

Warming sensitivity of spring phenology of deciduous species lies in their bud energy budget

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29 **Spring phenology is mainly driven by temperature in extratropical ecosystems. Contrasting**
30 **responses of foliar phenology to climatic warming, however, have been reported in recent decades,**
31 **raising important questions about the role of other environmental constraints, especially light. In**
32 **fact, temperatures differ substantially between plant tissues and the air because plants absorb and**
33 **lose energy. Yet, phenology studies always substitute plant tissue temperature by air temperature.**
34 **Here, we explored how solar radiation, wind, and bud traits might affect spring phenology of**
35 **deciduous forests through the energy budget of buds. We show that air temperature might be an**
36 **imprecise and biased predictor of bud temperature. Our current interpretation of the plant**
37 **phenological response to warming should be reconsidered, which will require new observations of**
38 **bud traits and temperature for accurately quantifying their energy budget.**
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Plant phenology, the study of the timing of life-cycle events, drives several ecosystem functions, such as plant productivity and biomass, but also local and global climates by affecting biogeochemical and biogeophysical processes, such as carbon storage and energy fluxes^{1,2}, and the abundance and diversity of local flora and fauna, such as pollinators and herbivores^{3,4}. Understanding the environmental controls and responses of plant phenology to climate change is thus essential for several sectors, e.g. agriculture, forestry and gardening⁵, but also for conservation⁶ and public health⁷ (e.g. allergies).

Foliar phenology and temperature

Leaves control plant water loss and carbon assimilation and are thus central to the growth of other plant organs. Temperature is one of the main drivers of foliar phenology in extratropical ecosystems⁸. Cold temperatures during winter and warm temperatures during spring control leaf unfolding and flowering at the beginning of the season. Temperature during the growing season will control foliar development, carbon assimilation, transpiration, plant growth and the establishment of new buds for the following year. Finally, cold temperatures at the end of the growing season are sensed by plants as a signal for foliar senescence⁹.

Climatic warming has strongly shifted phenophases in the Northern Hemisphere in recent decades^{1,10–12}. Rising temperatures have lengthened the annual growth cycle by advancing leaf unfolding in spring and delaying leaf fall in autumn¹³, albeit with variations among species¹⁴ and regions¹⁵. Recent evidence, though, suggests that the sensitivity of spring phenology to warming is decreasing in northern forests¹⁶ and that the rate of change in plant productivity does not match that of air temperature¹⁷. Indeed, plant phenology may be acclimated to long-term biogeographical constraints^{18–20} and may be co-limited by several other factors, such as light²¹, water^{9,22,23} and nutrients²⁴. These observations suggests that warming does not have the same effect everywhere²⁵, which has increased interest in other environmental drivers in recent decades, especially illustrated by multiple debates about the specific role of light (and photoperiodism) in spring phenology^{21,26–33}.

The controversial effect of light: different definitions

How light affects spring phenology remains an open question. Most commonly, its effect is considered via photoperiod, often referred to as daylength. The daylength hypothesis implies that the quality and/or quantity of light is somehow directly sensed by plants through biochemical mechanisms. Some recent studies suggest that the spectral composition of light can indeed influence foliar phenology^{34,35}. Light also plays a key role in regulating phytohormones, but the underlying mechanisms remain unknown³² and clearly require more investigation. More sporadically, the effect of light has been

treated as the sum of insolation over a specific period³⁶, for which plants need a specific quatum for a phenological event to occur. The quantity and quality of light depend on plant location, which is the main reason why a response to daylength has often been proposed as a safety mechanism against frost at high latitudes and elevations. Only 35% of the woody species in the Northern Hemisphere, however, depend on daylength as a direct signal for leaf-out²¹, and these species are mainly at mid- to low latitudes

Light effect on spring phenology is still being debated. Recent studies nonetheless suggest a complex interaction between temperature and light. Daytime and nighttime temperatures during winter and spring have an asymmetrical effect on leaf unfolding^{37–41}, with a greater weight of temperature during the day^{38,42,43}. Whether or not plants are able to sense light, radiation has a physical impact on plants: it affects the temperatures of their tissues. We will use the example of budburst in the following arguments to illustrate that omitting this radiation effect introduces large biases into the interpretation of spring phenological responses based on air temperature.

The forgotten effects of radiation and wind

Bud temperature (T_{bud}) depends on its energy balance⁴⁴. During the day, plant tissues absorb both shortwave (SW, visible and near-infrared) and longwave (LW, infrared) radiation from the sky but also radiation emitted and reflected by the surrounding environment (vegetation, soil) (Figure 1a). Only a fraction (α , absorptivity) of SW radiation will be absorbed depending on bud traits such as color, coating, shape and size (Figure 1b), while most LW radiation will be absorbed by buds. According to the Stefan-Boltzmann law, buds lose energy via LW radiation emission, while they absorb LW radiation emitted from surrounding objects. Finally, a part of their energy is lost by conduction and mostly by convection^{45,46} (e.g. due to wind) while leaves lose an important part of their energy via transpiration.

T_{bud} increases when energy gains exceed losses (Figure 2a) and vice-versa. T_{bud} can thus be lower than air temperatures (T_{air}) on clear nights⁴⁵ or because of wind. On the other hand, T_{bud} can be significantly higher than T_{air} during the day. The link between T_{bud} and energy balance has been known for more than 30 years^{44,45}. Since then, all major studies linking temperature and photoperiod to phenological changes, however, have not accounted for the true temperature of plant organs.

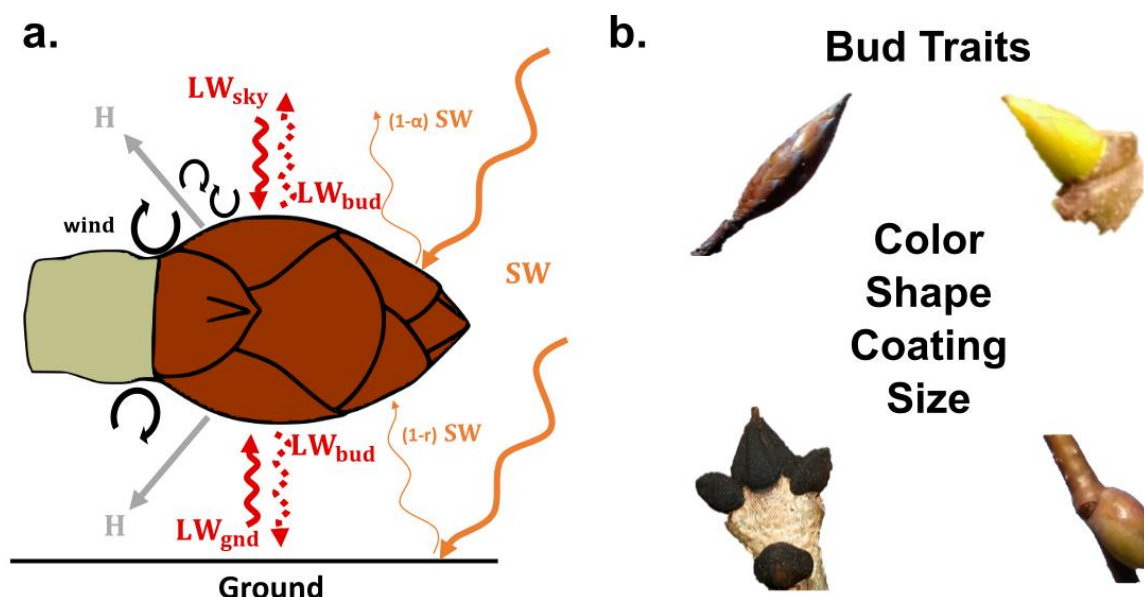


Figure 1 | Energy budget of buds and bud traits. **a.** Buds lose energy through convection and conduction (H). Buds absorb incoming shortwave (visible and near-infrared, SW) and longwave (infrared, LW) radiation from the sky (LW_{sky}) and the surrounding environment (here simplified as LW radiation from the ground, LW_{gnd}). Buds emit LW radiation as a function of their temperature (LW_{bud}). Only a fraction (α) of SW radiation is absorbed by buds, depending on the properties of their surfaces. Buds also absorb a small fraction of SW reflected from the ground ($1-r$). **b.** Illustration of bud traits influencing solar absorptivity, heat conduction and convection processes, and hence, bud temperature.

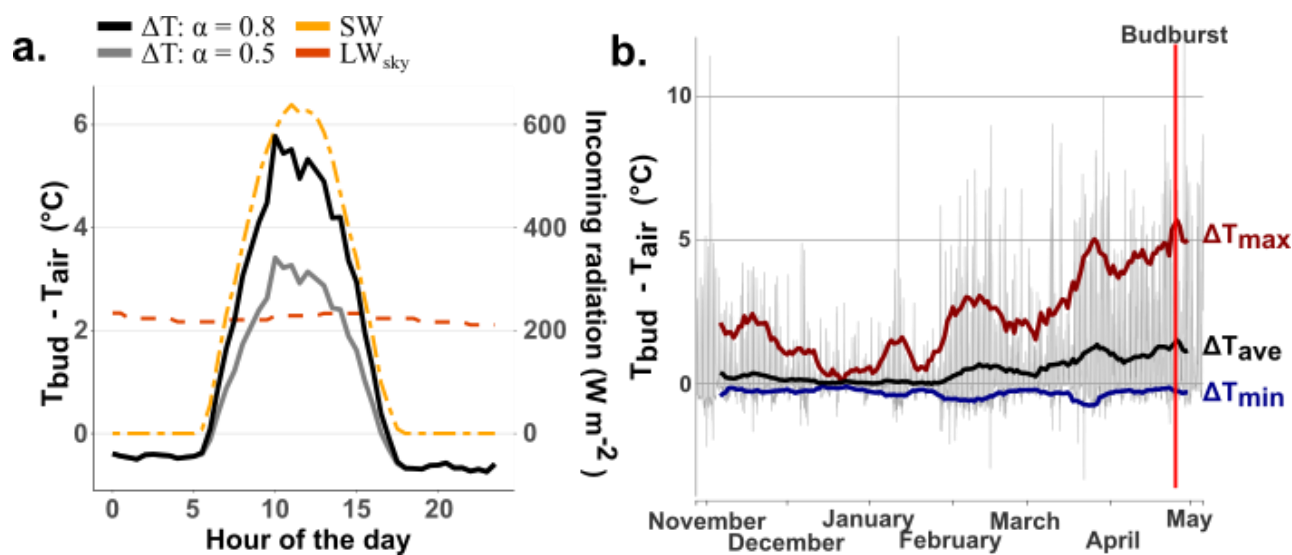


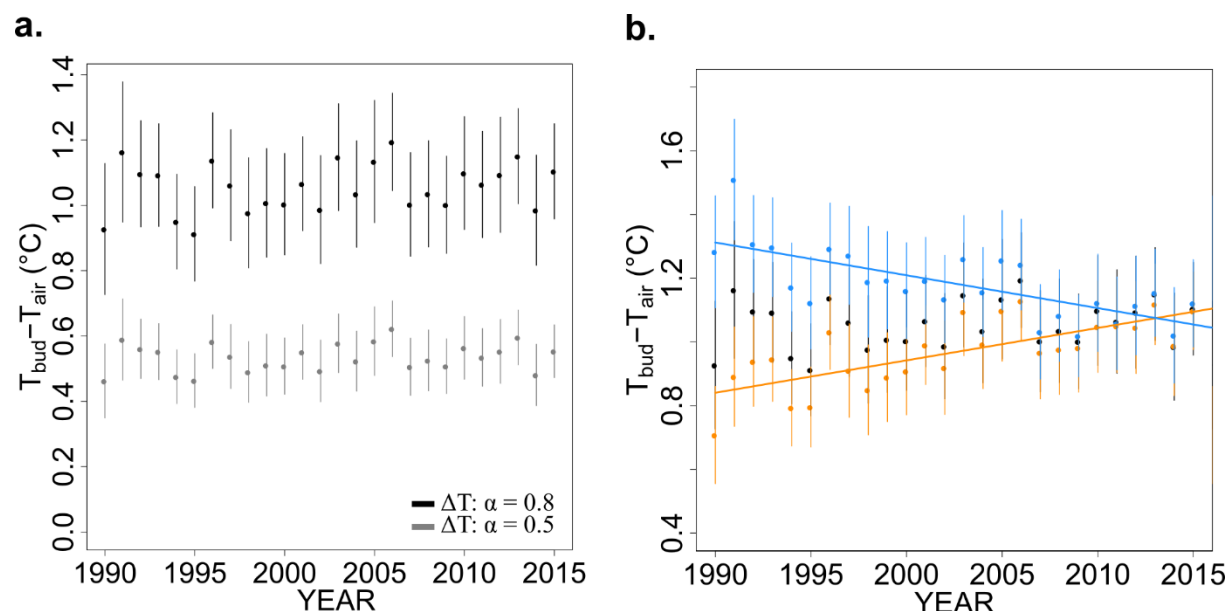
Figure 2 | Simulated differences in temperature between buds and the air (ΔT) from energy balance. **a.** Daily variation in ΔT for an exposed bud and a typical day in April for two solar absorptivities: $\alpha=0.5$ (typical for broadleaves⁴⁷) and $\alpha=0.8$ (typical for needle leaves⁴⁷). **b** Example of ΔT simulated under idealized conditions (e.g. exposed buds in a deciduous canopy) using meteorological observations for winter and spring collected at the Hesse FLUXNET site⁴⁸ (Beech forest, France). The grey lines represent half-hourly differences in temperature simulated using an energy-budget model. The blue, black and red curves represent the 10-d rolling mean of the minimal (ΔT_{min}), average (ΔT_{ave}) and maximal (ΔT_{max}) temperature differences, respectively. Approximative leaf flushing date is illustrated by the red vertical line (April 25th).

A complex and non-linear response of plant tissue temperature to radiation and wind

What can we expect if we account for the energy budgets of buds in phenological studies? Unfortunately, the lack of *in situ* observations for bud temperature does not allow to answer this question. As part of the reflection, we thus applied existing energy balance approaches^{44,45,49} to explore the potential variability in temperature of an isolated bud (Supplementary material). This situation is well representative of the conditions encountered by sun-exposed buds of a tree and especially of deciduous species (i.e. with no or minimum shading). As a first example, we looked at the variability in T_{bud} estimated from its energy balance and site meteorological observations for an European Beech forest⁴⁸. On average, T_{bud} is expected to be higher than T_{air} during the preseason ($\sim 1^{\circ}\text{C}$ in our example; Figure 2b). Day and night T_{bud} are higher or lower than T_{air} by several degrees. The temperature of buds thus strongly depends on the diurnal radiative cycle and the spectral composition of the light (SW/LW radiation), echoing the observed asymmetrical effect of diurnal temperatures on leaf unfolding^{38,42,43}. Applied on four other sites, this approach leads to similar results despite differences in T_{bud} profiles induced by differences in radiation along a latitudinal gradient (Supplementary Figure 1). Spring phenology does not only respond to average preseason temperature, but mainly to the accumulated effect of temperature and its dynamics. It is often assumed that chilling and forcing temperature required for budburst are only effective over specific windows, generally between 0 and 5 °C and over 5°C, respectively. Daily bud temperature variability might thus be the most important factor influencing leaf unfolding, not necessarily its average temperature. We could expect that the difference in extremum temperature sensed by buds over the preceding months (ΔT_{min} and ΔT_{max} , Figure 2b) will inevitably affect the apparent forcing and chilling requirement for leaf unfolding.

Accounting for the energy budget of buds for six common species across Europe (Supplementary Figure 2) we also expect a stronger interannual variability in T_{bud} than T_{air} , as well as different temporal evolutions over the last decades (Figure 3). In our example, buds are expected to warm faster or slower than air depending on location and species, with 20% and 7% of the sites exhibiting an increase and a decrease in ΔT over 1990-2015, respectively. Even if these trends represent idealized sun-exposed conditions here, we observe that the heterogeneity in ΔT evolution results from a complex and non-linear response to the amount of absorbed radiation and convection processes (Supplementary Figure 3). Because leaf unfolding is earlier in 2015 than in 1990, the average amount of absorbed radiation during the preseason slightly decreased over this period, while most of the interannual variability in ΔT is driven by conduction and convection (i.e. wind). The difference in air-bud temperature and their non-linear and non-proportional relationship suggests that our current interpretation of the apparent bud sensitivity to warming is incorrect.

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Figure 3 | Potential changes in $T_{bud}-T_{air}$ over Europe. **a.** Each point corresponds to the mean ΔT simulated for six deciduous species across Europe (1059 sites) under idealized conditions (i.e. sun-exposed buds) using field observation of budburst and global meteorological data (see Supplementary Material). All sites and species were pooled together. Two solar absorptivity values were tested, 0.5 (grey) and 0.8 (black). The error bars represent the spatial and species variability (± 1 SD around the mean). **b.** Under these conditions, ΔT is expected to decrease (blue) over the period 1990-2016 for 356 sites*species (7%) and increase for 902 sites*species (orange, 18%) over a total of 5050 sites*species. The black points correspond to all sites pooled together.

Response to warming will depend on organ properties and local environment

We illustrated the role of bud energy balance through an idealized and constant representation of buds and their environment for all sites and species. Larger spatial and temporal variations are expected due to the effect of topography, ground albedo (e.g. snow, understory), differences in bud traits (Figure 1b) and micrometeorological conditions⁵⁰ that will affect plant tissues energy balance. By affecting the amount of radiation reaching the buds (Figure 1a), varying ground albedo from 0.1 (~wet bare soil) to 0.9 (~snow) leads to a doubling in pre-season ΔT (Supplementary Figure 4). Since ground albedo strongly vary in space and over the pre-season (e.g. snow), we can expect substantial differences in the phenological signal at the regional scale induced by radiation, as already observed from leaf unfolding observations¹⁸.

Different bud colors or coating will also affect solar absorption of specific wavelengths, while shape and size will modify convection processes and the amount of intercepted radiation (Supplementary Figure 5), and hence, bud temperature. For example, Common Ash (*Fraxinus excelsior*) has black buds while sycamore (*Acer pseudoplatanus*) has green buds and mountain ash (*Sorbus aucuparia*) have dense white trichomes (i.e. hairs) on their surfaces. In our example, a difference in solar absorptivity of 0.3

leads to a doubling in ΔT (Figure 2a, Figure 3a). The differences in bud traits can thus partly account for the observed interspecific differences in heat requirement and apparent sensitivity to temperature. This suggests that the phenological response of plants to warming might be more species-specific than we thought, which should be accounted for in large scale studies.

Despite its central role at the organ level^{50,51}, micrometeorology is rarely accounted for in phenology studies because rarely measured, or simply because it is impossible to account for its effect such as in remote sensing analysis or terrestrial biosphere modelling. Instead, phenology studies, either local or regional, often use meteorological and climate dataset with hourly to daily time resolutions. The use of a steady state energy balance is easily justified under such conditions since thermal time constants of tree buds varies between a few seconds to about ten minutes⁵². Accounting for average preseason radiation and wind conditions might better explain the observed variability in plant phenology than air temperature alone. Here, we only explored spring T_{bud} variability in the case of sun-exposed buds with no shading. Accounting for the potential protecting effect of leaves or needles in evergreen species might substantially attenuate the effects of radiation and wind on intra- and bottom-canopy buds. The concomitant use of high-resolution microclimate data and transient energy budget models will be needed to quantify such effects.

Towards a better understanding of the environmental control of plant phenology

Drivers of phenological events and light are virtually impossible to separate, because daylength and radiation are strongly correlated with the time of year. Accounting for organ energy balances is thus promising for separating the environmental drivers of phenology using a single approach and potentially for reconciling the differences observed in the field. Applying existing modelling approaches in the context of sun-exposed buds suggested that air temperature might be an imprecise and biased predictor of bud temperature and more importantly of its variability over the months preceding leaf unfolding, which might introduce biases in the analysis of chilling and forcing requirement for budburst. However, we also showed that bud temperature results from a complex combination of several biotic and abiotic factors, and under certain conditions air temperature might remain a good proxy for bud temperature. The examples we have presented demand the reassessment of past results and interpretations that were solely based on air temperature, however current observations do not allow such reassessment. Bud traits and *in situ* temperature observations are scarcely described in the literature. New experiments and observations are clearly needed for accurately assessing the energy balances of plant organs. Existing studies have mostly focused on leaves, but other organs should also be investigated. Key traits that will need to be measured to assess the interspecific variability of phenology include organ traits influencing

solar absorptivity and heat storage, but organ temperatures (i.e. using thermocouples) concomitant with micrometeorological variables will also need to be directly measured. Because buds do not transpire, their energy budget is simpler than for leaves. Properly calibrated, accounting for bud energy balance could improve the accuracy of phenological models that are still unable to predict the spatiotemporal variability of plant dynamics with satisfactory accuracy⁵³.

Finally, we stress that energy balance affects the temperature extrema sensed by plants (Figure 2b). The lengthening of the growing season in recent decades has also been associated with an increase in environmental risks. For example, earlier leaf unfolding exposes plants late frost⁵⁴⁻⁵⁶ in spring, potentially resulting in dramatic impacts on agriculture⁵⁷⁻⁵⁹ and forestry^{60,61}. The use of energy balances to study and better predict these environmental risks can provide novel insights into the responses of plants to extreme temperatures and offer more robust predictive tools, which are essential for mitigating the ecological and economic impacts. Temperature of plant organs and their dynamics are still overlooked in both environmental studies and modeling exercises⁶². Energy balance thus plays a key role, not only for plant phenology but also for all other processes since plant tissue temperature will govern key mechanisms such as photosynthesis and respiration and the general functioning of the plant.

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Supplementary information

Already existing models and data were used to support this perspective. This work did not attempt to develop, nor validate, a new model. The full description of the energy budget model (and underlying assumptions) as well as supplementary figures and tables are provided in the Supplementary information. The R code of the model of energy budgets and data sets used to generate the figures and analysis of this manuscript are available from Github: <https://github.com/mpeaucelle/Tbud>
A version of the git repository is archived on Zenodo at <https://zenodo.org/record/4173415>.

References

1. Peñuelas, J. & Filella, I. Phenology. Responses to a warming world. *Science (New York, N.Y.)* **294**, 793–795; 10.1126/science.1066860 (2001).
2. Peñuelas, J., Rutishauser, T. & Filella, I. Ecology. Phenology feedbacks on climate change. *Science (New York, N.Y.)* **324**, 887–888; 10.1126/science.1173004 (2009).
3. Ramos-Jiliberto, R., Moisset de Espanés, P., Franco-Cisterna, M., Petanidou, T. & Vázquez, D. P. Phenology determines the robustness of plant-pollinator networks. *Scientific reports* **8**, 14873; 10.1038/s41598-018-33265-6 (2018).
4. Chuine, I. Why does phenology drive species distribution? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**, 3149–3160; 10.1098/rstb.2010.0142 (2010).
5. Chmielewski, F.-M. Phenology in Agriculture and Horticulture. In *Phenology: An Integrative Environmental Science*, edited by M. D. Schwartz. 2nd ed. (Springer Netherlands; Springer e-books; Imprint: Springer, Dordrecht, 2013), pp. 539–561.
6. Morellato, L. P. C. *et al.* Linking plant phenology to conservation biology. *Biological Conservation* **195**, 60–72; 10.1016/j.biocon.2015.12.033 (2016).
7. Katelaris, C. H. & Beggs, P. J. Climate change: allergens and allergic diseases. *Internal medicine journal* **48**, 129–134; 10.1111/imj.13699 (2018).
8. Schwartz, M. D. (ed.). *Phenology: An Integrative Environmental Science*. 2nd ed. (Springer Netherlands; Springer e-books; Imprint: Springer, Dordrecht, 2013).
9. Delpierre, N. *et al.* Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France. *Agricultural and Forest Meteorology* **149**, 938–948; 10.1016/j.agrformet.2008.11.014 (2009).
10. Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A. & SCHWARTZ, M. D. Shifting plant phenology in response to global change. *Trends in ecology & evolution* **22**, 357–365; 10.1016/j.tree.2007.04.003 (2007).
11. Fu, Y. H. *et al.* Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology and Biogeography* **23**, 1255–1263; 10.1111/geb.12210 (2014).
12. Jeong, S.-J., HO, C.-H., GIM, H.-J. & BROWN, M. E. Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982–2008. *Global change biology* **17**, 2385–2399; 10.1111/j.1365-2486.2011.02397.x (2011).
13. Liu, Q. *et al.* Delayed autumn phenology in the Northern Hemisphere is related to change in both climate and spring phenology. *Global change biology* **22**, 3702–3711; 10.1111/gcb.13311 (2016).
14. Vitasse, Y. *et al.* Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology* **149**, 735–744; 10.1016/j.agrformet.2008.10.019 (2009).
15. Wang, S. *et al.* Temporal Trends and Spatial Variability of Vegetation Phenology over the Northern Hemisphere during 1982–2012. *PloS one* **11**, e0157134; 10.1371/journal.pone.0157134 (2016).
16. Fu, Y. H. *et al.* Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–107; 10.1038/nature15402 (2015).
17. Huang, M. *et al.* Velocity of change in vegetation productivity over northern high latitudes. *Nature ecology & evolution* **1**, 1649–1654; 10.1038/s41559-017-0328-y (2017).

18. Peaucelle, M. *et al.* Spatial variance of spring phenology in temperate deciduous forests is constrained by background climatic conditions. *Nature communications* **10**, 5388; 10.1038/s41467-019-13365-1 (2019).
19. Zohner, C. M., Mo, L., Pugh, T. A. M., Bastin, J.-F. & Crowther, T. W. Interactive climate factors restrict future increases in spring productivity of temperate and boreal trees. *Global change biology*; 10.1111/gcb.15098 (2020).
20. Montgomery, R. A., Rice, K. E., Stefanski, A., Rich, R. L. & Reich, P. B. Phenological responses of temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit, and geographic range. *Proceedings of the National Academy of Sciences of the United States of America* **117**, 10397–10405; 10.1073/pnas.1917508117 (2020).
21. Zohner, C. M., Benito, B. M., Svenning, J.-C. & Renner, S. S. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Clim Change* **6**, 1120–1123; 10.1038/nclimate3138 (2016).
22. Peñuelas, J. *et al.* Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist* **161**, 837–846; 10.1111/j.1469-8137.2004.01003.x (2004).
23. Papagiannopoulou, C. *et al.* Vegetation anomalies caused by antecedent precipitation in most of the world. *Environ. Res. Lett.* **12**, 74016; 10.1088/1748-9326/aa7145 (2017).
24. Fu, Y. H. *et al.* Nutrient availability alters the correlation between spring leaf-out and autumn leaf senescence dates. *Tree physiology* **39**, 1277–1284; 10.1093/treephys/tpz041 (2019).
25. Seyednasrollah, B., Swenson, J. J., Domec, J.-C. & Clark, J. S. Leaf phenology paradox: Why warming matters most where it is already warm. *Remote Sensing of Environment* **209**, 446–455; 10.1016/j.rse.2018.02.059 (2018).
26. Chuine, I., Morin, X. & Bugmann, H. Warming, photoperiods, and tree phenology. *Science (New York, N.Y.)* **329**, 277–8; author reply 278; 10.1126/science.329.5989.277-e (2010).
27. Vitasse, Y. & Basler, D. What role for photoperiod in the bud burst phenology of European beech. *Eur J Forest Res* **132**, 1–8; 10.1007/s10342-012-0661-2 (2013).
28. Way, D. A. & Montgomery, R. A. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, cell & environment* **38**, 1725–1736; 10.1111/pce.12431 (2015).
29. Caffarra, A., Donnelly, A. & Chuine, I. Modelling the timing of *Betula pubescens* budburst. II. Integrating complex effects of photoperiod into process-based models. *Clim. Res.* **46**, 159–170; 10.3354/cr00983 (2011).
30. Körner, C. & Basler, D. Plant science. Phenology under global warming. *Science (New York, N.Y.)* **327**, 1461–1462; 10.1126/science.1186473 (2010).
31. Fu, Y. H. *et al.* Daylength helps temperate deciduous trees to leaf-out at the optimal time. *Global change biology* **25**, 2410–2418; 10.1111/gcb.14633 (2019).
32. Singh, R. K., Svystun, T., AlDahmash, B., Jönsson, A. M. & Bhalerao, R. P. Photoperiod- and temperature-mediated control of phenology in trees - a molecular perspective. *New Phytologist* **213**, 511–524; 10.1111/nph.14346 (2017).
33. Flynn, D. F. B. & Wolkovich, E. M. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* **219**, 1353–1362; 10.1111/nph.15232 (2018).

34. Brelsford, C. C., Nybakken, L., Kotilainen, T. K. & Robson, T. M. The influence of spectral composition on spring and autumn phenology in trees. *Tree physiology* **39**, 925–950; 10.1093/treephys/tpz026 (2019).
35. Strømme, C. B. *et al.* UV-B and temperature enhancement affect spring and autumn phenology in *Populus tremula*. *Plant, cell & environment* **38**, 867–877; 10.1111/pce.12338 (2015).
36. Fu, Y. H. *et al.* Increased heat requirement for leaf flushing in temperate woody species over 1980–2012: effects of chilling, precipitation and insolation. *Global change biology* **21**, 2687–2697; 10.1111/gcb.12863 (2015).
37. Huang, Y., Jiang, N., Shen, M. & Guo, L. Effect of pre-season diurnal temperature range on the start of vegetation growing season in the Northern Hemisphere. *Ecological Indicators* **112**, 106161; 10.1016/j.ecolind.2020.106161 (2020).
38. Meng, F. *et al.* Opposite effects of winter day and night temperature changes on early phenophases. *Ecology* **100**, e02775; 10.1002/ecy.2775 (2019).
39. Zhang, S., Isabel, N., Huang, J.-G., Ren, H. & Rossi, S. Responses of bud-break phenology to daily-asymmetric warming: daytime warming intensifies the advancement of bud break. *International journal of biometeorology* **63**, 1631–1640; 10.1007/s00484-019-01776-0 (2019).
40. Meng, L. *et al.* Divergent responses of spring phenology to daytime and nighttime warming. *Agricultural and Forest Meteorology* **281**, 107832; 10.1016/j.agrformet.2019.107832 (2020).
41. Bigler, C. & Vitasse, Y. Daily Maximum Temperatures Induce Lagged Effects on Leaf Unfolding in Temperate Woody Species Across Large Elevational Gradients. *Frontiers in plant science* **10**, 398; 10.3389/fpls.2019.00398 (2019).
42. Fu, Y. H. *et al.* Three times greater weight of daytime than of night-time temperature on leaf unfolding phenology in temperate trees. *The New phytologist* **212**, 590–597; 10.1111/nph.14073 (2016).
43. Piao, S. *et al.* Leaf onset in the northern hemisphere triggered by daytime temperature. *Nature communications* **6**, 6911; 10.1038/ncomms7911 (2015).
44. HAMER, P. The heat balance of apple buds and blossoms. Part I. Heat transfer in the outdoor environment. *Agricultural and Forest Meteorology* **35**, 339–352; 10.1016/0168-1923(85)90094-2 (1985).
45. Landsberg, J. J., Butler, D. R. & Thorpe, M. R. Apple bud and blossom temperatures. *Journal of Horticultural Science* **49**, 227–239; 10.1080/00221589.1974.11514574 (1974).
46. Grace, J. The temperature of buds may be higher than you thought. *New Phytologist* **170**, 1–3; 10.1111/j.1469-8137.2006.01675.x (2006).
47. Jones, H. G. *Plants and microclimate. A quantitative approach to environmental plant physiology* (Cambridge university press, Cambridge, 2013).
48. Granier, A., Bréda, N., Longdoz, B., Gross, P. & Ngao, J. Ten years of fluxes and stand growth in a young beech forest at Hesse, North-eastern France. *Ann. For. Sci.* **65**, 704; 10.1051/forest:2008052 (2008).
49. Muir, C. D. tealeaves: an R package for modelling leaf temperature using energy budgets. *AoB PLANTS* **11**, plz054; 10.1093/aobpla/plz054 (2019).
50. Zellweger, F. *et al.* Forest microclimate dynamics drive plant responses to warming. *Science (New York, N.Y.)* **368**, 772–775; 10.1126/science.aba6880 (2020).

- 367 51. Bailey, B. N., Stoll, R., Pardyjak, E. R. & Miller, N. E. A new three-dimensional energy balance
368 model for complex plant canopy geometries: Model development and improved validation
369 strategies. *Agricultural and Forest Meteorology* **218-219**, 146–160;
370 10.1016/j.agrformet.2015.11.021 (2016).
- 371 52. Michaletz, S. T. & Johnson, E. A. A heat transfer model of crown scorch in forest fires. *Can. J. For.*
372 *Res.* **36**, 2839–2851; 10.1139/x06-158 (2006).
- 373 53. Richardson, A. D. *et al.* Terrestrial biosphere models need better representation of vegetation
374 phenology: results from the North American Carbon Program Site Synthesis. *Glob Change Biol* **18**,
375 566–584; 10.1111/j.1365-2486.2011.02562.x (2012).
- 376 54. Liu, Q. *et al.* Extension of the growing season increases vegetation exposure to frost. *Nature*
377 *communications* **9**, 426; 10.1038/s41467-017-02690-y (2018).
- 378 55. Ma, Q., Huang, J.-G., Hänninen, H. & Berninger, F. Divergent trends in the risk of spring frost
379 damage to trees in Europe with recent warming. *Global change biology* **25**, 351–360;
380 10.1111/gcb.14479 (2019).
- 381 56. Zohner, C. M. *et al.* Late-spring frost risk between 1959 and 2017 decreased in North America but
382 increased in Europe and Asia. *Proceedings of the National Academy of Sciences of the United States*
383 *of America*; 10.1073/pnas.1920816117 (2020).
- 384 57. Xiao, L. *et al.* Estimating spring frost and its impact on yield across winter wheat in China.
385 *Agricultural and Forest Meteorology* **260-261**, 154–164; 10.1016/j.agrformet.2018.06.006 (2018).
- 386 58. Unterberger, C. *et al.* Spring frost risk for regional apple production under a warmer climate. *PloS*
387 *one* **13**, e0200201; 10.1371/journal.pone.0200201 (2018).
- 388 59. Leolini, L. *et al.* Late spring frost impacts on future grapevine distribution in Europe. *Field Crops*
389 *Research* **222**, 197–208; 10.1016/j.fcr.2017.11.018 (2018).
- 390 60. Greco, S. *et al.* Late Spring Frost in Mediterranean Beech Forests: Extended Crown Dieback and
391 Short-Term Effects on Moth Communities. *Forests* **9**, 388; 10.3390/f9070388 (2018).
- 392 61. Augspurger, C. K. Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate
393 deciduous forest. *Functional Ecology* **23**, 1031–1039; 10.1111/j.1365-2435.2009.01587.x (2009).
- 394 62. Dong, N., Prentice, I. C., Harrison, S. P., Song, Q. H. & Zhang, Y. P. Biophysical homeostasis of
395 leaf temperature: A neglected process for vegetation and land-surface modelling. *Global Ecol*
396 *Biogeogr* **26**, 998–1007; 10.1111/geb.12614 (2017).