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Research

# Increased autumn productivity permits temperate trees to compensate for spring frost damage

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## Summary

- Climate warming is leading to earlier budburst and therefore an increased risk of spring frost injury to young leaves. But to what extent are second-cohort leaves, which trees put out after leaf-killing frosts, able to compensate incurred losses?
- To investigate whether second-cohort leaves behave differently from first-cohort leaves, we exposed saplings of beech (*Fagus sylvatica*), oak (*Quercus robur*), and honeysuckle (*Lonicera xylosteum*) to experimental treatments mimicking either a warm spring or a warm spring with a leaf-killing frost.
- Refoliation took 48, 43, and 36 d for beech, oak and honeysuckle, respectively. In beech and oak, autumn Chl content and photosynthesis rates were higher in second- than in first-cohort leaves, senescence in second-cohort leaves occurred *c*. 2-wk-later, and autumn bud growth in beech was elevated 66% in frost-damaged plants compared with the warm spring treatment. No differences in autumn phenology and growth were observed for honeysuckle.
- Overall, in beech and oak, delayed Chl breakdown in second-cohort leaves mitigated 31% and 25%, respectively, of the deficit in growing-season length incurred by spring frost damage. These results reveal an unexpected ability of second-cohort leaves of beech and oak to compensate for spring frost damage, and demonstrate that long-lived trees vary their autumnal phenology depending on preceding productivity.

## Introduction

The most critical extreme-temperature event for temperate zone woody plants is late frost, that is, below-zero temperatures following conditions that allowed spring leaves to be pushed out. Neither winter minimum temperatures nor early autumn frosts are as critical as spring frosts because dormant buds can withstand low temperatures. It is therefore the frequency of late spring frosts that largely shapes the northern distribution limit of trees (Cannell *et al.*, 1985; Heide, 1993; Lenz *et al.*, 2013, 2016a,b; Kollas *et al.*, 2014; Vitasse *et al.*, 2014b; Muffler *et al.*, 2016).

Counterintuitively, the selective importance of frost damage to young leaves is increasing with the ongoing rapid climate warming: the earlier a species' leaf-out, the more often its young leaves will be exposed to late spring frosts (Cannell & Smith, 1986; Hänninen, 1991), and there is evidence from both North America and Europe that this is happening (Augspurger, 2013; Liu *et al.*, 2018; Vitasse *et al.*, 2018). Thus, warmer spring temperatures and greater temperature fluctuations have led to greater frost damage in 20 woody species monitored from 1993 to 2012 in Champaign County, Illinois, USA (Augspurger, 2013), and in the Swiss Alps, spring frost risk has increased in four tree species monitored from 1975 to 2016 (Vitasse *et al.*, 2018). Once frost damage to the young leaves has occurred, rapid reflushing is key, and depending on species, this takes 16–34 d (Augspurger, 2009). Photosynthesis, growth, and bud set should all be set back severely, and indeed, studies comparing individual tree-ring widths in *Fagus sylvatica* between years with and without frost damage have shown that the loss of the first cohort of leaves (and growing a second cohort) delayed seasonal wood formation and reduced annual ring width in the same year (Dittmar *et al.*, 2006; Príncipe *et al.*, 2017). In 2007, a severe late frost event reduced gross ecosystem productivity by 7–14% across 8753 $km^2$ of high-elevation North American forest (Gu *et al.*, 2008; Hufkens *et al.*, 2012).

Despite such setbacks as a result of frost damage, ring width in the year following the frost damage in *F. sylvatica* is comparable to 'normal' years (Príncipe *et al.*, 2017). This is unexpected because, as a determinate-growth species, the number of leaves that are put out in one season (and thus the amount of photosynthetically active tissue) is completely determined by previous years' bud growth (Cochard *et al.*, 2005; Zohner & Renner, 2018), which should have been highly reduced as a result of frost damage. This raises the question as to whether trees employ compensatory mechanisms, such as extended autumn activity, to mitigate growth losses induced by spring frost damage. Second sets of leaves produced after the first cohort has been killed, for example, might not undergo senescence at the same time as the first

cohort would have, allowing trees to stay photosynthetically active later into the fall.

The answer to this question is not self-evident because bud set and leaf senescence are largely controlled by declining day length after the summer solstice (Wareing, 1956; Cooke *et al.*, 2012). In species where this is the case, delaying autumn leaf senescence to compensate for frost damage in spring may not be possible. Recent studies, however, have shown that in some species, the timing of preceding phenological stages modifies the timing of autumn phenology (Fu *et al.*, 2014; Keenan & Richardson, 2015; Liu *et al.*, 2016; Signarbieux *et al.*, 2017). In the northeastern United States, monitoring of American beech (*F. grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*) revealed that earlier/later spring leaf-out was associated with earlier/later autumn senescence, but the trees had not experienced frost damage. To our knowledge, Augspurger's (2009) observations of spring frost damage to young tree leaves in Illinois are the only data on the senescence behaviour of second-cohort leaves. Comparisons of senescence dates in a year in which trees experienced frost damage and grew a second cohort of leaves to senescence dates in 3 yr without spring frost showed that second-cohort leaves in *Celtis* and *Quercus* senesced 2–3 wk later than first-cohort leaves, while second-cohort leaves of *Aesculus glabra* senesced 3 wk earlier than first-cohort leaves (but all in different years).

Here, we set out to test whether growth deficits incurred by spring frost damage can be mitigated by increased autumn productivity. To directly compare first- and second-cohort leaves in the same year, we carried out experiments on saplings of beech (*F. sylvatica*), oak (*Q. robur*), and honeysuckle (*Lonicera xylosteum*) in which we could manipulate all leaves and measure growth, photosynthesis, Chl content, and bud set throughout the season. Saplings of the three species, two of them dominant European trees, the other an understorey shrub, were exposed to experimental treatment that mimicked a 'normal' spring, a warm spring, or a warm spring with a leaf-killing frost (Fig. 1). Our study presents the first experimental approach to study how the physiology of first- and second-cohort leaves may differ.

## Materials and Methods

### Treatments

The experiment was conducted in the Munich Botanical Garden (48°09′N, 11°30′E; 501 m above sea level (asl)) between February and December 2017 on 3-yr-old saplings of beech (*Fagus sylvatica*), oak (*Quercus robur*), and honeysuckle (*Lonicera xylosteum*). Thirty individuals per species were exposed to three treatments, and the effects on phenology and growth then followed until winter. Plants were obtained from a local nursery in autumn 2016, transferred to plastic pots (40 × 40 cm) with sandy soil, and kept outdoors under uniform conditions until the start of the experiment (1 February 2017). Throughout the experiment, pots were watered once or twice a week to keep soil moisture constant.

Ten individuals per species were kept at ambient conditions (± 0°C) outdoors (unmodified spring treatment). Twenty individuals per species were exposed to conditions 4°C warmer than the outside air temperature in a climate-controlled glasshouse with an openable top from 1 February 2017 until all individuals had leafed out (Fig. 1). The glasshouse provided a stable warming treatment, and actual warming was within ± 20-% of the prescribed value. Day length and light intensity in the glasshouse did not differ from outdoor conditions. After full leaf expansion in all individuals (honeysuckle, 28 March; oak, 10 May; beech, 15 May), 10 of the 20 individuals were transferred to ambient conditions outdoors (warm spring treatment), while the other 10 were exposed to a simulated leaf-killing frost event destroying all newly formed leaves before being moved outside (warm spring + frost treatment). To carry out the frost treatment, we used a customized commercial freezer, with freezing and rethawing rate of 10 K $h^{-1}$, and kept samples for 1 h at the target freezing temperature. For each species, a temperature *c.* 2°C below the reported $LT_{50}$ values (Lenz *et al.*, 2013) was chosen as target freezing temperature to ensure 100% leaf frost damage in all individuals (−14.0°C for *L. xylosteum*, −8.2°C for *Q. robur*, and −6.8°C for *F. sylvatica*). During summer and autumn, individuals were kept under uniform conditions, arranged in a randomized block design; each block consisted of one individual from each of the three treatments.

### Phenological observations, leaf seasonal index, and bud development measurements

Observations and trait measurements were made on all 30 individuals for each of the three species. Leaf-out observations were conducted twice a week in spring 2017. A bud was considered as having leafed out when its leaves had unfolded and pushed out all the way to the petiole. The day on which three branches on a

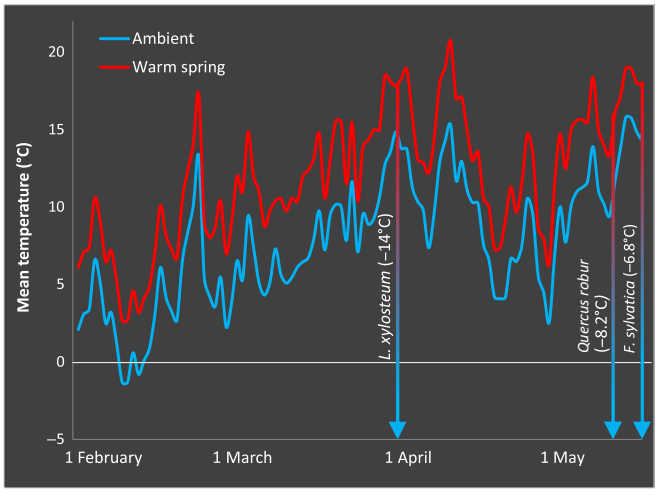


**Fig. 1** Temperature profiles (daily mean air temperatures) of the three treatments applied in this study. Individuals in the warm spring treatment and the frost treatment (red line ± arrows) were both exposed to 4°C warmer spring temperatures than ambient (blue line), with those in the frost treatment in addition being exposed to a late frost that killed all their first-cohort leaves, forcing the production of a second cohort of leaves. Arrows indicate the dates at which killing frosts were applied to the respective species (minimum temperatures shown in brackets).

plant had leafed-out buds was considered that individual's leaf-out date (Zohner & Renner, 2014). For each individual, we also calculated the proportion of leafed-out buds by dividing the number of leafed-out buds by the number of total buds of an individual.

To quantify seasonal changes in Chl content in first- and second-cohort leaves, we measured the leaf spectral index (LSI) at, on average, 2 wk intervals during spring and autumn and 4 wk intervals during summer with a SPAD-502 Plus (Soil Plant Analysis Development, Minolta Camera Co., Ltd, Tokyo, Japan). Per individual, SPAD readings from 10 leaves selected at random were averaged. To calculate LSI per individual, we additionally included the percentage of opened buds in spring and leaf abscission in autumn for each individual, that is, the still-closed buds in spring or the already-dropped leaves in autumn have an LSI of 0. For example, an individual that lost already 50% of leaves with an LSI of 30 for the remaining leaves has a total LSI of 15 ($30 \times 0.5$). We defined individual leaf senescence as the date when LSI had decreased by 50% relative to maximum LSI in summer. Growing season length was defined as the period between leaf-out and leaf senescence.

In beech, the longest apical branch in each of the 30 individuals was labelled with coloured strings, and lengths of the three longest buds were then measured once per month during the 2017 growing season (from 8 June 2017 until 4 November 2017) (buds of the other two species were too small to take such measurements). From this, we calculated an average length per individual. Completion of bud set (hereafter referred to as bud set) was defined as the date on which the buds of an individual had reached > 95% 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, for example, 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.

### Seasonal photosynthesis

Net leaf photosynthetic rates were monitored three times in autumn (September, October, beginning of November) on one leaf of each individual using photosynthetic light curves (pulse-amplitude modulated (PAM) chlorophyll fluorometry; Walz, Effeltrich, Germany). To standardize temperature, measurements were taken on days with an air temperature between 16 and 20°C. We used a customized program that logged at 10 s intervals, starting with equilibration for 2 min at 800 µmol photon $m^{-2}$ $s^{-1}$ and 6 min at 66 µmol photon $m^{-2}$ $s^{-1}$, which preliminary trials in 2017 suggested was sufficient for leaf equilibration to different light intensities. Measurements were taken daily on a species-rotating basis between 09:00 and 12:00 h with replicate individuals of each species done on two consecutive days.

### Data analysis

The experiment followed a three-factor design with repeated measurements. The studied factors consisted of three treatments: unmodified spring temperatures, warm spring temperatures, and warm spring temperatures followed by a leaf-killing frost event, forcing the production of a second cohort of leaves (Fig. 1). The experimental and observational unit was a pot with a single individual. To test for differences among groups, an ANOVA was performed in case of homoscedastic, normally distributed vectors. A Kruskal–Wallis *H*-test was performed when a normal distribution and/or homoscedasticity could not be assumed. *Post hoc* analyses followed the same guidelines: in the case of homoscedastic, normally distributed vectors, we used a Tukey–Kramer test; when vectors were not normally distributed, the Kruskalmc method (multiple comparison after Kruskal–Wallis) was used (Siegel & Castellan, 1988). All analyses were performed in R 3.4.1 (R Core Team, 2018).

## Results

### Refoliation and seasonal activity of first- and second-cohort leaves

Refoliation occurred, on average, after 36 d in honeysuckle, 43 d in oak, and 48 d in beech (Fig. 2). In beech, six of 10 individuals recovered after the frost treatment (40% mortality rate), while in oak and honeysuckle, all 10 individuals survived. The leaf spectral index shows that second-cohort leaves of the tree species senesced significantly later than first-cohort leaves of the warm spring treatment, namely by 14 d in beech (Fig. 2f) and by 11 d in oak (Fig. 2e). In beech, second-cohort leaves senesced 10 d later than first-cohort leaves of the cold spring treatment (Fig. 2f). In beech and oak, second-cohort leaves also increased their autumn photosynthetic activity (Fig. 3b,c). In *L. xylosteum*, second-cohort leaves did not differ from first-cohort leaves in leaf senescence dates and autumn photosynthetic activity (Figs 2a,d, 3a).

When keeping autumn senescence dates constant (using the average senescence dates of all individuals within a species), the vegetation periods of second-cohort leaves in honeysuckle, oak, and beech were, respectively, 36 d (16%), 43 d (23%), and 47 d (26%) shorter than those of the warm spring treatment. When actual senescence dates of each treatment were used to calculate the length of the vegetation period, vegetation periods of second-cohort leaves were 32 d (15%), 32 d (17%), and 33 d (18%) shorter, respectively. In beech and oak, 31% and 25% of the vegetation period deficit of second-cohort leaves were thus mitigated by extended autumn phenology. In honeysuckle, autumn phenology did not mitigate spring frost deficits.

### Seasonal primary growth following a leaf-killing spring frost

For *F. sylvatica*, we quantified bud growth (length increment in mm) during spring/summer and autumn following the three treatments (Fig. 4). At the end of the year, bud lengths in the frost treatment and the unmodified spring treatment were reduced by 27% and 10% compared with the warm spring treatment (mean bud length after growth cessation: frost treatment, 11.7 mm; ambient spring treatment, 14.5 mm; warm spring

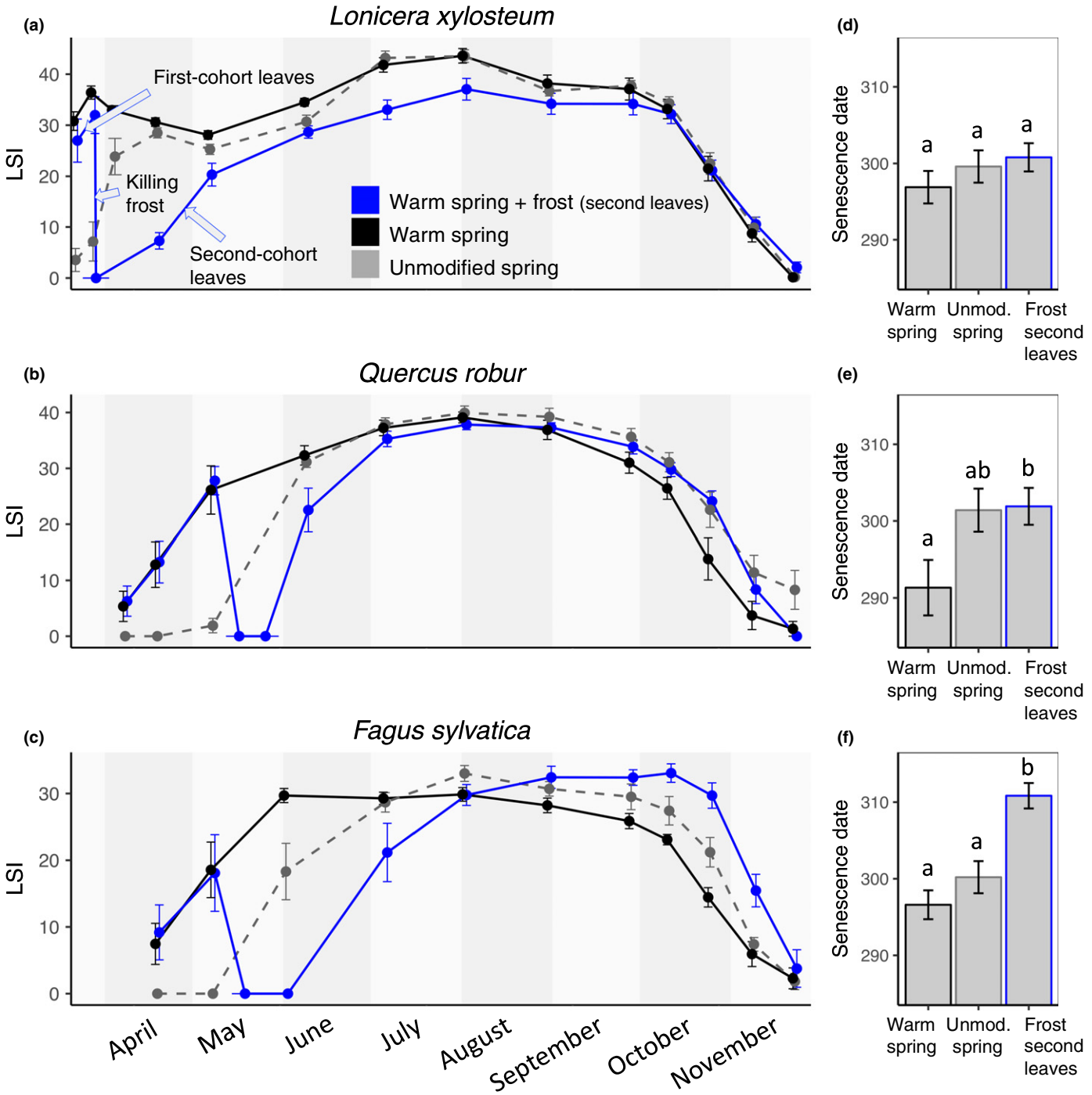


**Fig. 2** Leaf-spectral indices (LSI; mean ± SE) in 2017 under warm spring conditions (black circles and lines), warm spring conditions followed by a killing-frost event (second-cohort leaves; blue circles and lines), and unmodified spring conditions (grey circles and dashed grey lines) for: (a) *Lonicera xylosteum*, (b) *Quercus robur*, and (c) *Fagus sylvatica*. (d–f) Mean leaf senescence dates (50% Chl breakdown) ± SE for the three treatments. Different letters denote a significant difference (at $P < 0.05$). $n = 10$ individuals ($n = 6$ individuals for the frost treatment in *F. sylvatica* as a result of 40% mortality).

treatment, 16.0 mm). However, compared with the warm spring treatment, autumn bud growth was 66% (2.1 mm) higher in plants with second-cohort leaves (Fig. 4b), because bud set in the latter plants was delayed by 16 d compared with the warm spring treatment (Fig. 4c). Thus, while autumn growth (growth after 1 September) contributed only 20% to the final bud length in the warm spring treatment, it contributed 46% to final bud length in the plants that had lost their first-cohort leaves (Fig. 4b). In the ambient treatment, the contribution of autumn growth was intermediate (33%). Overall, 23% of the growth deficit was mitigated by extended autumn growth in plants with second-cohort leaves, because buds of the frost treatment continued to grow after buds of the spring warming treatment had already ceased growth, reducing the size difference between the treatments from 35% to 27%.

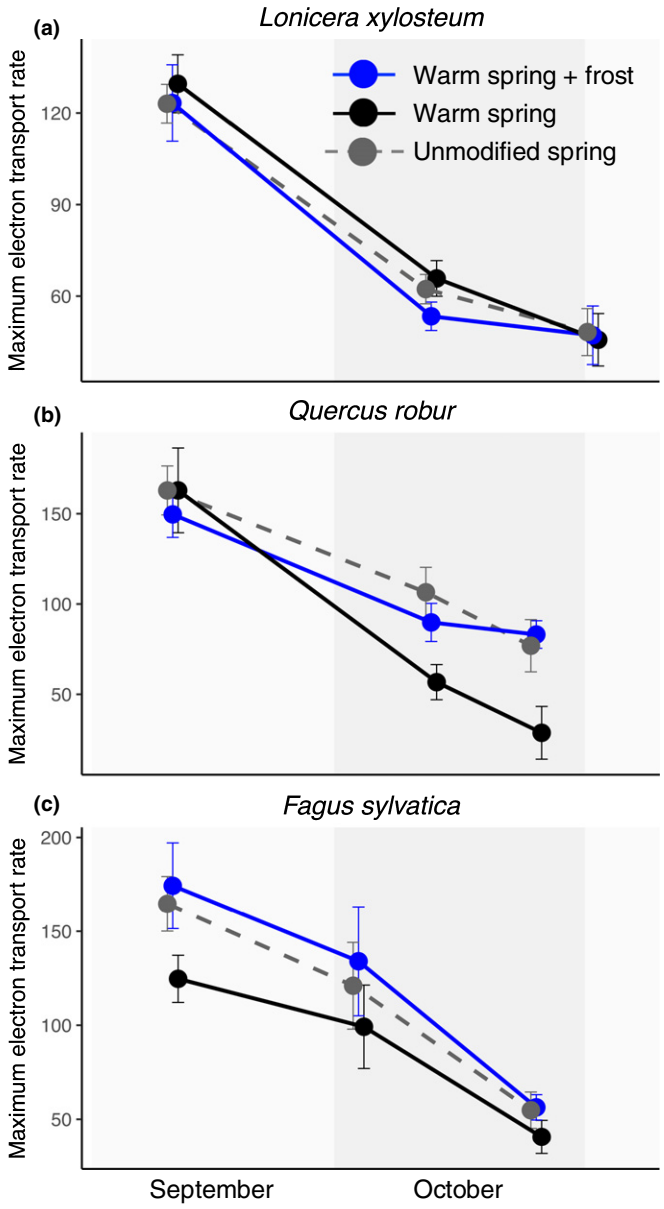


**Fig. 3** Late-season photosynthetic activity of (a) *Lonicera xylosteum*, (b) *Quercus robur*, and (c) *Fagus sylvatica* for the three treatments (warm spring, warm spring + frost (second-cohort leaves), and unmodified spring). Values are mean electron transport rates ± SE for each treatment. In *F. sylvatica* and *Q. robur*, maximum electron transport rates of the frost treatment were significantly higher compared with the warm spring treatment (linear mixed-effects model including date as a random effect: *F. sylvatica*, $P < 0.05$; *Q. robur*, $P < 0.05$; *L. xylosteum*, $P = 0.43$).

## Discussion

In response to global warming, spring leaf unfolding in temperate woody plants is shifting towards ever earlier dates (Zohner & Renner, 2014). As a result, the risk of young leaves being exposed to freezing temperatures is elevated in many regions (Augspurger, 2013; Liu *et al.*, 2018; Vitasse *et al.*, 2018). Studying how plants may compensate for spring tissue damage is therefore key to assessing the ecological consequences of an increasing frost damage risk. We investigated here the behaviour of first- and second-cohort leaves of saplings because young understorey trees leaf-out earlier than mature individuals and thus have a higher likelihood of experiencing frost damage (Vitasse, 2013; Vitasse *et al.*, 2014a). Also, young individuals are more vulnerable to frost damage than are mature trees. This is because long-lived trees will usually have the resources to be able to form several sets of leaves without this threatening their survival. For seedlings, having to form new leaves strongly increases mortality (Augspurger, 2013). In our experiments, only six out of 10 beech saplings recovered after the frost treatment (40% mortality rate). In oak and honeysuckle, all individuals survived the frost treatment.

We discovered an unexpected difference between the first leaves produced by beech and oak, and the new leaves produced after spring frost damage. In both species, the second-cohort leaves senesced *c.* 2 wk later than the first-cohort leaves (produced in the same year by control individuals exposed only to spring warming), which led to significantly elevated autumnal photosynthetic rates. Overall, 31% and 25% of the growing season deficits in beech and oak, respectively, were mitigated by delayed autumn senescence. Similar delayed autumn senescence has been found in North American species of *Celtis* and *Quercus*, but those observations were made on leaves produced in different years (Augspurger, 2009).

In beech, we also investigated seasonal primary growth patterns (bud development) and found that individuals affected by spring frost elevated autumn bud growth by 66% owing to a delay in bud set of 16 d compared with the warm spring reference (Fig. 4b,c). This demonstrates that the phenological delay in autumn directly compensates for summer growth deficits. That individuals exposed to cold spring conditions (without a killing frost) also showed elevated autumn bud growth and senesced their leaves later than individuals exposed to warm spring conditions, albeit to a lesser degree than individuals that experienced a spring frost (Figs 2c, 4b), shows that the onset of the growing season is a strong determinant of autumn phenology, highlighting internal phenological self-regulation. Thus, while most studies assume that autumn phenology is mainly triggered by external abiotic stimuli, such as decreasing day length, temperature, and water supply (Keskitalo *et al.*, 2005; Gallinat *et al.*, 2015), developmental carryover effects appear to be equally important and need to be considered in future projections of growing season length. To date, a limited carbohydrate storage capacity is the most likely mechanism explaining how trees can vary their autumn phenology despite uniform summer/autumn conditions (Fu *et al.*, 2014). In this study, beech buds with the smallest growth rates in spring/summer had the highest growth rates in autumn (Fig. 4b), providing evidence for preceding productivity (and thus carbon storage) being linked to autumn phenology. However, further studies on seasonal sugar content are needed to validate this.

A side-effect of later bud hardening and leaf senescence in autumn to compensate for spring frost damage is that leaves then face an increased risk of autumn frost damage. It is thus also possible that there is no maximum carbon-storage capacity *per se*,

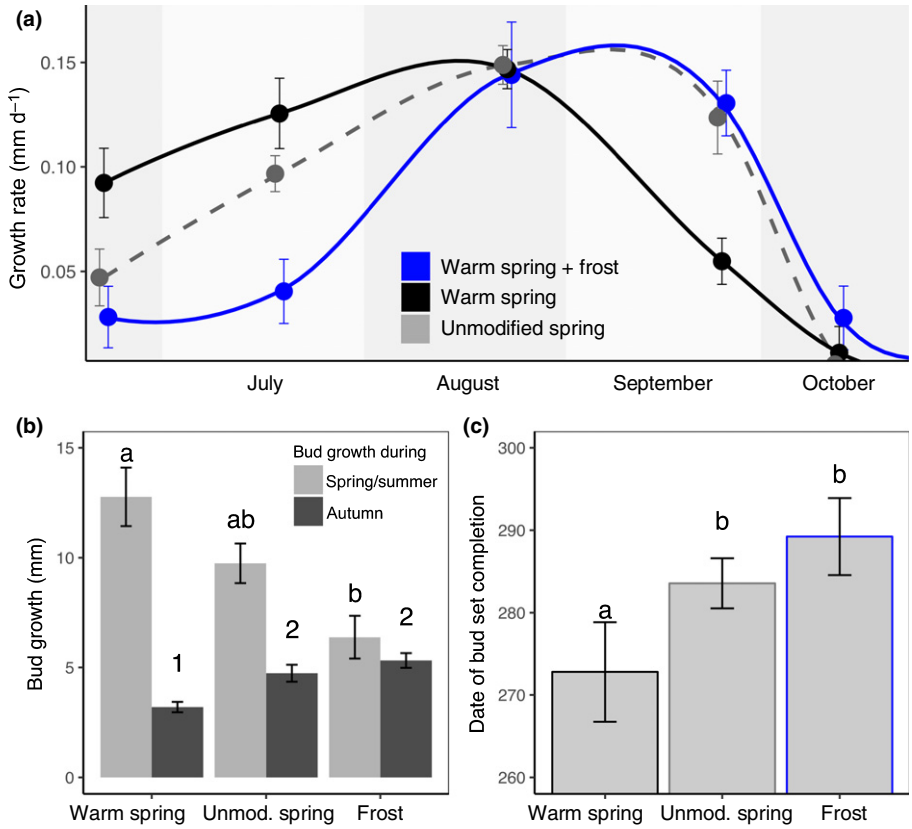


**Fig. 4** (a) Seasonal primary growth in *Fagus sylvatica* under warm spring conditions (black circles and lines), warm spring conditions followed by a killing-frost event (blue circles and lines), and unmodified spring conditions (grey circles and dashed grey lines). (b) Spring/summer and autumn (after 1 September) bud growth. Bud length increment (in mm) before and after 1 September. (c) Bud set dates (day of year when buds reached > 95% of their final size) for the control, cold spring, and late-frost treatment. Values are means ± SE for each treatment. Overall model fit: $R^2 = 0.38$ ($F$-value = 6.61 with 22 df). Different letters denote a significant difference ($P < 0.05$). $n = 10$ individuals per treatment ($n = 6$ individuals for the frost treatment in *F. sylvatica* as a result of 40% mortality).

but that the tradeoff between reduced autumn activity/autumn frost risk and increased autumn activity/autumn frost risk has led to the evolution of finely tuned carryover effects allowing trees to adjust their autumn phenology to preceding amounts of carbon storage.

Spring frost damage had no effect on autumn phenology in honeysuckle, and the second-cohort leaves in this species were produced *c.* 1 wk faster than in beech and oak (after 36 d, on average, compared with after 48 and 43 d; Fig. 2). As is typical for understorey shrubs, honeysuckle undergoes leaf-out very early (*c.* 1 month earlier than oak and beech) and produces several flushes per season (polycyclism), which could be crucial parameters in refoliation and explain the missing carryover effects between spring and autumn phenology. Also, because of its early onset and comparably fast refoliation, frost damage-induced losses in growing season length were smaller than in oak and beech despite no delays in autumn phenology (15%, 17% and 18% loss, respectively). Given the high frost tolerance of honeysuckle ($LT_{50}$ *c.* −12°C), frost damage in this species might be less common than in beech and oak. On the other hand, strong advances in leaf unfolding can be expected in the future (no/minimal chilling or day-length constraints; Zohner *et al.*, 2017), possibly increasing the frequency of lethal spring temperatures that honeysuckle leaves will experience.

## Conclusions

This study is the first to experimentally compare first- and second-cohort (i.e. reflushed) leaves and provides insights into the ability of two dominant tree species to compensate for frost damage to their first cohort of leaves. In oak and beech, some 31% and 25% of the growing season deficits incurred by frost damage were mitigated by the delayed senescence of their second-cohort leaves. Autumn phenology remains less understood than spring phenology. Our study now underscores earlier evidence that the autumnal phenology of long-lived trees varies depending on preceding productivity (Fu *et al.*, 2014; Keenan & Richardson, 2015; Zohner & Renner, 2018).

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## Author contributions

CMZ planned and designed the research. CMZ and AR performed the experiment and analysed data. CMZ, AR and SSR wrote the manuscript.

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