant roots: The hidden half* (3rd ed., pp. 205–220). Marcel Dekker Inc.

Reich, P. B., Luo, Y., Bradford, J. B., Poorter, H., Perry, C. H., & Oleksyn, J. (2014). Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the National Academy of Sciences of the United States of America*, 111(38), 13721–13726. https://doi.org/10.1073/pnas.1216053111

Richardson, A. D., Andy Black, T., Ciais, P., Delbart, N., Friedl, M. A., Gobron, N., Hollinger, D. Y., Kutsch, W. L., Longdoz, B., Luyssaert, S., Migliavacca, M., Montagnani, L., William Munger, J., Moors, E., Piao, S., Rebmann, C., Reichstein, M., Saigusa, N., Tomelleri, E., ... Varlagin, A. (2010). Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3227–3246. https://doi.org/10.1098/rstb.2010.0102

Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M. (2013). Climate change, phenology, and phenological

control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169(February), 156–173. https://doi.org/10.1016/j.agrformet.2012.09.012

Signarbieux, C., Toledano, E., Sanginés de Carcer, P., Fu, Y. H., Schlaepfer, R., Buttler, A., & Vitasse, Y. (2017). Asymmetric effects of cooler and warmer winters on beech phenology last beyond spring. *Global Change Biology*, 23(11), 4569–4580. https://doi.org/10.1111/gcb.13740

Steinaker, D. F., Wilson, S. D., & Peltzer, D. A. (2010). Asynchronicity in root and shoot phenology in grasses and woody plants. *Global Change Biology*, 16(8), 2241–2251. https://doi.org/10.1111/j.1365-2486.2009.02065.x

Vitasse, Y. (2013). Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist*, 198(1), 149–155. https://doi.org/10.1111/nph.12130

Way, D. A., & Oren, R. (2010). Differential responses to changes in growth temperature between trees from different functional groups and biomes: A review and synthesis of data. *Tree Physiology*, 30(6), 669–688. https://doi.org/10.1093/treephys/tpq015

White, M. A., Thornton, P. E., Running, S. W., & Nemani, R. R. (2000). Parameterization and sensitivity analysis of the BIOME–BGC terrestrial ecosystem model: Net primary production controls. *Earth Interactions*, 4(3), 1–85. https://doi.org/10.1175/1087-3562(2000)004<0003:pasaot>2.0.co;2

Woo, H. R., Kim, H. J., Lim, P. O., & Nam, H. G. (2019). Leaf senescence: Systems and dynamics aspects. *Annual Review of Plant Biology*, 70(1), 347–376. https://doi.org/10.1146/annurev-arplant-050718-095859

Zani, D., Crowther, T. W., Mo, L., Renner, S. S., & Zohner, C. M. (2020). Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees. *Science*, 370, 1066–1071. https://doi.org/10.1126/science.abd8911

Zhang, Y., Commane, R., Zhou, S., Williams, A. P., & Gentine, P. (2020). Light limitation regulates the response of autumn terrestrial carbon uptake to warming. *Nature Climate Change*, 10(8), 739–743. https://doi.org/10.1038/s41558-020-0806-0

Zohner, C. M., Benito, B. M., Svenning, J. C., & Renner, S. S. (2016). Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change*, 6(12), 1120–1123. https://doi.org/10.1038/nclimate3138

Zohner, C. M., Mo, L., Pugh, T. A. M., Bastin, J. F., & Crowther, T. W. (2020). Interactive climate factors restrict future increases in spring productivity of temperate and boreal trees. *Global Change Biology*, 26, 4042–4055. https://doi.org/10.1111/gcb.15098

Zohner, C. M., & Renner, S. S. (2014). Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. *Ecology Letters*, 17(8), 1016–1025. https://doi.org/10.1111/ele.12308

Zohner, C. M., & Renner, S. S. (2017). Innately shorter vegetation periods in North American species explain native-non-native phenological asymmetries. *Nature Ecology and Evolution*, 1(11), 1655–1660. https://doi.org/10.1038/s41559-017-0307-3

Zohner, C. M., & Renner, S. S. (2019). Ongoing seasonally uneven climate warming leads to earlier autumn growth cessation in deciduous trees. *Oecologia*, 189(2), 549–561. https://doi.org/10.1007/s00442-019-04339-7

Zohner, C. M., Renner, S. S., Sebald, V., & Crowther, T. W. (2021). Data from: How changes in spring and autumn phenology translate into growth - experimental evidence of asymmetric effects [dataset]. *Zenodo*, https://doi.org/10.5281/zenodo.4727525

Zohner, C. M., Rockinger, A., & Renner, S. S. (2019). Increased autumn productivity permits temperate trees to compensate for spring frost

damage. *New Phytologist*, *221*, 789–795. https://doi.org/10.1111/nph.15445

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.