Warming nondormant tree roots advances aboveground spring phenology in temperate trees

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Summary

- Climate warming advances the onset of tree growth in spring, but above- and belowground phenology are not always synchronized. These differences in growth responses may result from differences in root and bud dormancy dynamics, but root dormancy is largely unexplored.
- We measured dormancy in roots and leaf buds of *Fagus sylvatica* and *Populus nigra* by quantifying the warming sum required to initiate above- and belowground growth in October, January and February. We furthermore carried out seven experiments, manipulating only the soil and not air temperature before or during tree leaf-out to evaluate the potential of warmer roots to influence budburst timing using seedlings and adult trees of *F. sylvatica* and seedlings of *Betula pendula*.
- Root dormancy was virtually absent in comparison with the much deeper winter bud dormancy. Roots were able to start growing immediately as soils were warmed during the winter. Interestingly, higher soil temperature advanced budburst across all experiments, with soil temperature possibly accounting for *c.* 44% of the effect of air temperature in advancing aboveground spring phenology per growing degree hour.
- Therefore, differences in root and bud dormancy dynamics, together with their interaction, likely explain the nonsynchronized above- and belowground plant growth responses to climate warming.

Introduction

The timing of the start of the growing season in trees impacts primary productivity (Kindermann *et al.*, 1996; Richardson *et al.*, 2010), carbon and water cycles (Piao *et al.*, 2019; Lian *et al.*, 2020), and plant–animal interactions, including foraging and pollination (Hegland *et al.*, 2009). Tree growth encompasses both root and shoot phenology, which are not in sync with each other (Steinaker *et al.*, 2010; Abramoff & Finzi, 2015; Blume-Werry *et al.*, 2016; Radville *et al.*, 2016; Makoto *et al.*, 2020; Blume-Werry, 2022; Liu *et al.*, 2022). Such a mismatch in the growth onset may occur because leaf bud dormancy prohibits growth under otherwise favorable growth conditions, in particular during late autumn and winter (Champagnat, 1989; Cooke *et al.*, 2012; Beil *et al.*, 2021). Root growth, on the contrary, often slows down or ceases but does occur even during winter (Radville *et al.*, 2016), as suggested by roots of temperate species still growing at 2–4°C (Schenker *et al.*, 2014). Roots may employ

a riskier strategy than leaf and flower buds as root-zone temperatures rarely reach air temperature extremes, and strong temperature fluctuations do not occur in deeper rooting depths. The chance of a damaging frost event following a warm thaw spell is therefore higher for aboveground tissue compared with deeper roots. As a possible consequence, roots do not form dormant buds as found on stems. Thus, roots of temperate zone trees may not go dormant at all, although explicit experiments testing this are lacking. Whether differences in dormancy in above- and belowground tissue are responsible for seasonal mismatches in growth is unknown as the status of above- and belowground tissues has not yet been investigated concurrently.

Leaf and flower buds of temperate trees enter a state of rest, termed dormancy, preventing frost damage due to premature growth onset during winter warm periods (Vitasse *et al.*, 2014; Vitra *et al.*, 2017). A temperature sum above a standard threshold of 5°C is commonly used to quantify the dormancy depth in terms of the number of degree days (GDDs), or more precisely

growing degree hours (GDH) required to initiate growth (Fu *et al.*, 2015). As leaf buds gradually enter dormancy in the fall, the thermal sum required for dormancy release and budburst increases up to a specific date. In this so-called endodormancy, leaf buds cannot become active even under favorable growing conditions. After reaching peak dormancy, dormancy depth decreases toward the end of winter and the GDDs required to initiate budburst progressively diminish. The timing of progression to ecodormancy, when buds remain closed mainly due to an absence of sufficient minimum threshold of GDDs, is dependent on the sum of ambient chilling temperatures and photoperiod (Harrington *et al.*, 2010; Malyshev *et al.*, 2018; Fu *et al.*, 2019; Baumgarten *et al.*, 2021).

While wide-spread advances in spring phenology have been documented aboveground, it is also becoming increasingly clear that belowground phenology, such as timing of the start and the end of the growing season or periods of highest production, is not in sync with aboveground phenology in many species and ecosystems (e.g. Blume-Werry *et al.*, 2016; Radville *et al.*, 2016; Makoto *et al.*, 2020). There is thus increasing evidence that root growth can occur independently from an influx of photosynthates (Radville *et al.*, 2016; Blume-Werry *et al.*, 2017), likely by using stored nonstructural carbohydrates for growth of young roots (Solly *et al.*, 2018). Furthermore, a recent meta-analysis suggests that these phenological mismatches may become more pronounced in the future as above- and belowground plant parts do not respond to warming in the same way (Blume-Werry, 2022; Liu *et al.*, 2022). This may occur at least partly because the sensitivity of belowground phenology of woody plants to warming is particularly high (Liu *et al.*, 2022), suggesting that tree roots are less dormant than shoots.

Active and growing roots not only determine the plants' ability to take up water and nutrients, but also strongly influence carbon and nutrient cycling of the whole ecosystem, by influencing biomass allocation in the plants, as well as carbon fluxes belowground in the form of root litter and exudates. This carbon flux belowground is substantial; in addition to produced root biomass, root exudation alone can comprise up to 10% of photosynthetically fixed carbon (Jones *et al.*, 2009). There is thus an urgent need to increase our understanding of belowground phenological changes in response to climate warming.

In addition to roots potentially not going dormant, there are indications that warming-induced advanced root activity may also influence aboveground phenological responses. For example, root-zone warming has been shown to advance aboveground growth onset in vines and apple trees (Greer *et al.*, 2006; Rogiers *et al.*, 2009), while having antagonistic effects on aboveground growth depending on time since soil warming in spruce (Lahti *et al.*, 2005). While the exact mechanism remains elusive, this finding indicates that root phenology might additionally play a role in determining aboveground phenology.

Here, we set up a series of experiments to first quantify dormancy patterns in leaf buds and roots of juvenile trees and to, second, manipulate soil but not air temperature to find out whether warming roots alone influences timing of above- and belowground activity, that is root growth and budburst. We did this

for mature trees in the field and for potted saplings in a common garden and in climate chambers. Specifically, we hypothesized that:

(**1**) Unlike aboveground phenology, root growth of temperate forest trees can be initiated at any time with warming during winter due to a lack of dormancy.

(**2**) Higher root-zone temperature advances budburst in temperate forest tree species.

Materials and Methods

Experiment 1 addressed temporal differences in root and shoot dormancy depth in tree saplings while Experiments 2–8 tested the influence of soil temperature on budburst timing in tree saplings and mature trees. In Experiment 9, a subset of tree seedlings from Experiment 8 was concurrently exposed to air warming in glasshouses to compare the effect of root and air warming on phenology (vs only root warming as in 8). The warming temperature sum required to initiate root growth/budburst (at date t_{growth}) from the placement of samples to the growth chambers (t_0) was used as a proxy of dormancy depth. Growing degree hours were calculated as:

$$GDH = \sum_{t_0}^{t_{growth}} (T_{mean} - T_{base})$$

where T_{mean} is the hourly temperature and T_{base} is the base temperature (considered as the threshold value required for budburst activity; Fu *et al.*, 2015), which was set to $+5°C$.

Experiment 1: root vs leaf bud dormancy

Saplings of *Fagus sylvatica* L. and stem cuttings of *Populus nigra* L. were planted in 20-l pots at the common garden facility of the University of Greifswald, Germany (54°05′30.6″N, 13°21′53.2″E) in 2020 and grown outside from fall 2020 to fall 2021. Mean temperature and total precipitation during the growing period of our experiment were 10.2°C and 758 mm, respectively. The growth substrate was composed of 50% fine sand and 50% peat (volume percentage). Per pot, 50 g of slow release NPK fertilizer, 2.8 g of micronutrients and 7 g of chalk were added.

Fagus sylvatica saplings (0.8–1 m in height; 2 yr old) were acquired from a Belgian nursery with the seed sources being Boisd'Hé and Coco. Cuttings of Brandaris genotypes of *P. nigra* (*c.* 30 cm long) were obtained from a short-rotation coppice experimental plantation at Lochristi, Belgium (51°06′N, 03°51′E) in February 2020. The Brandaris genotype was bred by the Research Institute for Forestry and Urban Ecology 'De Dorschkamp' (Wageningen, the Netherlands) in 1964. Clonally propagated saplings of *P. nigra* were then grown from 30-cm stem cuttings in Greifswald under the same growth conditions as *F. sylvatica*. Trees were watered as required.

Rhizotrons were created by cutting rectangular openings (10 cm × 20 cm) from the bottom of cylindrical pots, which were 30 cm in diameter and 40 cm in height (Supporting Information

Fig. S1). The openings were replaced with transparent Plexiglas (PLEXIGLAS® XT antireflex 2 mm). The Plexiglas opening was kept away from the light by placing each rhizotron pot into another pot of the same dimensions. Soil root balls remained intact while switching pots.

From 2021 to 2022, on October 25, January 12 and February 28, 4-yr-old *F. sylvatica* ($n = 15$) and 2-yr-old *P. nigra* saplings ($n = 6$) were transferred from the field site to a growth room. Light was provided 16 h per day with lamps (D193 Papillon 315 W; CDM-TP Elite MW, Phillips, Amsterdam, the Netherlands), positioned *c.* 1 m above the top branches of trees, resulting in *c.* 100 µmol s^{-1} m^{-2}. A temperature of 20°C (± 2°C) and a humidity of 50% (± 10%) was maintained in the growth room. Temperature and light were both kept constant on each sampling date to ensure differences in warming sums required to initiate growth were attributable to the date of sampling and not to dormancy test conditions.

Root dormancy and bud dormancy depth were quantified as the number of days needed to initiate root growth or bud burst, respectively. The start of root growth was assessed from photographs taken with a camera (NIKON D850 with Micro-Nikkor 105 mm f/2.8G IF-ED lens, Nikon Corp., Tokyo, Japan) from below the pots, which were positioned 1 m above the floor on a stand. The camera settings were kept constant: cover F/16, exposure time 1/4 s, ISO 100, focal length 105 mm, resolution 5512 × 8280 and focus AF-S. Photographs were taken every 3 d after the move to the growth room (first photograph taken after 48 h of warming) and visually analyzed by a trained person, detecting the date on which new root growth could be observed (Fig. S1). Buds were checked for budburst on the same days when the photographs were taken, as the first day on which one or more buds showed the first green part of a leaf.

Experiments 2–8: influence of soil temperature on the timing of budburst

Experiment 2 used soil insulation required to manipulate soil temperature in several locations for adult trees. Experiments 3 and 4 applied an *in situ* soil insulation method, allowing for naturally high temperature fluctuations. Experiments 5–7 maximized soil temperature differences, being necessary to achieve sufficient replication and administer warming during different periods. Using heated wires in Experiment 8 allowed to warm a greater soil amount, reducing temperature fluctuations (vs Experiments 3–7).

Experiment 2: soil temperature manipulation by insulation (adult trees) Soil warming treatments were applied to adult *F. sylvatica* trees at nine locations along a winter temperature gradient of > 4°C in Northeastern Germany and Northern Poland (Weigel *et al.*, 2021). At each location, adult *F. sylvatica* trees representative for the respective stand were selected based on radial growth patterns of the preceding 30 yr (Weigel *et al.*, 2018, 2021).

Soil temperature was manipulated in winter 2016/2017 by covering the ground of *c.* 5 m radius around 1 adult target tree for each of the nine sites, respectively, with white gardening fleece made from thermally bound polypropylene fibers (70 g m^{-2};

Hermann Meyer KG). The material is highly reflective and water-permeable, thereby insulating the soil from air temperatures without affecting the soil moisture content. The soil of the controls was left untreated. The fleece insulation increased the soil surface temperature over the 90 d before sampling by 0.79 ± 0.30°C (mean ± SD) across all sites, for mean GDH differences and site-specific soil temperature differences see Tables 1, 2, respectively.

A slingshot (Notch BIG SHOT Standard Kit, SHERRILLtree, Greensboro, NC, USA) was used to reach and cut branches of *c.* 5 cm in diameter from the upper tree canopy of a total of the nine trees experiencing control and from nine trees experiencing insulating conditions. Ten smaller twigs containing at least one terminal and several lateral buds of *c.* 10 cm length were sampled from each tree, kept moist with wet paper towels, wrapped in aluminum foil and packed in a cool box (mean temp. 7°C) for the transport during the period of 10 March–22 March. The twigs were placed in a glasshouse, and time to budburst was monitored under optimal growing conditions (mean temp. 20°C; 16 h day length at 100–200 µmol m^{-2} s^{-1}). Terminal buds were removed and twigs were trimmed to *c.* 6 cm to standardize the samples and remove the influence of terminal buds on lateral budburst via correlative inhibition. The air-exposed twig end was covered with wax to prevent desiccation. Twigs were placed in PVC foam mats placed in trays of distilled water, trimming 0.5 cm of every twig weekly and changing water twice-weekly. Twigs were observed every 2 d until budburst (Experiment 1).

Experiment 3: soil temperature manipulation by Styrofoam insulation (tree seedlings) Three-year-old *B. pendula* Roth seedlings from seeds stemming from northern Germany were acquired from a local tree nursery in 2019. The 1.0–1.3-m-tall seedlings were repotted into 15 cm × 15 cm × 22 cm pots with the substrate comprising of a 1 : 1 : 1, sand : peat : local forest soil mixture. Two treatments differing in soil insulation were realized over the winter of 2019/2020 at the common garden facility of the University of Greifswald. The pots of the insulation treatment ($n = 9$) were insulated by 5-cm-thick Styrofoam walls, buried to the top of the pot in sand and their upper surface insulated by water-permeable 1-cm coco fiber mats. Control pots had no insulation ($n = 9$) and were placed in dug-out sand holes (60 cm in diameter; 60 cm apart) of the same depth as insulated pots.

The soil temperature was recorded by EM60/EM60G (Meter Group, Pullman, WA, USA) and TMS-4 (TOMST, Praha, Czech Republic) data loggers, which continuously monitored soil temperature at 5 cm depth. Although mean temperature was the same in the control treatment and in the insulation treatment, more GDH accumulated in the noninsulated treatment (4.0 ± 1.4°C; 876 GDH in warming vs 4.0 ± 2°C 413 GDH in control). This was likely due to sunlight that warmed the black noninsulated pots. At the end of February, all plants were placed in the climate chamber (model: LT-36VLX; CLF Plant Climatics GmBH, Wertingen, Germany) and kept at 23°C mean temperature, 60–70% air humidity and light intensity between 200 and 300 µmol m^{-2} s^{-1} until 50% budburst occurred in each tree (Experiment 1).

Table 1 Summary of all experiments carried out to relate root and leaf bud dormancy (Experiment 1) as well as to determine the influence of warmer soil temperature on the timing of budburst (Experiments 2–8).

Goal	Experiment	Plant material	Species	Temperature manipulation period (s)	Soil temperature manipulation	Soil temperature of warmer treatment (°C)	Soil temperature of colder treatment (°C)	Budburst test conditions
Root vs leaf bud dormancy	(1) Growth room	Potted tree seedlings	Fagus sylvatica, Populus nigra	25 October 2021–1 January 2022; 12 January 2022–28 February 2022; 28 February–3 March 2022	na			Growth room 20°C; 16-h light (buds and roots)
Ambient root temperature manipulation via insulation	(2) Root insulation	Twig cuttings from adult trees	Fagus sylvatica	10 December 2016–10 March 2017	Fleece cover at tree base	3 (± 0.6) 456 GDH	2.3 (± 0.5) 233 GDH	Glasshouse 20°C; 16 h light
	(3) Root insulation	Potted tree seedlings	Betula pendula	3 December 2019–29 February 2020	Styrofoam root insulation	4.0 (± 1.4) 876 GDH	4.0 (± 2.0) 413 GDH	Growth room 23°C; 16 h light
	(4) Root insulation	Potted tree seedlings	Betula pendula	10 November 2021–9 February 2022	Coconut fibers and insulating foam	3.4 (± 2.7) 1644 GDH	3.3 (± 3.7) 1315 GDH	Climate chamber 13°C; 12 h light
Controlled root temperature manipulation via climate chambers	(5) Chamber warming	Potted tree seedlings	Fagus sylvatica	26 February 2020–15 April 2020	Pots inserted in climate chambers; stems exposed to room temperature via slits in foam chamber door	13.4 (± 1.6) 8808 GDH	5.9 (± 1.0) 373 GDH	Glasshouse 20°C; natural light
	(6) Chamber warming	Potted tree seedlings	Betula pendula	11 January 2021–2 February 2021		12.0 (± 0.5) 3179 GDH	6.0 (± 0.4) 436 GDH	Climate chamber 20°C; 12 h light
	(7) Chamber warming	Potted tree seedlings	Betula pendula	8 December 2021–5 January 2022		10.0 (± 1.0) 7248 GDH	1.7 (± 0.6) 0 GDH	Climate chamber 16°C; 12 h light
Ambient root temperature manipulation via buried wires	(8) Wire soil warming	Potted tree seedlings	Betula pendula	8 March 2020–9 April 2020	Heating wires wrapped around bamboo sticks inserted close to roots	11.9 (± 5.0) 5023 GDH	6.4 (± 5.4) 1432 GDH	In-situ spring conditions
Controlled root and air temperature manipulation in glasshouse	(9) Aboveground (air) warming	Potted tree seedlings	Betula pendula	14 February 2020–23 March 2020	Glasshouse (air) warming	Air temperature: 14.6 (± 4.0) 8485	Air temperature: 8.0 (± 4.3) 2966	Glasshouse conditions

Accumulated growing degree hours (GDH) in warmer and colder soils show the relative warming effects, in addition to the difference in °C. In Experiment 9, a subset of tree seedlings from Experiment 8 was concurrently exposed to different air temperatures in glasshouses to compare the effect of combined root and air warming to soil warming only (Experiment 8). Numbers in brackets indicate SD; na, not applicable.

Table 2 Coordinates of locations used in the snow manipulation experiment with respective mean annual precipitation and mean minimum monthly air temperature between 1961 and 1990 (Marchi *et al.*, 2020).

Location	°E	°N	Δ Soil temp (°C)	Air temperature (°C)	Mean annual precipitation (mm)
Billenhagen	12.32	54.12	0.92	−0.53	588
Hanshagen	13.51	54.05	0.66	−0.95	569
Neustrelitz	13.14	53.39	1.29	−1.45	580
Afrika	13.83	53.11	0.95	−1.94	568
Gryfino	14.73	53.32	0.86	−2.62	568
Debno	14.56	52.71	0.87	−2.87	540
Wejherowo	18.08	54.72	0.68	−3.03	623
Kolbudy	18.43	54.25	1.15	−4.35	592
Kartuzy	18.15	54.24	0.44	−4.74	621

ΔTemp indicates the average difference in temperature at soil surface 90 d before twig samples were taken from trees under the fleece insulation treatment or the untreated control. The resulting mean growing degree hour sums of the two treatments are shown in Table 1.

Experiment 4: soil temperature manipulation by insulating foam (tree seedlings) The location, plant material and substrate were identical to Experiment 3. Different from Experiment 3 was the smaller pot size (10 cm × 10 cm × 25 cm) and the insulation treatment. For the soil insulation treatment ($n = 10$), each pot was inserted into a bigger empty pot (25 cm diameter and 30 cm deep), and the space between the two pots was filled with Polyurethane spray foam. Mats of coco fibers were used to cover the soil surface and pots were buried and distributed in the sand as in Experiment 3. Data loggers (EL-USB-TC Logger with T-type Probe, Erie, PA, USA) were inserted in all 20 pots at a depth of 5 cm. More GDH accumulated in the noninsulated pots.

On 10 February, all trees were placed in a climate chamber (see Experiment 3 for details) with temperature and photoperiod simulating spring conditions (16°C during the day (i.e. 07:00 h : 19:00 h) and 10°C at night; Table 1) until 50% budburst occurred in each tree (Experiment 1).

Experiment 5: soil temperature manipulation by chamber warming (tree seedlings) Three-year-old *F. sylvatica* seedlings were acquired (northern German seed source), transplanted into 15 cm × 15 cm × 30 cm pots in October 2019 with a substrate composition of 50% fine sand and 50% peat (volume percentage) and from then on watered as needed to keep the substrate moist. From 26 February to 15 April 2020, the potted seedlings were transferred to two climate chambers (model: LT-36VLX; CLF Plant Climatics GmBH), set to 13°C and 6°C, respectively. The trees were placed horizontally in the chambers on metal racks so that the pots and substrate were inside the chamber while the stem was outside with the stems stuck out through the rubber seam between the door and chamber wall. Slits around stems were additionally sealed with foam and tape. Soil and air temperature was measured by RT-1 temperature sensors (Meter Group) at 5 cm depth in the soil and by taping them to twigs. No difference in air temperature outside the chambers was detected (19.6°C in both treatments on average). The seedlings

and the chamber settings were switched between chambers every 4 d, receiving natural light through a glass roof until 50% budburst occurred in each tree (Experiment 1).

Experiment 6: soil temperature manipulation by chamber warming (tree seedlings) Three-year-old *B. pendula* seedlings were acquired from the same nursery as in Experiment 3 in October 2020. Trees were grown outside, had a height of 0.6–1.2 m and were potted in 10 cm × 10 cm × 15 cm pots. From 11 January to 2 February 2021, 12 seedlings were placed in each of two climate chambers (CLF Model LT-36VLX, LT-36VL; CLF Plant Climatics GmBH) with the setup allowing only the soil temp to differ. The original door was removed and replaced by an aluminum frame. The frame held 4-cm-thick Styrofoam blocks, which insulated the chamber. The Styrofoam blocks were inserted into the door frame, with stems of seedlings sticking out through the horizontal slits between the blocks (Fig. S2). Temperatures were measured both inside and outside (close to stem) the climate chambers using RT-a sensors (Meter Environment). Trees were watered every 3 d to keep soil moist in all pots. A 9-h photoperiod was set for the leaf buds, using an outlet timer to turn on and off the lights (2230 V, 200 lm, 6.5 W, 1300 K, Paulmann LED lamp; Paulmann Licht GmbH, Springe, Germany). Soil temperatures were monitored continuously with temperature sensors (TMS-4, TOMST for soil temperature and RT1 temperature logger). At the first visible cell swelling of the first bud on the first tree (before budburst), all seedlings were placed in the same chamber at once and spring temperature, and photoperiod was simulated until 50% budburst occurred in each tree (Experiment 1): 15/5°C, 12-h day length and light intensity of 200–300 μmol m^{-2} s^{-1}.

Experiment 7: soil temperature manipulation by chamber warming (tree seedlings) Soil temperature was manipulated as in Experiment 6. The control plants were placed in a climate chamber ($n = 12$; model: LT-36VLX; CLF Plant Climatics GmBH) set at 10°C and the treatment plants ($n = 12$) in another climate chamber set at 0°C. Temperature of soil inside the chambers and air outside the chambers on the bud surface was measured by temperature sensors (EL-USB-TC Logger with T-type Probe). Bud temperatures did not differ between treatments (12.6°C in control ± 3.8°C; 12.1°C in warm treatment ± 3.6°C). The plant positions were swapped every week. The soil manipulation lasted for 28 d (8 December 2021 to 5 January 2022). Plant positions and chamber settings were switched once a week. After temperature manipulation, all seedlings were placed in the same chamber (both soil and stems). The temperature inside the climate chamber was set to 16°C and the night temperature to 10°C. A 12-h photoperiod was set as in Experiment 6. The plants were inspected every 2 d until 50% budburst occurred in each tree (Experiment 1). Seedlings were watered as necessary to keep soil moisture even.

Experiment 8: soil temperature manipulation by wire warming (tree saplings) Three-year-old *B. pendula* saplings with the seed source as in Experiments 3 and 4 were purchased from the same tree nursery. The seedlings (1.5–1.8 m tall) were transplanted

into 20-l pots (30 cm in diameter and 30 cm tall) in October 2019 with a substrate composition of 50% fine sand and 50% peat (volume percentage) and watered as needed. Heating wires (BLOCK resistance wire: 1.5 mm 0.277 Ωm^{-1} A) were wrapped around bamboo sticks (1 cm in diameter and 30 cm long) and buried in the pots during the transplanting, with no current going through the control pots. The current was programmed to maintain a temperature close to 6°C warmer than control via a computer (Raspberry Pi 8968 860 3 Model B All-in-One Desktop PC). Electricity was provided by an extension cable from the main power socket. Trees were observed every second day until 50% budburst occurred in each tree (Experiment 1). All pots were watered as needed, and no significant difference in soil moisture was observed between treatments to a depth of 20 cm (Spectrum Technologies – FieldScout TDR 100).

Experiment 9: soil and air temperature manipulation (tree saplings) Concurrently with the soil manipulation in the field (Experiment 8), a subset of tree saplings was used to estimate the effect of combined air and soil temperature manipulation (vs soil only as in Experiments 2–8). Thirty *B. pendula* saplings were placed in each of two glasshouses and kept until 50% budbreak from 14 February to 23 March 2020. Temperature was kept *c.* 6°C warmer in the warmer glasshouse (14.6 ± 4°C vs 8.0 ± 4.6°C). Trees were observed every second day till 50% budburst (Experiment 1).

Statistical analysis

Experiment 1: A three-factorial ANOVA was used to test how tissue type (roots/buds), time of warming (October/January/February) and species (*F. sylvatica*/*P. nigra*) and their interactions affected the number of GDH required to initiate growth. Normal distribution and homogeneity of variance in the residuals were checked by diagnostic plots (residual vs fitted and normal Q–Q plots), and data were rank-transformed if not meeting these parametric assumptions. Statistical analyses and data visualization were conducted with the Program R (R Core Team, 2021) and packages 'GGPLOT2' (Wickham, 2016), 'EMMEANS' (Lenth, 2022) and 'DPLYR' (Wickham *et al.*, 2022).

Experiments 2–8: A meta-analysis was carried out to test for the effects of the soil temperature treatments (warmer vs colder) on the GDH required for budburst across the Experiments 2–8, as they all differed in experimental setup, sample size, timing, target species, temperature effect of the treatments, etc. The goal was to obtain robust pooled summary estimates from the individual experiments by taking the heterogeneity among them into consideration. Aggregating from the individual studies leads to higher statistical power of meta-analyses. We used the function metacont() of the R-package 'META' (Balduzzi *et al.*, 2019) to calculate common and random effects estimates for a meta-analysis with continuous outcome data, using inverse variance weighting for pooling.

Furthermore, we tested for the quantitative influence of soil temperature on bud burst by a linear least-squares regression, correlating the difference in soil GDH between the warmer and the colder treatment with the standardized mean difference of the GDH required to reach 50% budburst between the warmer and colder treatment for each experiment. The standardized mean was the difference in the mean of between warmer and colder treatments divided by the standard deviation of GDH in the respective experiment. The metric was used instead of mean differences as it allows more generalized analyses across different studies (Takeshima *et al.*, 2014). *Y*-intercept was set to 0.

For Experiment 9, a *t*-test was used to test the difference in mean GDH required for 50% budburst in the warming and control trees in the two glasshouses.

Results

### Experiment 1: shoots are dormant in winter, roots are not

Bud dormancy depth, expressed in the number of GDH to initiate growth was significantly greater than root dormancy depth ($F = 59.1$, $P < 0.001$; Fig. 1). While shoots showed the highest dormancy in late autumn and reduced dormancy depth thereafter, root dormancy was very low throughout the whole study period (Interaction Tissue × Time of sampling: $F = 35.1$, $P < 0.001$; Fig. 1). While the two tree species differed in dormancy and dormancy dynamics over time (Fig. 1; Table 3), they did not differ in the patterns of root vs shoot dormancy (no significant interaction between tissue and species in Table 3), thereby indicating that the observed differences between root and shoot dormancy patterns are generalizable across two species differing strongly in aboveground spring phenology. The higher variation in *F. sylvatica* leaf-out compared with *P. nigra* likely reflected the genetic variation within *F. sylvatica* in contrast to clonally propagated *P. nigra*.

Experiments 2–8: higher root-zone temperature advances budburst

Across all treatments, higher soil temperature resulted in buds requiring on average 390 less GDH as compared with buds of seedlings in nonwarmed soil ($P < 0.01$; Fig. 2 top panel), amounting to 0.75 GDH less warming required to initiate leaf-out per each additional GDH of soil warming. Standardizing the mean differences in GDH required for leaf-out between colder treatments and warmer treatments (C–W) confirmed that root warming advanced leaf-out (mean difference of −0.63 standard deviations; $P < 0.01$; Fig. 2 bottom panel). In experiments where more GDH was administered to roots relative to control, a greater advance in budburst timing was observed comparing warming treatment to control ($P = 0.004$, $r^2 = 0.75$; Fig. 3).

Comparison between soil (Experiment 8) vs air (and soil) warming effects on budburst timing (Experiment 9)

Experiments 8 and 9 allowed us to compare the effects of warming the soil only and warming the air and the soil via two subsets of tree seedlings, where one subset experienced different soil temperatures outside while another subset experienced different air
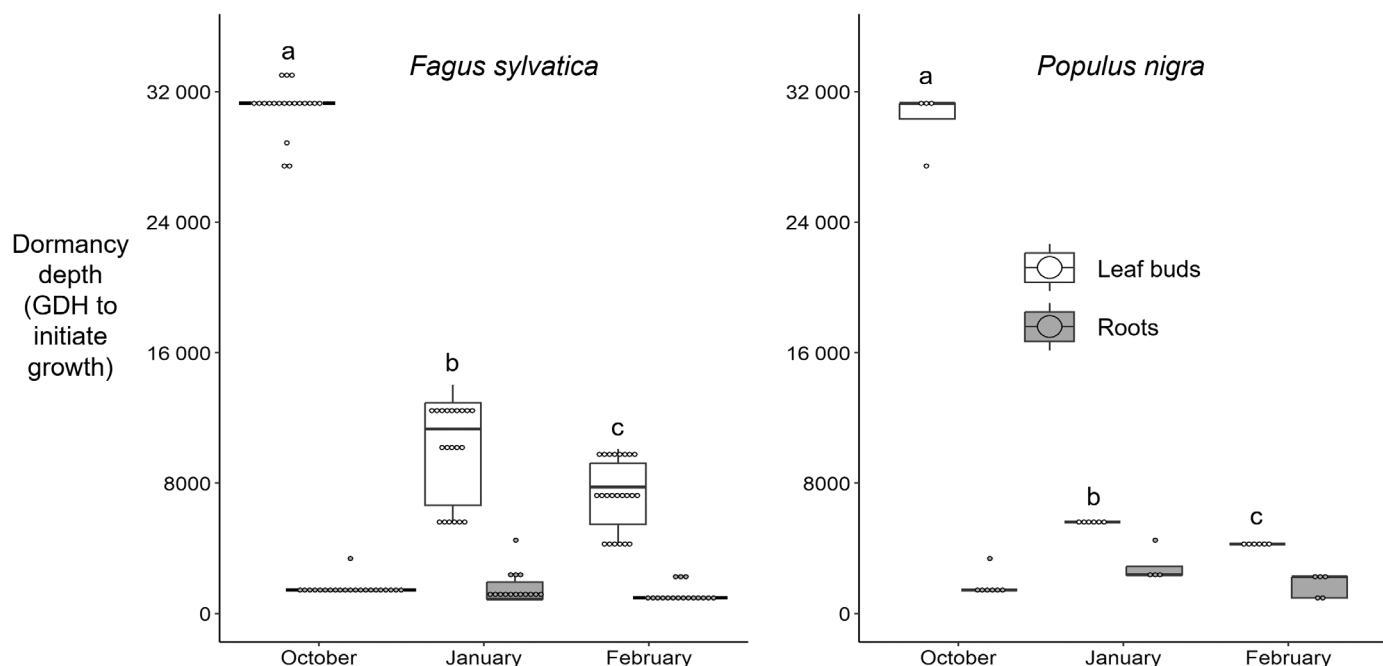
Fig. 1 Relative dormancy depth expressed as the number of growing degree hours $> 5°C$ required to initiate growth of buds and roots of two tree species sampled in different months. ANOVA results are found in Table 3. Horizontal lines show the medians, boxes indicate the 25th and 75th percentiles and the whiskers are ×1.5 the interquartile range. Lower case letters indicate homogeneous groups over time, separated by species, according to Tukey *post hoc* tests for shoots only as roots showed no significant changes with time. Each point represents a tree seedling.

and soil temperatures in two glasshouses. Soil warming alone via heated wires resulted in the accumulation of 3591 more GDH in the root-zone vs the control, resulting in 3.2-d advance in bud-burst. Air and soil warming, administered via warming in two separate glasshouse compartments resulted in the warmer compartment accumulating 5519 GDH more than the control and advancing budburst by 11 d. Soil warming thus resulted in 1025 GDH being required to advance budburst by 1 d while air warming (combined with soil warming) resulted in 488 GDH being required to advance budburst by 1 d. Therefore, the impact of soil warming alone made up 44% of the total spring warming effect on budburst timing. In terms of temporal leaf-out, warming of roots and buds advanced leaf-out by $1.7\,d\,°C^{-1}$ while warming roots alone advanced leaf-out by $0.6\,d\,°C^{-1}$, with root warming alone making up 34% of total temporal shift of spring phenology due to warming.

Table 3 Three-way ANOVA results from Experiment 1 testing the effect of species (*Fagus sylvatica* vs *Populus nigra*), time of sampling (October, January, February) and tissue type (roots vs shoots) on GDH required to initiate growth.

| Factor	df	F	P
Species	1	16.6	**< 0.001**
Time of sampling	2	132.3	**< 0.001**
Tissue	1	59.1	**< 0.001**
Species × Time of sampling	2	4.0	**0.02**
Species × Tissue	1	0.02	0.90
Time of sampling × Tissue	2	35.1	**< 0.001**
Species × Time of sampling × Tissue	2	1.2	0.29

Bold letters indicate significant effects.

Discussion

Shoots are dormant over winter, roots not

As expected, we found a clear pattern of very high dormancy in shoots in late autumn being gradually lifted over the course of the winter. These findings support the vast amount of knowledge on patterns of leaf bud dormancy (Laube *et al.*, 2014; Malyshev *et al.*, 2018; Beil *et al.*, 2021). However, in contrast to leaf buds, we observed no dormancy in roots (Fig. 1). Roots started to grow right after soils warmed, and thus clearly demonstrate the ability to grow under favorable conditions during the 'off-season' which buds and shoots do not. It had been previously shown that root growth can occur during winter (Radville *et al.*, 2016) and that roots of several temperate juvenile trees species are able to grow $> 2–4°C$ soil temperature (Schenker *et al.*, 2014). Root-zone temperature of the potted trees likely went $< 0°C$ before the January sampling date in Experiment 1 as mean daily air temperature reached $−6.7°C$ (soil was not insulated) at the field site 2 wk before sampling, being $−3°C$ a day before sampling. Readiness to start rapid regrowth in roots was thus not even influenced by prior sub-zero temperatures. The minimum warming sum required to visually detect root growth is likely to be even less than here reported as root photographs before 48 h of warming were not available across sampling dates. Additionally, root growth has been reported to occur before leaf-out in several temperate tree species (Reich *et al.*, 1980; Pritchard *et al.*, 2008; McCormack *et al.*, 2014). Several other previous studies have shown no earlier root growth with warming in (sub-)arctic plant communities (Radville *et al.*, 2016, 2018; Blume-Werry *et al.*,

Fig. 2 Upper panel: mean difference (MD) in the growing degree hours (GDH) required to reach 50% budbreak in *Fagus sylvatica* or *Betula pendula* for each experiment (see Table 1 for experiment details) and aggregated across all experiments (bold). Lower panel: standardized mean difference (SMD) in GDH required to reach 50% budbreak in warmed and non-warmed soil. Negative mean values indicate less GDH required to reach 50% budbreak in warmed soil. CI indicates the 95% confidence interval. I^2, the percentage of variation across studies that is due to heterogeneity rather than chance; P value, the probability of the null hypothesis that there is no heterogeneity between studies; Weight, weight of each individual experiment; τ^2, an estimate of the variance of the underlying distribution of true effect sizes.
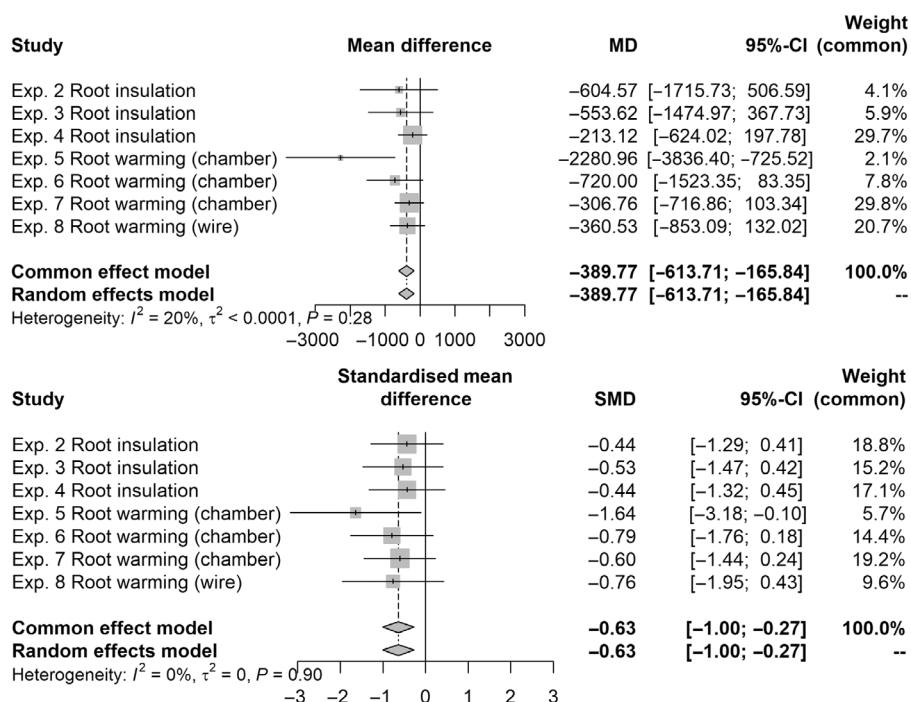
Fig. 3 Standardized mean difference (SMD) in the warming required to initiate budburst (growing degree hours, GDH) in warmer vs colder root soil temperature treatments, as explained by the difference in the GDH administered to tree roots in each experiment (5 cm depth). Each point represents a separate experiment on *Fagus sylvatica* or *Betula pendula* (see Table 1 for experiment details). Gray area shows the 95% confidence interval for the slope. Significance value (P) and coefficient of variation (r^2) of the linear regression with slope 0 are displayed.
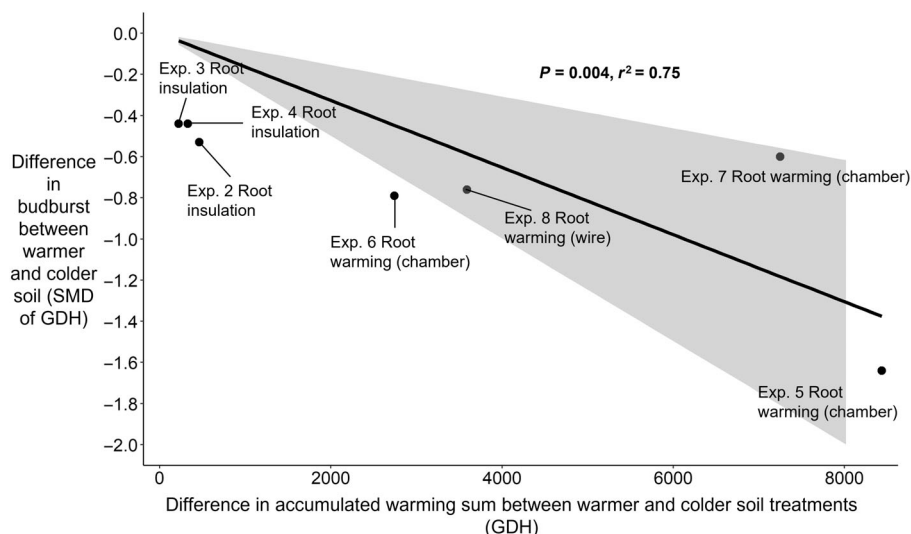
2017), potentially indicating that temperate species have a higher ability to resume root growth under favorable conditions whereas more northern species may possess some form of root dormancy.

Populus genus constitutes pioneer tree species whereby spring shoot phenology is mainly driven by chilling and warming sums (Laube *et al.*, 2014; Pliura *et al.*, 2014) while *F. sylvatica* is one of the latest flushing species of temperate Europe, relying on photoperiod in addition to chilling and warming sums (Vitasse & Basler, 2013; Malyshev *et al.*, 2018). Finding the same pattern of high shoot dormancy late in autumn which is lifted over winter vs no root dormancy throughout the winter in these two contrasting species supports the generality of our findings across tree species.

A lack of dormancy of roots in temperate forests has important biogeochemical implications. About 22% of biomass in forests is belowground (Ma *et al.*, 2021) and 22% of global terrestrial net primary production ends up belowground (McCormack *et al.*, 2015). Carbon is transferred to the soil via root exudation, which can comprise up to 10% of photosynthetically fixed carbon (Jones *et al.*, 2009) while additionally being supplemented by root turnover (McCormack *et al.*, 2014). If indeed roots can resume growth and activity at any time upon warming, warmer winters due to climate change, in particular in warm-temperate ecosystems not affected by snow (Kreyling *et al.*, 2020), will inevitably prolong the root growing season, increasing the input of labile carbon into the soil over winter. The initiation of root

growth and subsequent soil frost can also lead to reduced stem growth (Reinmann *et al.*, 2019; Weigel *et al.*, 2021). Root damage initiates compensatory root growth and the C allocation toward roots and short-term increase of the belowground C sink due to increased fine-root turnover decreases the energy reserves that could be invested into aboveground growth in a scenario of declining snow cover and increasing soil frost exposition (Gaul *et al.*, 2008). The fate of the additional carbon input into the soil, potentially leading to increased soil carbon accumulation or, on the contrary, boosted decomposition of soil organic matter due to a priming effect (Kuzyakov, 2010; Keuper *et al.*, 2020), remains to be studied. Apart from carbon fluxes, the timing of root growth also influences seasonal fluxes of water and nutrients, timing of soil resource uptake (Matamala *et al.*, 2003), and competition between plant species (Harris, 1977). Despite this importance, root phenology is usually not specifically implemented in models, most terrestrial ecosystem models are based on leaf phenology only and implicitly assume the same timing for belowground production and activity (Delpierre *et al.*, 2016). However, if roots are not dormant and start to grow under higher soil temperatures outside the 'growing season', we may be missing out on important biogeochemical patterns.

A recent meta-analysis suggested that there is a potential for continued future decoupling of above and belowground phenology in woody plants with warming extending the belowground growing season by 2.25 d per degree of increase in temperature and no aboveground changes (Blume-Werry, 2022; Liu *et al.*, 2022). While their meta-analysis suggested a stronger decoupling of above and belowground growth with warming, Liu *et al.* (2022) could only include < 10 studies that measured both above and belowground phenology on the same plants or plant communities. Our study, thus, is an important contribution and further shows that solely concentrating on growth patterns of aboveground phenology misses out on important belowground patterns and illustrates a potential mechanism for the responsiveness of roots, that is a lack of dormancy and, thus, an ability to resume growth whenever conditions are favorable.

Warmer soils speed up leaf bud burst

We showed here that soil warming during winter and spring speeds up aboveground phenology over a range of different experimental settings and in two contrasting tree species (Figs 2, 3). The strong relationship between the amount of soil warming and the advance in aboveground bud burst (Fig. 3) supports the causality of this effect. Based on the readiness of roots to grow as soon as the soil temperature rises (Fig. 1; Schenker *et al.*, 2014), we assume that root activity hastens budburst. Nonetheless, physiological root activity increase with warming has not been quantified in this study and requires further tests. Similar to the here observed advance in budburst when soils are warmed, bud burst in several fir and pine species has been shown to be delayed by cold soils (Lopushinsky & Max, 1990), and shoot growth of peach seedlings was suppressed by cooler root-zone temperature (Tagliavini & Looney, 2019). As our warming treatments started

at the end of autumn, lasting at times up to budburst, it is likely that the buds underwent the transition from endodormancy and ecodormancy during the warming treatment. Thus, the specific effects of warming on bud dormancy during different dormancy stages need further testing. Although roots required the same minimum warming sum to start growing in the fall and winter, the warming sum needed to initiate above- and belowground growth is similar in the spring and diverges more earlier in the winter. Thus, the earlier the warming will take place in the future, the more likely will the roots start growing much earlier than the leaves, increasing the aboveground vs belowground growth differences.

How exactly increased root activity due to higher soil temperatures may advance aboveground growth initiation is not clear, although it is reasonable to assume that plant hormones, which are transported upwards in the xylem from roots to shoots and buds signal the initiation of aboveground growth (Lacombe & Achard, 2016). One of these potential compounds is gibberellin, which is needed for shoot elongation, and bud burst is dependent on sufficient gibberellin levels (Cooke *et al.*, 2012). Root-borne gibberellin likely plays an important role in growth responses to temperature of the whole plant (Tagliavini & Looney, 2019). For example, low soil temperatures delay bud activity of Douglas fir, via delayed gibberellin transport from roots to shoots (Lavender *et al.*, 1973). Recently, it has also been demonstrated that temperature affects the concentration of gibberellin in the xylem of Arabidopsis and that root-derived gibberellin contributes substantially to temperature-induced shoot growth (Camut *et al.*, 2019). Additionally, root warming may increase root-synthesized cytokinins and abscisic acid, which can hasten budbreak (Greer *et al.*, 2006). Another mechanism might be an imbalance of plant activity and, thus, a metabolic sink-source relationship that leads to an earlier bud burst to compensate for the increased root activity upon soil warming (Cooke *et al.*, 2012), as higher root-zone temperature mobilizes root carbohydrate reserves (Rogiers *et al.*, 2009). The effect size of soil warming on aboveground spring phenology was surprisingly high in our experiments. Per GDH, soil root warming resulted in 44% of the budburst advance vs when air (and soil) was warmed. The relative soil warming effect can only be taken as a preliminary estimate as other factors such as soil warming not uniformly warming adult trees roots at different depths were not addressed. For example, species or younger trees that have shallower rooting depths may be more strongly affected as a higher percentage of their roots will experience stronger temperature changes when located in the upper soil horizon. Additionally, species with later aboveground dormancy release, such as beech, may have a different influence of root-zone temperature. As both effects commonly occur in combination, the substantial contribution of soil warming on bud burst timing has received little attention so far. Further experiments could keep soil temperature constant while air temperature is manipulated, to compare with solely root temperature manipulation, giving a more refined estimate of above- vs belowground warming effects.

Practically, there are conditions when air and soil temperatures are decoupled and the strong effect of soil temperature can result in contrasting responses of aboveground phenology to the

prevailing air temperature effects. Snow, for example, effectively insulates and thus decouples air from soil temperature (Sturm *et al.*, 1997; Groffman *et al.*, 2001) and can reduce soil frost or prevent soils from freezing even in boreal ecosystems with very cold winters (Isard & Schaetzl, 1998; Kreyling & Henry, 2011). This insulation likely contributes to allowing plants to resume activity relatively early in the spring. Snow cover, however, is declining by 5.3 d per decade since winter 1972–1973 in the northern hemisphere (Choi *et al.*, 2010), resulting in the phenomenon of 'colder soils in a warmer world' in cold-temperate regions (Groffman *et al.*, 2001). Here, frost events may still occur during single cold spells, but the insulating snow cover is starting to diminish (Kreyling *et al.*, 2020). In addition to snow, other soil insulation such as lichen, moss and leaf litter may also insulate soils from cold temperatures and in turn affect spring budburst. Colder soils due to missing snow cover may thus delay bud burst if the initiation of root growth is delayed due to increased soil frost duration (Blume-Werry *et al.*, 2016). On the contrary, more frequent warm spells, which cause declining snow cover, can also advance root production. In any case, earlier warming of the soil will likely advance leaf-out stronger as otherwise expected, with the potential for frost damage remaining in the future. Species-specific differences in root frost tolerance may also become more important in the future, with reduced snow cover and potentially continued occurrence of frosts (Kreyling *et al.*, 2020).

Climate change-induced warming is most pronounced in winter (IPCC, 2022), and it seems likely that the effects of warmer winters on bud burst, via their influence on root activity, depend on the site-specific soil temperature and prevailing winter temperature. As tree species distribution of *B. pendula* and *F. sylvatica* span from snow-free regions to regions of thick snow cover, the same change in air temperature may have differential effects on spring phenology in different areas due to different soil temperature changes.

In conclusion, warming nondormant roots of temperate trees is an important factor in regulating the aboveground growth onset. Belowground processes related to root activity will likely continue to temporally diverge from the onset of aboveground growth onset due to the absence of dormancy in temperate trees. The earlier the onset of warmer temperatures, the greater the mismatch will likely be, albeit factors such as snow cover and rooting depth may modify this trend. Soil processes coupled to root growth, such as nutrient cycling and carbon addition to the soil may accelerate greater under warming and need to be examined closer with respect to species-specific rooting profiles and leaf bud dormancy.

Competing interests

None declared.

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Data availability

Data used in the statistical analyses are available in the electronic supplementary table.

References

Abramoff RZ, Finzi AC. 2015. Are above- and below-ground phenology in sync? *New Phytologist* 205: 1054–1061.

Balduzzi S, Rücker G, Schwarzer G. 2019. How to perform a meta-analysis with R: a practical tutorial. *Evidence-Based Mental Health* 22: 153–160.

Baumgarten F, Zohner CM, Gessler A, Vitasse Y. 2021. Chilled to be forced: the best dose to wake up buds from winter dormancy. *New Phytologist* 230: 1366–1377.

Beil I, Kreyling J, Meyer C, Lemcke N, Malyshev AV. 2021. Late to bed, late to rise – warmer autumn temperatures delay spring phenology by delaying dormancy. *Global Change Biology* 27: 5806–5817.

Blume-Werry G. 2022. The belowground growing season. *Nature Climate Change* 12: 11–12.

Blume-Werry G, Jansson R, Milbau A. 2017. Root phenology unresponsive to earlier snowmelt despite advanced above-ground phenology in two subarctic plant communities. *Functional Ecology* 31: 1493–1502.

Blume-Werry G, Wilson SD, Kreyling J, Milbau A. 2016. The hidden season: growing season is 50% longer below than above ground along an arctic elevation gradient. *New Phytologist* 209: 978–986.

Camut L, Regnault T, Sirlin-Josserand M, Sakvarelidze-Achard L, Carrera E, Zumsteg J, Heintz D, Leonhardt N, Lange MJP, Lange T et al. 2019. Root-derived GA12 contributes to temperature-induced shoot growth in Arabidopsis. *Nature Plants* 5: 1216–1221.

Champagnat P. 1989. Rest and activity in vegetative buds of trees. *Annales des Sciences Forestières* 46: 9s–26s.

Choi G, Robinson DA, Kang S. 2010. Changing northern hemisphere snow seasons. *Journal of Climate* 23: 5305–5310.

Cooke JEK, Eriksson ME, Junttila O. 2012. The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms. *Plant, Cell & Environment* 35: 1707–1728.

Delpierre N, Vitasse Y, Chuine I, Guillemot J, Bazot S, Rutishauser T, Rathgeber CBK. 2016. Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. *Annals of Forest Science* 73: 5–25.

Fu YH, Piao S, Vitasse Y, Zhao H, De Boeck HJ, Liu Q, Yang H, Weber U, Hänninen H, Janssens IA. 2015. 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.

Fu YH, Zhang X, Piao S, Hao F, Geng X, Vitasse Y, Zohner C, Peñuelas J, Janssens IA. 2019. Daylength helps temperate deciduous trees to leaf-out at the optimal time. *Global Change Biology* 25: 2410–2418.

Gaul D, Hertel D, Leuschner C. 2008. Effects of experimental soil frost on the fine-root system of mature Norway spruce. *Journal of Plant Nutrition and Soil Science* 171: 690–698.

Greer DH, Wünsche JN, Norling CL, Wiggins HN. 2006. Root-zone temperatures affect phenology of bud break, flower cluster development, shoot extension growth and gas exchange of 'Braeburn' (*Malus domestica*) apple trees. *Tree Physiology* 26: 105–111.

Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL. 2001. Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry* 56: 135–150.

Harrington CA, Gould PJ, St.Clair JB. 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. *Forest Ecology and Management* 259: 798–808.

Harris GA. 1977. Root phenology as a factor of competition among grass seedlings. *Journal of Range Management* 30: 172.

Hegland SJ, Nielsen A, Lázaro A, Bjerknes A-L, Totland Ø. 2009. How does climate warming affect plant–pollinator interactions? *Ecology Letters* 12: 184–195.

IPCC. 2022. Climate change 2022: impacts, adaptation, and vulnerability. In: Pörtner H-O, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V *et al.*, eds. *Contribution of Working Group II to the sixth assessment report of the Intergovernmental Panel on Climate Change.* Cambridge, UK: Cambridge University Press, 3056.

Isard SA, Schaetzl RJ. 1998. Effects of winter weather conditions on soil freezing in southern Michigan. *Physical Geography* 19: 71–94.

Jones DL, Nguyen C, Finlay RD. 2009. Carbon flow in the rhizosphere: carbon trading at the soil-root interface. *Plant and Soil* 321: 5–33.

Keuper F, Wild B, Kummu M, Beer C, Blume-Werry G, Fontaine S, Gavazov K, Gentsch N, Guggenberger G, Hugelius G *et al.* 2020. Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere priming. *Nature Geoscience* 13: 1–6.

Kindermann J, Würth G, Kohlmaier GH, Badeck F-W. 1996. Interannual variation of carbon exchange fluxes in terrestrial ecosystems. *Global Biogeochemical Cycles* 10: 737–755.

Kreyling J, Henry HAL. 2011. Vanishing winters in Germany: soil frost dynamics and snow cover trends, and ecological implications. *Climate Research* 46: 269–276.

Kreyling J, Schumann R, Weigel R. 2020. Soils from cold and snowy temperate deciduous forests release more nitrogen and phosphorus after soil freeze–thaw cycles than soils from warmer, snow-poor conditions. *Biogeosciences* 17: 4103–4117.

Kuzyakov Y. 2010. Priming effects: interactions between living and dead organic matter. *Soil Biology and Biochemistry* 42: 1363–1371.

Lacombe B, Achard P. 2016. Long-distance transport of phytohormones through the plant vascular system. *Current Opinion in Plant Biology* 34: 1–8.

Lahti M, Aphalo PJ, Finér L, Ryyppö A, Lehto T, Mannerkoski H. 2005. Effects of soil temperature on shoot and root growth and nutrient uptake of 5-year-old Norway spruce seedlings. *Tree Physiology* 25: 115–122.

Laube J, Sparks TH, Estrella N, Höfler J, Ankerst DP, Menzel A. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20: 170–182.

Lavender DP, Sweet GB, Zaerr JB, Hermann RK. 1973. Spring shoot growth in Douglas-fir may be initiated by gibberellins exported from the roots. *Science* 182: 838–839.

Lenth R. 2022. EMMEANS: estimated marginal means, aka least-squares means. *R Package Version* 1: 2.

Lian X, Piao S, Li LZX, Li Y, Huntingford C, Ciais P, Cescatti A, Janssens IA, Peñuelas J, Buermann W *et al.* 2020. Summer soil drying exacerbated by earlier spring greening of northern vegetation. *Science Advances* 6: 1–12.

Liu H, Wang H, Li N, Shao J, Zhou X, van Groenigen KJ, Thakur MP. 2022. Phenological mismatches between above- and belowground plant responses to climate warming. *Nature Climate Change* 12: 97–102.

Lopushinsky W, Max TA. 1990. Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. *New Forests* 4: 107–124.

Ma H, Mo L, Crowther TW, Maynard DS, van den Hoogen J, Stocker BD, Terrer C, Zohner CM. 2021. The global distribution and environmental drivers of aboveground versus belowground plant biomass. *Nature Ecology and Evolution* 5: 1110–1122.

Makoto K, Wilson SD, Sato T, Blume-Werry G, Cornelissen JHC. 2020. Synchronous and asynchronous root and shoot phenology in temperate woody seedlings. *Oikos* 129: 643–650.

Malyshev AV, Henry HAL, Bolte A, Arfin Khan MAS, Kreyling J. 2018. Temporal photoperiod sensitivity and forcing requirements for budburst in temperate tree seedlings. *Agricultural and Forest Meteorology* 248: 82–90.

Marchi M, Castellanos-Acuña D, Hamann A, Wang T, Ray D, Menzel A. 2020. ClimateEU, scale-free climate normals, historical time series, and future projections for Europe. *Scientific Data* 7: 1–9.

Matamala R, Gonzàlez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH. 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* 302: 1385–1387.

McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM. 2014. Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* 95: 2224–2235.

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari HS, Hobbie EA, Iversen CM, Jackson RB *et al.* 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207: 505–518.

Piao S, Liu Q, Chen A, Janssens IA, Fu Y, Dai J, Liu L, Lian X, Shen M, Zhu X. 2019. Plant phenology and global climate change: current progresses and challenges. *Global Change Biology* 25: 1922–1940.

Pliura A, Suchockas V, Sarsekova D, Gudynaitė V. 2014. Genotypic variation and heritability of growth and adaptive traits, and adaptation of young poplar hybrids at northern margins of natural distribution of *Populus nigra* in Europe. *Biomass and Bioenergy* 70: 513–529.

Pritchard SG, Strand AE, McCormack ML, Davis MA, Finzi AC, Jackson RB, Matamala R, Rogers HH, Oren R. 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO_2-enrichment: a six-year-minirhizotron study. *Global Change Biology* 14: 588–602.

R Core Team. 2021. *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Radville L, McCormack ML, Post E, Eissenstat DM. 2016. Root phenology in a changing climate. *Journal of Experimental Botany* 67: 3617–3628.

Radville L, Post E, Eissenstat DM. 2018. On the sensitivity of root and leaf phenology to warming in the Arctic. *Arctic, Antarctic, and Alpine Research* 50: S100020.

Reich PB, Teskey RO, Johnson PS, Hinckley TM. 1980. Periodic root and shoot growth in oak. *Forest Science* 26: 590–598.

Reinmann AB, Susser JR, Demaria EMC, Templer PH. 2019. Declines in northern forest tree growth following snowpack decline and soil freezing. *Global Change Biology* 25: 420–430.

Richardson AD, Black TA, Ciais P, Delbart N, Friedl MA, Gobron N, Hollinger DY, Kutsch WL, Longdoz B, Luyssaert S *et al.* 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 365: 3227–3246.

Rogiers SY, Clarke SJ, Schmidtke LM. 2009. Elevated root-zone temperature hastens vegetative and reproductive development in Shiraz grapevines. *Australian Journal of Grape and Wine Research* 20: 123–133.

Schenker G, Lenz A, Körner C, Hoch G. 2014. Physiological minimum temperatures for root growth in seven common European broad-leaved tree species. *Tree Physiology* 34: 302–313.

Solly EF, Brunner I, Helmisaari HS, Herzog C, Leppälammi-Kujansuu J, Schöning I, Schrumpf M, Schweingruber FH, Trumbore SE, Hagedorn F. 2018. Unravelling the age of fine roots of temperate and boreal forests. *Nature Communications* 9: 1–8.

Steinaker DF, Wilson SD, Peltzer DA. 2010. Asynchronicity in root and shoot phenology in grasses and woody plants. *Global Change Biology* **16**: 2241–2251.

Sturm M, Holmgren J, König M, Morris K. 1997. The thermal conductivity of seasonal snow. *Journal of Glaciology* **43**: 26–41.

Tagliavini M, Looney NE. 2019. Response of peach seedlings to root-zone temperature and root-applied growth regulators. *HortScience* **26**: 870–872.

Takeshima N, Sozu T, Tajika OY, Hayasaka Y, Fukurawa T. 2014. Which is more generalizable, powerful and interpretable in meta-analyses, mean difference or standardized mean difference? *BMC Medical Research Methodology* **14**: 30.

Vitasse Y, Basler D. 2013. What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research* **132**: 1–8.

Vitasse Y, Lenz A, Körner C. 2014. The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science* **5**: 1–12.

Vitra A, Lenz A, Vitasse Y. 2017. Frost hardening and dehardening potential in temperate trees from winter to budburst. *New Phytologist* **216**: 113–123.

Weigel R, Henry HAL, Beil I, Gebauer G, Jurasinski G, Klisz M, van der Maaten E, Muffler L, Kreyling J. 2021. Ecosystem processes show uniform sensitivity to winter soil temperature change across a gradient from central to cold marginal stands of a major temperate forest tree. *Ecosystems* **24**: 1545–1560.

Weigel R, Muffler L, Klisz M, Kreyling J, van der Maaten-Theunissen M, Wilmking M, van der Maaten E. 2018. Winter matters: sensitivity to winter climate and cold events increases toward the cold distribution margin of European beech (*Fagus sylvatica* L.). *Journal of Biogeography* **45**: 2779–2790.

Wickham H. 2016. GGPLOT2: *elegant graphics for data analysis*. New York, NY, USA: Springer.

Wickham H, François R, Henry L, Müller K. 2022. DPLYR: a grammar of data manipulation. *R Package Version 1.0.9.*

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Results of the dormancy Experiment 1.

Dataset S2 Results of the root-zone warming experiments (Experiments 2–8).

Fig. S1 Rhizotron used in Experiment 1 with the transparent bottom of the pot.

Fig. S2 Experimental setup of methods used to create different root-zone temperatures in mature and juvenile trees.

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