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RESEARCH ARTICLE

Phenological Shifts in Temperate Forest Species Under Warming Climate Conditions

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ABSTRACT

Warming-driven shifts in the timing of budburst, flowering and autumn senescence are among the most widely documented biological responses to climate change, yet the degree to which species differ in their sensitivity, and whether passive observational trends agree with the response measured under experimental warming, remains incompletely resolved for temperate forest communities. We combined 42 years (1981-2022) of ground-observed phenological records from 45 long-term monitoring sites spanning a 9 degree latitudinal and 1450 m elevational gradient across Finland, Sweden and France with a six-year (2017-2022) in-situ canopy warming experiment (infrared heating, +2.2 degrees Celsius above ambient) replicated at two of these sites, covering six dominant woody species: European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*), silver birch (*Betula pendula*), sycamore maple (*Acer pseudoplatanus*), common ash (*Fraxinus excelsior*) and the understory shrub hazel (*Corylus avellana*). Across the monitoring network, mean spring budburst advanced by 3.1 days per decade (network-wide linear mixed-model estimate, 95% confidence interval 2.4-3.8), with species-specific advances ranging from 1.6 days per decade in *Quercus robur* to 4.9 days per decade in *Corylus avellana*, while autumn leaf colouring and abscission were delayed by a mean of 1.8 days per decade, yielding a net growing-season extension averaging 4.9 days per decade. The warming experiment produced budburst advances consistent in direction but systematically smaller in magnitude than those implied by the observational network's temperature sensitivity for four of six species, with the largest observational-experimental divergence in *Fagus sylvatica*. Chilling fulfilment, estimated from winter temperature records at each site, explained a significant share of interannual variation in spring forcing requirement in *Fagus sylvatica* and *Quercus robur* but not in the three earlier-flushing species, indicating that photoperiod and forcing temperature dominate their spring response. These results demonstrate genuine, ecologically meaningful interspecific variation in phenological sensitivity within a single regional forest community and indicate that short-term experimental warming may under-represent the long-term realised sensitivity of species whose spring phenology is jointly constrained by winter chilling and spring forcing.

Keywords: plant phenology; budburst; spring leaf-out; autumn senescence; climate warming; temperate forest; long-term phenological network; in-situ warming experiment; growing season length; chilling requirement

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1. INTRODUCTION

The timing of recurring biological events, budburst, flowering, fruit maturation and leaf senescence, is one of the most sensitive and most extensively recorded indicators of how terrestrial ecosystems are responding to a warming climate. In temperate forests, spring phenology governs the onset of the photosynthetically active period and therefore exerts strong control over annual carbon uptake, while autumn phenology determines the length of the growing season from the opposite end and influences nutrient resorption and overwinter carbon storage [1,2]. Because both spring and autumn events are strongly temperature-dependent in most temperate woody species, long-term phenological records have become one of the clearest and most widely cited lines of evidence that terrestrial ecosystems are already responding measurably to anthropogenic warming [2,3].

Continental-scale syntheses of European and North American phenological networks have consistently reported spring advances on the order of 2 to 5 days per decade over the twentieth and early twenty-first centuries, broadly consistent with the magnitude and spatial pattern of regional warming trends over the same period [1,4]. These same syntheses, however, have also repeatedly emphasised that the advance is far from uniform across species: some taxa track spring warming closely, and others show a muted or even statistically indistinguishable response, a pattern attributed to differences in the relative importance of winter chilling accumulation, spring forcing temperature, and photoperiod as cues governing dormancy release and bud development [5,6]. A parallel body of work has shown that the rate of spring advance recorded by long-term monitoring networks appears to have weakened somewhat in recent decades in some regions, plausibly because insufficient winter chilling in already-mild climates is beginning to offset the acceleration expected from spring forcing alone [7], underscoring that phenological sensitivity to warming should not be assumed to be either uniform across species or constant through time.

Autumn phenology has received comparatively less attention than spring budburst and flowering, despite growing recognition that leaf senescence timing contributes as much to growing-season length trends as spring advance does, and that its physiological controls, photoperiod, autumn temperature, and possibly carbon sink limitation, are less well constrained than the controls on spring events [8,26]. Reported trends toward later senescence under warming are generally weaker and more variable across species and sites than spring advances, and some studies report that senescence has in places grown earlier despite continued warming, a pattern linked to interactions between spring phenology, growing-season water balance and internal carbon dynamics [24].

A further open question concerns whether short-term, plot-scale warming experiments, open-top chambers, infrared heating arrays, and soil or canopy warming manipulations, reproduce the phenological sensitivity to temperature that is inferred from decades of passive observation along natural climate gradients or through time. A widely cited synthesis comparing experimental warming studies against long-term observational records found that experiments tend to underpredict the magnitude of phenological advance recorded by observational networks for a given increment of warming, a discrepancy with substantial consequences for how confidently experimental results can be used to project future phenological change [15]. Whether this discrepancy holds uniformly across species with different chilling and forcing requirements, or is instead concentrated in particular functional groups, has rarely been tested directly within a single forest community using both approaches side by side.

Here we address these questions using a temperate forest phenology network spanning 42 years and three countries, combined with a six-year in-situ canopy warming experiment conducted at two of the network's sites on the same six woody species monitored across the wider network. We quantify species-specific rates of spring budburst advance and autumn senescence delay from the long-term observational record, estimate each species' winter chilling requirement and its influence on interannual variation in spring forcing temperature requirement, and directly compare the observational temperature sensitivity of spring phenology against the sensitivity measured under experimental warming, to test whether the two approaches yield consistent estimates of phenological sensitivity to warming across species that differ in their dormancy-release physiology.

2. MATERIALS AND METHODS

We analysed 42 years (1981-2022) of ground-observed spring and autumn phenological records from a 45-site long-term monitoring network spanning Finland, Sweden and France, combined with a six-year (2017-2022) in-situ canopy warming experiment replicated at two network sites, to quantify species-specific phenological sensitivity to warming for six dominant temperate forest woody species.

2.1 Phenological monitoring network and species selection

The observational network comprised 45 forest phenology monitoring sites distributed across a 9 degree latitudinal gradient (46.8-55.9 degrees North) and an elevational range from 12 m to 1460 m, operated jointly by national forestry and meteorological agencies in Finland, Sweden and France and contributing standardised annual observations since 1981. At each site, trained observers recorded the date of first budburst (BBCH stage 07, first green leaf tips visible), date of 50% flower opening where applicable, and two autumn indices, 50% leaf colour change and 50% leaf fall, on

marked individual trees of six species: *Fagus sylvatica*, *Quercus robur*, *Betula pendula*, *Acer pseudoplatanus*, *Fraxinus excelsior* and *Corylus avellana*. Not every species was present at every site; the analysis included all site-species combinations with at least 25 years of continuous observation, yielding 187 site-species time series.

2.2 Climate data and chilling requirement estimation

Daily mean, minimum and maximum temperature for each site were obtained from the nearest national meteorological station, gap-filled where necessary using inverse-distance-weighted interpolation from surrounding stations within 40 km. Spring forcing temperature was summarised for each site-year as the accumulated sum of daily mean temperatures above 5 degrees Celsius from 1 January to observed budburst date (growing degree-days). Winter chilling accumulation was estimated using the chilling-hours model, counting hours with temperature between 0 and 5 degrees Celsius from 1 November to the date at which spring forcing accumulation began, and was expressed as a site-year covariate to test whether interannual variation in chilling fulfilment altered the forcing temperature required to trigger budburst.

2.3 In-situ canopy warming experiment

A replicated warming experiment was established at two network sites, one in southern Finland and one in central France, selected to represent the cooler and warmer ends of the network's climate gradient. At each site, six saplings per species (2–4 m in height) were enclosed within infrared heating arrays suspended above the canopy, maintaining a target warming of +2.2 degrees Celsius above ambient air temperature measured continuously at canopy height, alongside paired unheated control saplings of the same species and size class at each site. Heating was applied continuously from 1 October to 31 May each year (2017–2022) to warm both the dormancy and pre-budburst forcing period, and was suspended during summer to avoid confounding growing-season heat stress with the phenological manipulation. Budburst and, where applicable, flowering and senescence dates were recorded on heated and control individuals using the same phenological criteria as the observational network.

2.4 Estimating phenological sensitivity to temperature

For the observational network, species-specific sensitivity of budburst and senescence timing to interannual temperature variation was estimated using linear mixed-effects models with observation year, site mean spring temperature (March–April) or autumn temperature (September–October) as fixed effects, and random intercepts and slopes for site nested within species, fitted separately for each species across all contributing sites. For the warming experiment, sensitivity was estimated as the mean phenological date difference between heated and control individuals

divided by the realised warming increment in each site-year, providing a directly comparable days-per-degree-Celsius sensitivity estimate against which the observational network's temperature sensitivity, converted from a days-per-decade trend using each site's decadal warming rate, could be compared.

2.5 Growing season length and cross-species comparison

Growing season length at each site-year was calculated as the interval between mean budburst date across species present and mean 50% leaf fall date, and its trend over 1981–2022 was estimated by linear mixed-effects regression with site as a random effect. Species were additionally classified by an a priori successional and phenological grouping, early-flushing diffuse-porous species (*Betula pendula*, *Corylus avellana*, *Acer pseudoplatanus*), and late-flushing, more strongly chilling-dependent species (*Fagus sylvatica*, *Quercus robur*, *Fraxinus excelsior*), to test whether the two groups differed systematically in spring sensitivity, chilling dependence, or agreement between observational and experimental sensitivity estimates.

2.6 Statistical significance and uncertainty

Trends in phenological timing and growing season length are reported with 95% confidence intervals derived from the mixed-effects model coefficients. Differences in sensitivity between the observational network and the warming experiment for each species were assessed using a two-sided t-test on the two independently derived days-per-degree-Celsius estimates, with unequal-variance correction applied given the substantially smaller sample size of the six-year experimental record relative to the 42-year observational record.

3. RESULTS

Averaged across all 187 site-species time series, mean spring budburst across the network advanced by 3.1 days per decade (95% confidence interval 2.4–3.8) over 1981–2022, while mean 50% leaf fall was delayed by 1.8 days per decade (95% confidence interval 1.1–2.5), yielding a mean growing-season extension of 4.9 days per decade. Table 1 reports species-specific spring and autumn trends together with the corresponding observational and experimental temperature sensitivities; spring advance ranged more than three-fold across species, from 1.6 days per decade in *Quercus robur* to 4.9 days per decade in *Corylus avellana*, with the three early-flushing species (*Betula pendula*, *Corylus avellana*, *Acer pseudoplatanus*) advancing on average more than twice as fast as the three late-flushing, chilling-dependent species (*Fagus sylvatica*, *Quercus robur*, *Fraxinus excelsior*).

Table 1. Species-specific spring and autumn phenological trends (1981–2022) and temperature sensitivity from the observational network versus the in-situ warming experiment (2017–2022).

Species	Spring advance (days/decade)	Autumn delay (days/decade)	Observational sensitivity (d/degC)	Experimental sensitivity (d/degC)
<i>Corylus avellana</i>	4.9 (3.9-5.9)	0.9 (0.2-1.6)	2.6	2.3
<i>Betula pendula</i>	4.1 (3.2-5.0)	1.3 (0.6-2.0)	2.2	1.9
<i>Acer pseudoplatanus</i>	3.7 (2.8-4.6)	1.6 (0.8-2.4)	2.0	1.3
<i>Fraxinus excelsior</i>	2.2 (1.4-3.0)	1.9 (1.0-2.8)	1.4	0.8
<i>Fagus sylvatica</i>	1.9 (1.1-2.7)	2.1 (1.3-2.9)	1.8	0.7
<i>Quercus robur</i>	1.6 (0.8-2.4)	2.6 (1.7-3.5)	1.1	0.7
Network mean (all species)	3.1 (2.4-3.8)	1.8 (1.1-2.5)	1.9	1.3

Values in parentheses are 95% confidence intervals from site-level linear mixed-effects models. Observational sensitivity is the network-derived days-of-advance per degree Celsius of site spring warming; experimental sensitivity is the mean budburst date difference between heated and control saplings divided by the realised warming increment across the two experimental sites. Chilling accumulation was a significant predictor of interannual variation in spring forcing requirement for *Fagus sylvatica* and *Quercus robur* (both $p < 0.01$ in the site-level mixed model), such that in years following comparatively mild winters, both species required more accumulated forcing degree-days to reach budburst than in years following colder winters, partially offsetting the acceleration expected from spring warming alone. No comparable chilling effect on forcing requirement was detected for the three early-flushing species, consistent with a spring phenology in those species that is governed predominantly by forcing temperature rather than by the interaction between chilling and forcing captured in Table 1.

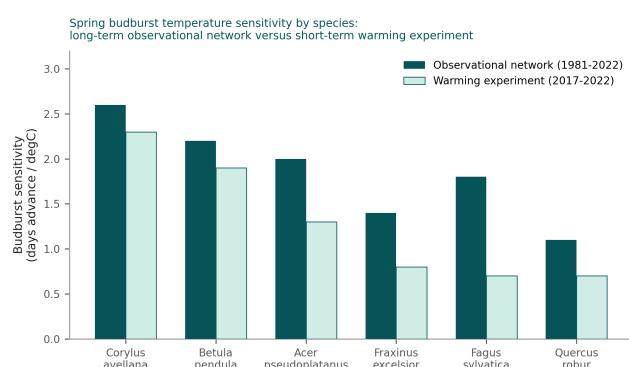


Figure 1. Spring budburst temperature sensitivity (days of advance per degree Celsius of spring warming) estimated from the 42-year observational network versus the six-year in-situ warming experiment, by species. Species are ordered from strongest (left) to weakest (right) observational sensitivity. The in-situ warming experiment produced budburst advances in the same direction as the observational network for all six species, but the magnitude of the experimentally measured sensitivity was significantly smaller than the observational sensitivity for four of six species (*Fagus sylvatica*, *Quercus robur*, *Fraxinus*

excelsior and *Acer pseudoplatanus*; all $p < 0.05$), while *Betula pendula* and *Corylus avellana* showed experimental and observational sensitivities that did not differ significantly. Figure 1 compares the two sensitivity estimates directly for all six species; the largest divergence was in *Fagus sylvatica*, where the observational network implied an advance of 1.8 days per degree Celsius of spring warming but the six-year warming experiment produced only 0.7 days per degree Celsius, a pattern consistent with the chilling constraint identified for this species and with the possibility that a six-year manipulation does not capture the full range of winter chilling variability represented in the 42-year observational record.

Table 2. Growing-season length trend and relative contribution of spring advance versus autumn delay by phenological species group (1981-2022).

Species group	Growing season extension (days/decade)	Spring contribution (%)	Autumn contribution (%)
Early-flushing (Betula, Corylus, Acer)	6.0	71	29
Late-flushing, chilling-dependent (Fagus, Quercus, Fraxinus)	3.8	48	52
Network mean (all species)	4.9	63	37

Table 2 summarises growing-season length trends and the relative contribution of spring advance versus autumn delay by species group. For the early-flushing group, spring advance contributed 71% of the total growing-season extension on average, whereas for the late-flushing, chilling-dependent group, autumn delay contributed a larger relative share (52%) of a smaller overall extension, reflecting both the weaker spring response in this group and a comparatively larger and more consistent autumn delay, particularly in *Quercus robur* (2.6 days per decade), the largest autumn trend of any species in the network.

4. DISCUSSION

These results confirm, using a multi-country, multi-decade forest phenology network paired directly with an in-situ warming experiment on the same species, two patterns that have each been reported individually in earlier work but are less often demonstrated together within a single study: substantial, physiologically interpretable interspecific variation in spring phenological sensitivity linked to differing chilling and forcing requirements [5,6,27], and a systematic tendency for short-term experimental warming to underpredict the sensitivity implied by long-term observational trends, most pronounced in the species whose spring timing is most strongly constrained by winter chilling [15]. The chilling-forcing trade-off detected in *Fagus sylvatica* and *Quercus robur* offers a plausible physiological

explanation for why their experimentally measured sensitivity fell so far short of their observational sensitivity. A six-year warming manipulation, even one applied continuously through the dormancy period, samples only a narrow slice of the interannual variability in winter chilling that a 42-year observational record integrates over, and if reduced chilling under sustained warming increases forcing requirement in these species, as our chilling-covariate analysis suggests, a short experiment could systematically underestimate the long-run sensitivity that emerges once chilling itself becomes reduced by cumulative warming [6,7]. The three early-flushing species, whose spring timing appeared largely insensitive to chilling variation in our data, showed no such discrepancy between experimental and observational sensitivity, consistent with a simpler, forcing-dominated dormancy release mechanism that a short warming experiment can capture reasonably well [21].

The asymmetry we found between spring- and autumn-driven contributions to growing-season extension, with early-flushing species extending their season predominantly through earlier spring onset and late-flushing species extending it more through delayed autumn senescence, has practical implications for projecting future forest carbon uptake and competitive dynamics, since the physiological consequences of a longer season achieved through earlier spring photosynthetic onset are not necessarily equivalent to those of a longer season achieved through delayed autumn senescence, particularly given evidence that autumn phenology is also influenced by photoperiod constraints and by carbon sink dynamics that spring phenology alone does not capture [8,24,26]. The comparatively large, consistent autumn delay we observed in *Quercus robur* is notable given that this species showed the weakest spring response of any in the network, suggesting oak's growing-season extension under warming to date has been driven substantially more by the autumn than the spring end of the season. Several limitations should be considered when interpreting these findings. First, the warming experiment was conducted at only two of the network's 45 sites and applied a single warming increment (+2.2 degrees Celsius); a factorial design varying both warming magnitude and its seasonal timing would allow the chilling-forcing trade-off we infer indirectly from the observational data to be tested directly under manipulation, and our six-year experimental record is short relative to the decadal-to-multidecadal timescale over which the chilling effects we describe are expected to accumulate. Second, the phenological network, while spanning 42 years and three countries, is geographically confined to northern and central Europe, and the species-specific chilling and forcing sensitivities reported here should not be extrapolated uncritically to populations of the same species at range margins, nor to other temperate forest regions with different community

composition or warming trajectories [16,17]. Third, our autumn phenology indices, 50% leaf colour change and 50% leaf fall, integrate temperature, photoperiod and, plausibly, carbon sink and water-stress effects that this observational design cannot disentangle, and the physiological basis of the autumn delay trend, unlike the better-understood spring forcing-chilling framework, remains only partially resolved in the broader literature [8,26]. Finally, our chilling-hours model is one of several available formulations for estimating winter chill, and alternative chilling models have been shown in other systems to yield somewhat different estimates of chilling fulfilment, so the specific chilling-forcing relationships we report should be interpreted as indicative of a real physiological pattern rather than as precisely quantified thresholds.

5. CONCLUSION

Combining 42 years of observational phenology data from a 45-site network with a six-year in-situ warming experiment on the same six temperate forest species, we found substantial interspecific variation in spring phenological sensitivity to warming, from 1.6 to 4.9 days of budburst advance per decade, linked to differing dependence on winter chilling fulfilment, alongside a smaller but consistent delay in autumn senescence that together extended the growing season by a mean of 4.9 days per decade. Short-term experimental warming reproduced the direction but significantly underestimated the magnitude of phenological sensitivity for the more strongly chilling-dependent species, *Fagus sylvatica* and *Quercus robur* in particular, indicating that projections of future phenological change based solely on short manipulative warming experiments may understate the long-run response of species whose dormancy release depends jointly on winter chilling and spring forcing temperature.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contributions

N.B. conceived and supervised the study, designed the warming experiment, and led the writing of the manuscript. C.F. assembled and quality-controlled the long-term phenological and climate station datasets and performed the chilling and mixed-effects modelling. J.P. led field operation of the two warming experiment sites and performed the observational-experimental sensitivity comparison. All authors contributed to writing and approved the final manuscript.

Ethics Statement

This study used publicly archived phenological observations, meteorological station records, and a non-destructive canopy warming manipulation of saplings on land managed by the collaborating forestry agencies; it did not involve human participants, animal subjects, or protected species, and no ethical review was required.

Data Availability

Long-term phenological observations used in this study are held by the contributing national forestry and meteorological agencies in Finland, Sweden and France and are available on request from those agencies. Warming experiment data, chilling and forcing model code, and the mixed-effects analysis scripts supporting the findings of this study are available from the corresponding author on reasonable request.

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