



Duration of wood formation phases in Scots pine and Norway spruce lengthens towards the south in the Nordic countries

Magdalena Held^{a,1,*}, Anna Lintunen^{a,b,2}, Tuula Jyske^{c,d,3}, Harri Mäkinen^{c,4}

^a Institute for Atmospheric and Earth System Research/Forest Sciences, Faculty of Agriculture and Forestry, University of Helsinki, Helsinki, Finland

^b Institute for Atmospheric and Earth System Research/Physics, Faculty of Science, University of Helsinki, Helsinki, Finland

^c Natural Resources Institute Finland, Helsinki, Finland

^d Faculty of Agriculture and Forestry, University of Helsinki, Helsinki, Finland

ARTICLE INFO

Keywords:

Wood growth
Xylem conduit formation
Picea abies
Pinus sylvestris
Tree growth
Environmental gradient

ABSTRACT

Environmental conditions such as temperature and light affect the wood formation of trees in complex ways, as cell division and each subsequent phase of wood formation may respond differently. We analyzed the influence of latitude and annual temperature sum on the dynamics of wood formation phases in the boreal conifers *Picea abies* (L.) Karst. and *Pinus sylvestris* L. Furthermore, we investigated the relationships of these dynamics with the number of conduits produced in a year. We found that wood formation phases started earlier and ended later at lower latitudes and years with higher temperature sum. However, latitude had a relatively weak explanatory power on the dynamics of the cell enlargement phase (i.e. the phase that starts earliest in the growing season) in *P. abies*, indicating a higher sensitivity to annually changing conditions like the temperature sum. Although the dynamics of the wood formation phases cannot directly affect the number of conduits produced, as this is determined by the preceding cell division, longer phases were associated with a greater number of conduits. This indicates that both cell division and the duration of the subsequent wood formation phases responded positively to the same conditions. Thus, in *P. abies* and *P. sylvestris* growing at latitudes from 60 ° to 67.5 °, warmer conditions, as expected under climate change, will enable a longer wood formation period and all its phases, and a higher wood production, at least until other factors become limiting.

1. Introduction

Wood formation varies greatly along environmental gradients, such as latitude, in response to changing growing conditions. Cells need to undergo different phases after cell division to become wood conduits. The timing, duration, and rate of each phase respond to environmental conditions in complex ways. Temperature, light, and water availability are the most important factors influencing the timing and rate of wood formation phases in Northern Hemisphere conifers (e.g., Buttò et al., 2012b; Cuny and Rathgeber, 2016; Huang et al., 2020; Jyske et al., 2014; Rossi et al., 2016).

Wood formation occurs above a certain temperature threshold, which can vary between sites and tree species (e.g., Anfodillo et al.,

2012; Deslauriers et al., 2008; Jyske et al., 2014). This makes ambient temperature a limiting factor in cold environments. Warm temperatures positively affect cambial activity, particularly in spring and early summer (Wodzicki, 1971; Lenz et al., 2013). Several studies have found an earlier onset of cambial activity, and thus wood formation, with increasing temperature along geographical gradients (Buttò et al., 2012b; Cuny et al., 2018; Deslauriers et al., 2008; Jyske et al., 2014; Rossi et al., 2016). Therefore, in temperature-limited environments, such as high-latitude and -altitude regions, where the growing season is lengthening due to climate warming, the period of wood formation may start earlier (Huang et al., 2020). This could result in a higher wood production during the growing season. However, a warmer cold season could have mixed effects on the onset of the growing season, as many

* Corresponding author.

E-mail address: magdalena.held@helsinki.fi (M. Held).

¹ orcid.org/0000-0001-5555-1385

² orcid.org/0000-0002-1077-0784

³ orcid.org/0000-0002-0459-4358

⁴ orcid.org/0000-0002-1820-6264

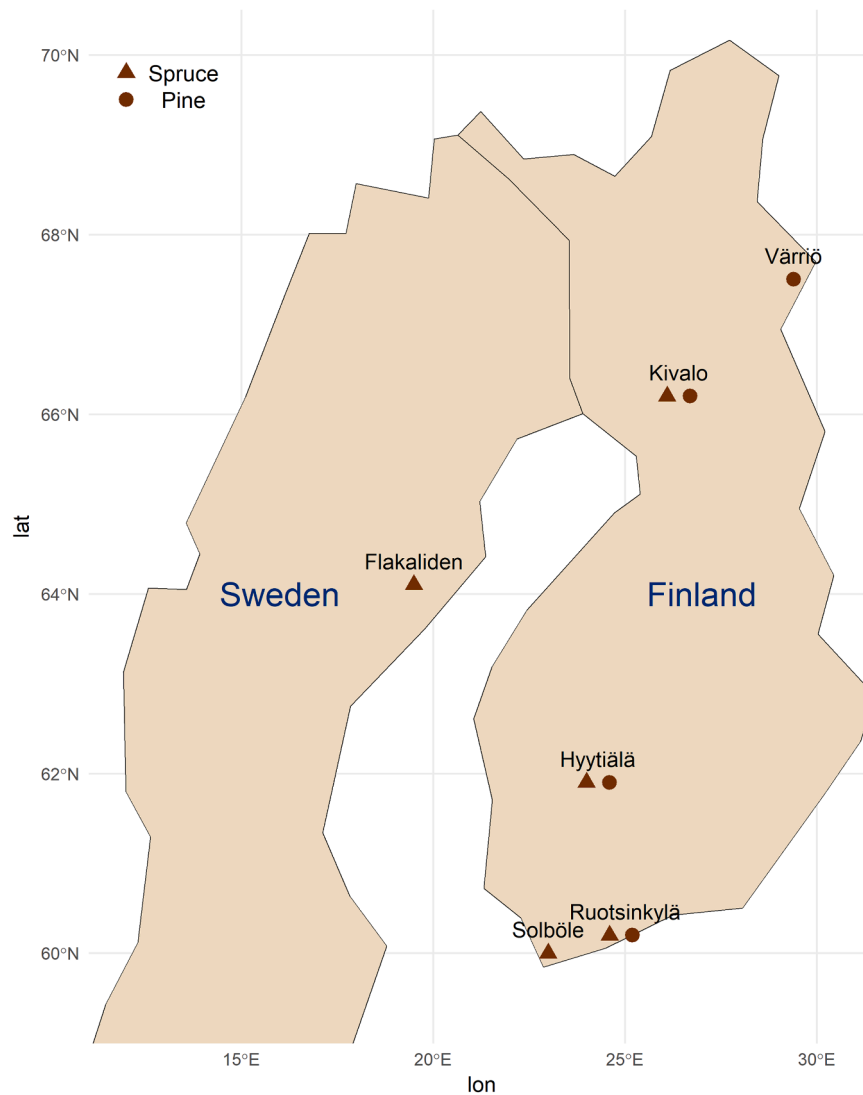


Fig. 1. Location of the study sites.

Table 1

Site characteristics.

Site a)	Latitude	Longitude	Altitude [m a. s. l.]	Mean annual temperature b)	Annual temperature sum c)	Forest type d)	Stand density [trees/ha]	Species e)	Sampled years	Country
Värriö	67.5	29.4	390	0.1 ± 0.8	688 ± 116	UEMT	770	Pine	2007–2009	Finland
Kivalo	66.2	26.4	140	2.1 ± 0.7	1099 ± 139	VMT	900	Spruce	2007, 2009, 2012	Finland
Flakaliden	64.1	19.5	310	2.7 ± 1.2	984 ± 125		2000	Pine	2007–2008	Sweden
Hyytiälä	61.9	24.3	181	4.1 ± 1	1255 ± 146	MT	1050	Spruce	2007–2010	Finland
						VT	1950	Pine	2007–2010	
Ruotsinkylä	60.2	25	60	6 ± 1	1605 ± 143	MT	1002	Spruce	2007–2012	Finland
Solböle f)	60	23	30	6.5 ± 1	1537 ± 110	OMT	380	Pine	2007–2010	
								Spruce	2007–2008	Finland

a) Finnish sites see Jyske et al. (2014), for Swedish site see Bergh et al. (1999)

b, c) from nearest weather station, averaged for the sampled years 2007–2012

d) forest types: MT = *Myrtillus* type, OMT = *Oxalis-Myrtillus* type, UEMT = *Uliginosum-Empetrum-Myrtillus* type, VMT = *Vaccinium myrtillus* type, VT = *Vaccinium* type

e) Tree species: Norway spruce (*Picea abies* [L.] Karst.), Scots pine (*Pinus sylvestris* L.).

f) trees from two different provenances: Muonio, Pieksämäki

tree species require a period of low temperatures to break winter dormancy (Delpierre et al., 2019). There is no consensus on the effect of temperature on the cessation of wood formation. Cuny et al. (2018) found no influence in *Picea abies* (L.) Karst. and *Larix decidua* Mill. trees

growing in Switzerland, however, Rossi et al. (2016) found wood formation to end later in warmer areas in Northern Hemisphere conifers, whereas (Buttò et al., 2012b) found an earlier cessation in *Picea mariana* (Mill.) B.S.P. in eastern Canada. In addition to cell division, the other

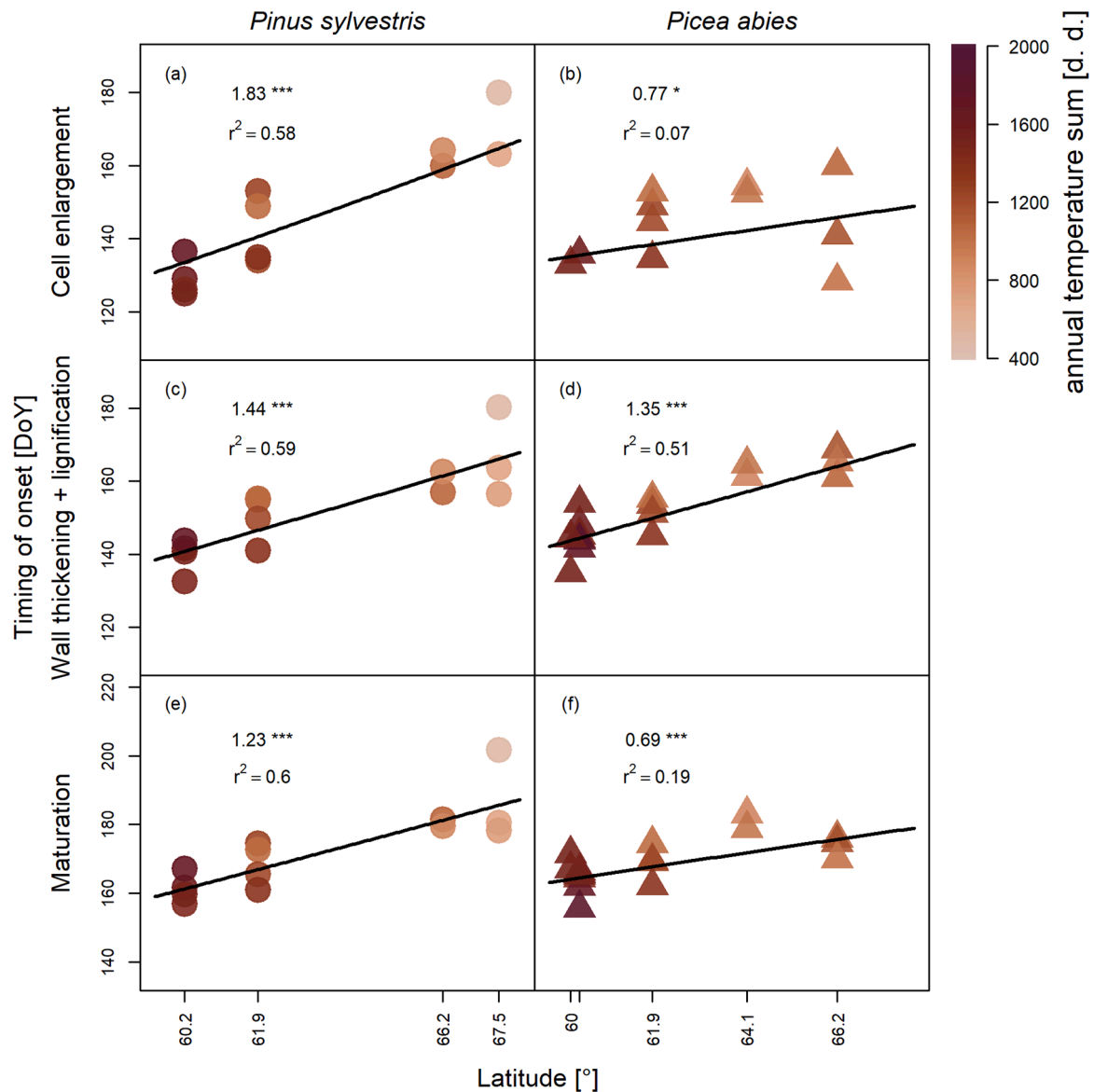


Fig. 2. Effect of latitude on the onset of the wood formation phases (cell enlargement, wall thickening and lignification, and maturation) in *Pinus sylvestris* and *Picea abies*. The lines were fitted with parameters resulting from REML models and indicate $p < 0.05$. The formulas show parameter b with its p -value (* < 0.05 , ** < 0.01 , *** < 0.001) and the marginal R^2 .

phases of wood formation have been found to start earlier in warmer environments (Deslauriers et al., 2008; Rossi et al., 2016). The annual cycle of light conditions is another key factor in the wood formation dynamics of Northern Hemisphere conifers (Buttò et al., 2012a; Huang et al., 2020).

In Finland, *P. sylvestris* and *P. abies* exhibit a shorter duration of wood formation at higher latitudes due to a later onset and earlier cessation of growth (Jyske et al., 2014). Similarly, Rossi et al. (2016) found an earlier onset, later cessation and longer duration of each wood formation phase with a higher mean annual temperature in conifers across the Northern Hemisphere.

Our study is a follow-up to Jyske et al. (2014) who analyzed the onset and cessation of conduit formation across a latitudinal gradient in Finland. We extend their study by analysing the dynamics of wood formation phases, i.e., the timing of onset and cessation, as well as the duration of each phase, in the two boreal conifer species *P. sylvestris* and *P. abies*. Our primary focus was to analyze how the dynamics of wood formation phases change along a latitudinal gradient and under different annual temperature sums. Furthermore, we investigated correlations

between the dynamics of wood formation phases and indicators of wood formation rate (i.e., number of conduits and ring width).

Our study aimed to analyze a) how the dynamics of wood formation phases vary with latitude and temperature sum, and b) the relationship between these dynamics with the final number of conduits and radial increment. We hypothesize that 1) at lower latitudes and higher temperature sums, the onset and cessation of wood formation phases occur earlier and later, respectively, resulting in longer durations, and 2) extended wood formation phases correlate with a higher final number of conduits and radial increment.

2. Material and methods

2.1. Species and sites

The material consisted of *Picea abies* and *Pinus sylvestris* trees in five stands across a latitudinal gradient ranging from 60 ° to 67.5 ° in Finland, as well as one *P. abies* stand in Sweden at 64.1 ° latitude (Fig. 1). Along with latitude, the altitude of the sites increased from 30 m a.s.l. in

Table 2
Site averages of timings and duration of wood formation phases.

Variable	Site/latitude	<i>Pinus sylvestris</i>	<i>Picea abies</i>
Onset of cell enlargement [DoY]	Värriö/67.5	170	
	Kivalo/66.2	164	140
	Flakaliden/64.1		153
	Hyytiälä/61.9	142	140
	Ruotsinkylä/60.2	131	136
	Solböle/60		133
	Värriö/67.5	167	
Onset of wall thickening and lignification [DoY]	Kivalo/66.2	160	165
	Flakaliden/64.1		163
	Hyytiälä/61.9	148	151
	Ruotsinkylä/60.2	140	146
	Solböle/60		137
	Värriö/67.5	187	
	Kivalo/66.2	180	174
Onset of maturation [DoY]	Flakaliden/64.1		181
	Hyytiälä/61.9	167	169
	Ruotsinkylä/60.2	161	125
	Solböle/60		169
	Värriö/67.5	215	
	Kivalo/66.2	176	207
	Flakaliden/64.1		242
Cessation of cell enlargement [DoY]	Hyytiälä/61.9	214	207
	Ruotsinkylä/60.2	245	231
	Solböle/60		243
	Värriö/67.5	236	
	Kivalo/66.2	244	236
	Flakaliden/64.1		252
	Hyytiälä/61.9	230	242
Cessation of wall thickening and lignification [DoY]	Ruotsinkylä/60.2	271	271
	Solböle/60		251
	Värriö/67.5	38	
	Kivalo/66.2	12	75
	Flakaliden/64.1		87
	Hyytiälä/61.9	69	62
	Ruotsinkylä/60.2	114	97
Duration of cell enlargement [days]	Solböle/60		82
	Värriö/67.5	76	
	Kivalo/66.2	75	69
	Flakaliden/64.1		89
	Hyytiälä/61.9	81	85
	Ruotsinkylä/60.2	129	125
	Solböle/60		113
Duration of wall thickening and lignification [days]	Värriö/67.5	57	
	Kivalo/66.2	66	62
	Flakaliden/64.1		71
	Hyytiälä/61.9	61	67
	Ruotsinkylä/60.2	108	108
	Solböle/60		75
	Värriö/67.5	70	
Duration of maturation [days]	Kivalo/66.2	80	100
	Flakaliden/64.1		98
	Hyytiälä/61.9	88	85
	Ruotsinkylä/60.2	141	133
	Solböle/60		118
	Värriö/67.5	70	
	Kivalo/66.2	80	100
Duration of wood formation [days]	Flakaliden/64.1		98
	Hyytiälä/61.9	88	85
	Ruotsinkylä/60.2	141	133
	Solböle/60		118
	Värriö/67.5	70	
	Kivalo/66.2	80	100
	Flakaliden/64.1		98

the south to 390 m a.s.l. in the northernmost site (Table 1). The southernmost stand (Solböle) belongs to a provenance trial comprising 19 provenances from Finland and Central Europe (Kalliokoski et al., 2012). However, we included only the two Finnish provenances in the present study. Further details of the sites can be found in the previous papers (Kalliokoski et al., 2012, 2013; Jyske et al., 2014; Mäkinen et al., 2018). For each site, we calculated daily temperature sums as the positive difference between the daily mean air temperature and a threshold of +5 °C and then summed these to give annual temperature sums (TS_{ann}), starting from the date when five consecutive days had a mean air temperature $\geq +5$ °C (Jyske et al., 2014). For details on the temperature data see Supplementary Table 1.

2.2. Sampling and sample preparation

From 2007–2012, three to nine dominant or co-dominant trees were sampled each study year at each site, but the number of study years varied from two to six between the sites (Table 1). Microcores were taken from each sample tree at breast height (1.3 m) using a Trephor tool (Rossi et al., 2006). This was done twice a week in spring and early summer and once a week in late summer and autumn.

The microcores were dehydrated using an ascending series of ethanol, cleared using Tissue-Clear (Tissue-Tek, Sakura Finetek, Tokyo, Japan), and immersed in liquid paraffin. The microcores were then embedded in paraffin blocks, from which radial sections were cut using a rotary microtome (Leitz 1516, Leica Microsystems, Wetzlar, Germany). These sections were then treated to remove the paraffin, stained and mounted on microscopic slides (see Jyske et al., 2014, for details).

2.3. Cell analysis

The number and width of current-year conduits were measured from digital images of the samples. Three phases of conduit differentiation were identified: (I) radial cell enlargement; (II) secondary cell wall thickening and lignification; and (III) mature conduits. Conduits in the enlargement phase are larger than cambial cells in the radial direction, and their primary cell walls show no birefringence under polarized light, allowing to distinguish the phases. In the secondary wall deposition and lignification phase, the cell walls of the conduits are birefringent and exhibit red and blue colors. The distinction between conduits forming a secondary wall and mature conduits was based on color (the cell walls of mature conduits are completely red, whereas the cell walls of conduits in the secondary wall deposition phase have also some blue) and cell wall thickness (the cell walls of mature conduits are thicker; Savidge, 2003).

2.4. Data preparation and analysis

For statistical analyses, we used R (version 4.5.0, R Core Team, 2025) in RStudio (version 2025.05.1 +513, Posit Posit team, 2025) by applying the package *tidyverse* (Wickham et al., 2019) for basic functions. We used the package *khroma* (Frerebeau, 2024) and the website *coblis* (Colblindor, accessed, 2025) to select a color scheme that is accessible to people with color vision deficiency for the plots.

We performed all analyses for each species and tree individual separately. For plotting, we averaged the data among tree individuals by year.

2.4.1. Determination of the onset, cessation, and duration of wood formation phases

The sampling interval varied between sites and years, and often also within years. In order to estimate the timing of wood formation phases (i.e., the date of onset and cessation, DoY) independently of the sampling interval, we applied generalized additive models (GAMs) to each tree in each year using the package *mgcv* (Wood, 2011).

Before applying the GAMs, we cleaned the dataset by removing cases where sampling started too late in spring or stopped too early in autumn,

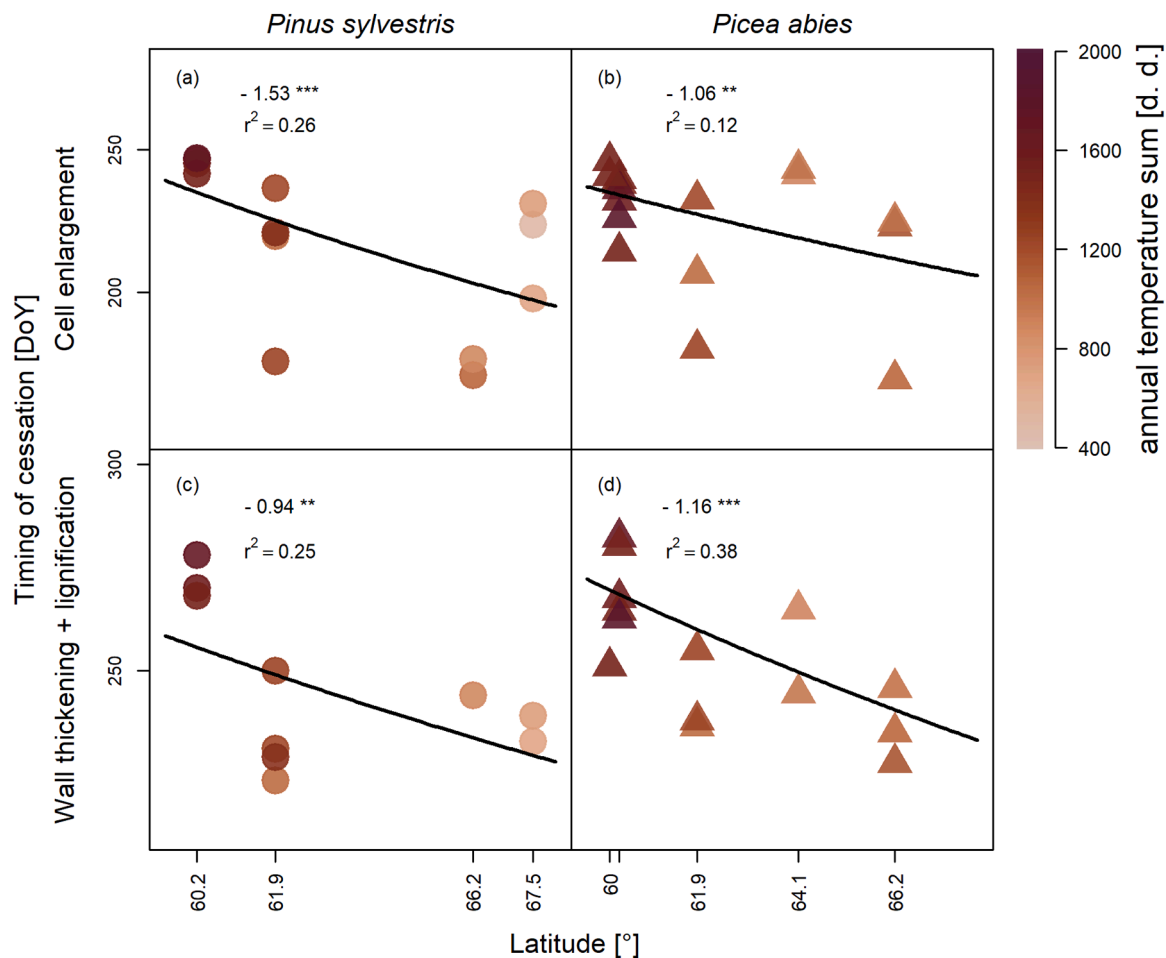


Fig. 3. Effect of latitude on the cessation of the wood formation phases (cell enlargement, and wall thickening and lignification) in *Pinus sylvestris* and *Picea abies*. Maturation ends when no more conduits are in any previous phase, thus we defined maturation to end together with wall thickening and lignification. The lines were fitted with parameters resulting from REML models and indicate $p < 0.05$. The formulas show parameter b with its p -value (* < 0.05 , ** < 0.01 , *** < 0.001) and the marginal R^2 .

resulting in the missed onset or cessation of some wood formation phases. If only the onset or cessation was missed, we still used that case to analyze the other. To determine whether the onset or cessation of a phase had been missed, we calculated a cut-off as 10% of the mean number of cells (excluding zeros and missing values) in the respective phase. We excluded cases in which the first or last observation of the growing season had a cell number higher than the cut-off from analyzing the timing of the onset or cessation, respectively.

We then created a function that applied GAMs to each tree, for each year, and then returned the first or last DoY at which the cell number in the respective phase exceeded a certain threshold. For onsets, we set the threshold to one cell. For cessations, we reduced the threshold, so that the model produced a value between the last day with a cell number above 0 and the next recorded day. We chose a threshold of 0.3 cells for the cessation of phase I and 0.4 cells for the cessation of phase II (phase III ends with phase II).

We calculated the duration of phases I and II by subtracting the DoY of onset from the DoY of cessation of the respective phase. To calculate the duration of phase III, we subtracted the DoY of phase III onset from the DoY of phase II cessation. To calculate the duration of wood formation, we subtracted the DoY of the phase I onset from the DoY of the phase II cessation. We performed these calculations for each tree separately. Cases where the onset or cessation of a phase was missed were omitted from the calculations.

2.4.2. Testing the effect of the site on the dynamics of wood formation

To test the effects of latitude and annual temperature sum on the dynamics of wood formation, we first used Shapiro-Wilk tests to check the variables for normality. As at least one variable did not meet the normality assumption in every tested relationship, we log10-transformed all data to comply with the assumptions of normality and homoscedasticity (Zar, 1999). Then, we applied linear mixed-effects models fitted with restricted maximum likelihood (REML) using the package *lme4* (Bates et al., 2015) to test the effects of latitude or TS_{ann} on the dynamics of wood formation, i.e., on the onset, cessation, and duration of each growth phase and the duration of wood formation. In each case, we included the effects of year and tree individual as random factors. We extracted R^2 using the package *MuMIn* (Bartoń, 2025) and p -values using the package *lmerTest* (Kuznetsova et al., 2017).

2.4.3. Testing the effect of wood formation phases and site on the wood production

We only selected trees in each year for which the cessation of wood formation (i.e., the cessation of wall thickening and lignification) was successfully recorded. Then, on the last recorded DoY, we extracted the total number of mature conduits (N) and summed the radial diameter of each matured conduit to calculate the total radial increment (R), representing the tree ring width. For phase II, we calculated the number of conduits in each sample throughout the growing season. After excluding cases with missed onset or cessation, we estimated the timing of maximum cell number ($max_{phaseII}$). We did not calculate this variable for

Table 3

Linear mixed-effects models with restricted maximum likelihood (REML) testing the effects of annual temperature sum and latitude on the listed variables. For the effects of latitude on variables of wood formation dynamics see Figs. 2–4.

	<i>Pinus sylvestris</i>			<i>Picea abies</i>		
	<i>b</i>	<i>p</i>	R_m^2	<i>b</i>	<i>p</i>	R_m^2
Annual temperature sum						
Onset of cell enlargement [DoY]	-	***	0.58	-	***	0.29
Onset of wall thickening and lignification [DoY]	-0.2	***	0.66	-	***	0.59
Onset of maturation [DoY]	-	***	0.65	-	***	0.39
Cessation of cell enlargement [DoY]	0.17	**	0.15	0.15	*	0.08
Cessation of wall thickening and lignification [DoY]	0.17	***	0.36	0.19	***	0.32
Duration of cell enlargement [days]	0.82	.	0.09	1.76	**	0.14
Duration of wall thickening and lignification [days]	0.65	***	0.43	0.81	***	0.4
Duration of maturation [days]	0.8	***	0.43	0.77	***	0.1
Duration of wood formation [days]	0.83	**	0.53	0.18		0.01
Final conduit number	0.96	***	0.32	1.22	***	0.33
Radial increment [mm]	0.88	***	0.23	1.42	***	0.26
timing of $max_{phaseII}$ [DoY]	-	***	0.86	-	***	0.66
	0.01			0.01		
Latitude						
Final conduit number	-6.6	***	0.29	-6	***	0.22
Radial increment [μ m]	-	***	0.22	-5.8	***	0.13
	6.46					
timing of $max_{phaseII}$ [DoY]	-		< 0.01	0.01		< 0.01
	0.01					

b = slope of the curve $y = a + x^b$ fitted with REML models
 $max_{phaseII}$ = maximum cell number in phase wall thickening and lignification
 $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, R_m^2 = R^2 marginal.

phase I, as cases with a missed onset may have also missed the timing of maximum cell number. We tested the variables for normality, log10-transformed the data if necessary and applied REML. We tested models with the effects of growth dynamics (i.e., onset, cessation, or duration of wood formation phases or wood formation), latitude, or TS_{ann} on N and R . Furthermore, we tested models with the effects of latitude or temperature on the timing of $max_{phaseII}$. We included the effects of tree individual and year as random factors.

3. Results

In both *P. sylvestris* and *P. abies*, the onset of all three phases of wood formation occurred earlier (Fig. 2; Table 2) and the cessation later (Fig. 3; Table 2) at lower latitudes and in years with a higher annual temperature sum (TS_{ann} ; Table 3). However, the marginal R^2 (R_m^2) indicates that latitude had low explanatory power, particularly for the onset of phases I and III, as well as the cessation of phase I in *P. abies*.

Consequently, all phases of wood formation were longer in both species at lower latitudes and with higher TS_{ann} (Fig. 4a–f; Table 3). As for onset and cessation, R_m^2 indicates that latitude had low explanatory power for phase I duration in *P. abies*. Notably, the explanatory power of latitude on the duration of phases II and III was lower in *P. sylvestris* than *P. abies*. The total duration of wood formation showed higher plasticity with latitude and TS_{ann} in *P. sylvestris* than in *P. abies* (Fig. 4g, h; Table 3).

A higher TS_{ann} allowed for an earlier occurrence of the $max_{phaseII}$ in both species (Table 3). However, there was no effect of latitude on the timing of $max_{phaseII}$ in either species (Supplementary Figures S1 and S2).

In both *P. sylvestris* and *P. abies*, an earlier onset and later cessation of each wood formation phase indicated a greater number of mature conduits (N) and higher radial increment (R ; Figs. 5–8). In *P. sylvestris*, a longer duration of phases I–III indicated higher N and R (Figs. 5f–h and 7f–h), though the correlation between phase I and R was only tendential

($p < 0.1$). In *P. abies*, only the duration of phases II and III positively correlated with N and R (Figs. 6g–h and 8g–h), indicating that phase I had minimal impact on radial increment in both species. In both species, TS_{ann} had a positive effect, while latitude had a negative effect on N and R (Table 3).

4. Discussion

Our study provides new evidence that changes in temperature and light along a latitudinal gradient greatly affect the dynamics of wood formation phases in the two boreal conifer species, *Pinus sylvestris* and *Picea abies*. More favorable conditions for growth in the south allow for longer duration of wood formation phases, and a higher number of conduits and annual radial wood increment.

4.1. Growth dynamics

Overall, the changes in the timing of the wood formation phases in *P. sylvestris* and *P. abies* along a latitudinal gradient from 60° to 67.5° are consistent with our preceding study (Jyske et al., 2014) and with Rossi et al. (2016) findings for conifers in the Northern Hemisphere. Lower latitudes allow for an earlier onset and later cessation of each wood formation phase, resulting in a longer duration. However, in our study, the timing and duration of phase I (cell enlargement) in *P. abies* had only weak relationships (low R_m^2) with latitude due to high annual variation (Figs. 2b, 3b, and 4b). This implies that the phase I in *P. abies* is affected by annually changing environmental conditions, such as temperature, rather than the fixed, latitude-dependent factor of light. According to Cuny et al. (2015), the onset of wood formation is controlled by temperature and synchronizes with the photoperiodic cycle later in the season, enabling the conduits to mature before winter, which may partly explain the higher annual variability in phase I than phases II and III. In *P. abies*, the onset of phase I was more strongly related to TS_{ann} than to latitude. However, the cessation and duration of phase I were not related to TS_{ann} . Furthermore, the year with the earliest onset of phase I at the northernmost *P. abies* site was not the year with the highest TS_{ann} on that site (Fig. 2b). This indicates that factors other than light cycle and temperature during the growing season affect the onset of phase I in this species. For example, wood formation is more sensitive to frost during the preceding winter in *P. abies* than in *P. sylvestris* (Lebourgeois et al., 2010), although both species require winter chilling to break the dormancy (Delpierre et al., 2019). Interestingly, in *P. sylvestris*, the correlations of the onset, cessation, and duration of phase I were weaker with TS_{ann} than with latitude, underlining that *P. sylvestris* is less temperature sensitive and more affected by the light cycle than *P. abies* (see also Delpierre et al., 2019). Global warming may thus have a greater advancing effect on the onset of phase I in *P. abies* than in *P. sylvestris*.

Phase II (cell wall thickening and lignification) also depends on temperature, both during and outside of the growing season. In both species, along phase II lasted longer (Fig. 4c, d) and $max_{phaseII}$ occurred earlier under higher TS_{ann} (Table 3). This relationship means that the highest rate of carbon sequestration into the wood also occurred earlier, because the amount of cell wall material remains constant throughout most of the growing season (Cuny et al., 2014). Warmer temperatures during the growing season allow for higher enzymatic activity, benefiting all wood formation phases, though the processes of phase II are particularly temperature dependent (Cuny, Rathgeber, 2016). Higher temperatures outside the wood formation period in the stem enable trees to accumulate the resources needed for this process by promoting root growth and mycorrhizal activity and, in evergreen conifers such as our study species, allowing for sugar accumulation through photosynthesis (Ding et al., 2019; Jyske et al., 2014; Kulmala et al., 2019; Lebourgeois et al., 2010). Although TS_{ann} does not include late winter or early spring temperatures, sites with higher growing season temperatures likely have higher temperatures also outside the growing season. Thus, the earlier onsets of all wood formation phases

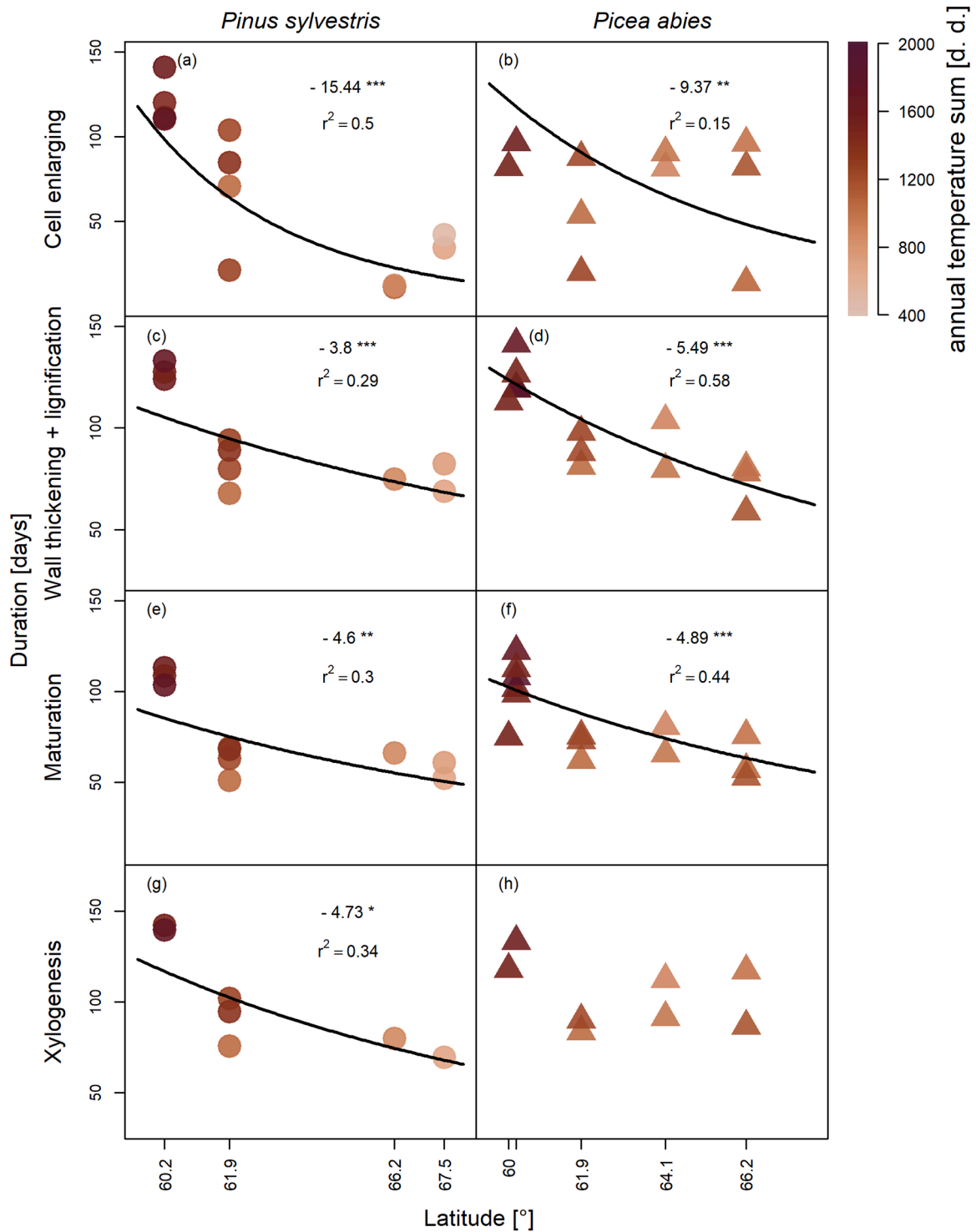


Fig. 4. Effect of latitude on the duration of the wood formation phases (cell enlargement, wall thickening and lignification, and maturation), and of total wood formation, in *Pinus sylvestris* and *Picea abies*. The lines were fitted with parameters resulting from REML models and indicate $p < 0.05$. The formulas show parameter b with its p -value (* < 0.05 , ** < 0.01 , *** < 0.001) and the marginal R^2 .

and the earlier occurrence of $max_{phaseII}$ in warmer sites are both likely direct effects of higher temperatures during the growing season and indirect effects due to higher temperatures before the onset of wood formation. A more detailed analysis would be necessary to understand the effect of annual temperature differences within a site.

The earlier onset of phase III at lower latitudes or with a higher TS_{ann} is consistent with an earlier onset of phases I and II (Fig. 2), as the intervals between the phases of wood formation are constant across

ecosystems and conifer species within the Northern Hemisphere (Rossi et al., 2016).

The sensitivity of the onset and cessation of wood formation phases, as well as of $max_{phaseII}$, to TS_{ann} indicates that global warming could alter the timing of these events and related processes. For example, it could advance the timing of primary growth, including shoot and needle formation (Buttò et al., 2012a) and peak carbon sequestration. However, photoperiod may limit this advancement by becoming the dominant

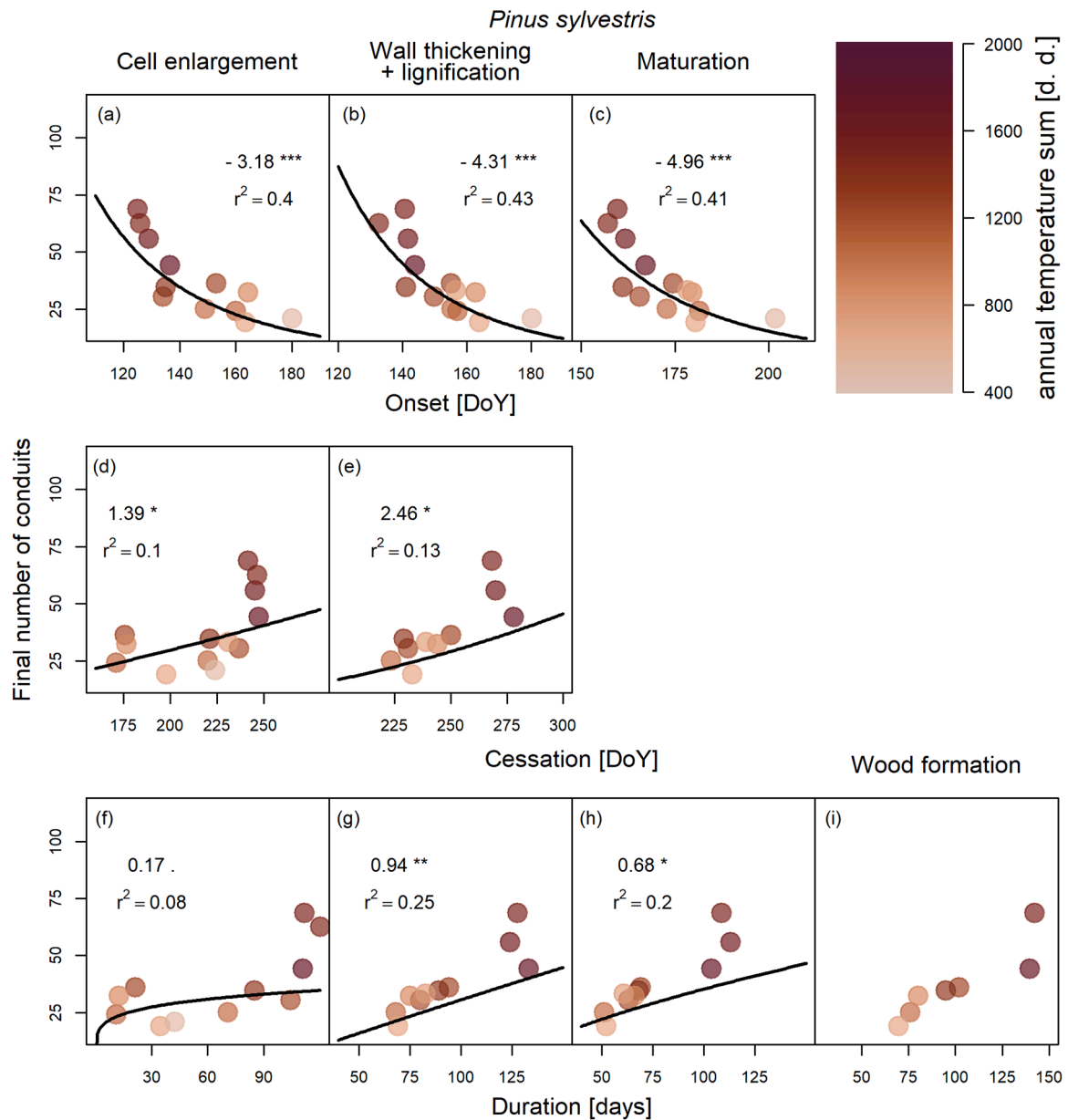


Fig. 5. Relationship of onset, cessation, and duration of wood formation and its phases (cell enlargement, wall thickening and lignification, and maturation) with the final number of conduits in one radial file in *Pinus sylvestris*. Maturation ends when no more conduits are in any previous phase, thus we defined maturation to end together with wall thickening and lignification. The lines were fitted with parameters resulting from REML models and indicate $p < 0.01$. The formulas show parameter b with its p -value ($^* < 0.05$, $^{**} < 0.01$, $^{***} < 0.001$) and the marginal R^2 .

regulator. Indeed, [Huang et al. \(2020\)](#) found that temperature and photoperiod interact tightly for conifers in the Northern Hemisphere, but the latter is the key driver for the onset of wood formation. Furthermore, higher winter temperatures may have ambivalent effects on the onset of wood formation in conifers like *P. abies* and *P. sylvestris*, as these species need both chilling and forcing temperatures to break winter dormancy ([Delpierre et al., 2019](#)). TS_{ann} accounts for spring forcing, as the calculation starts when temperatures reach the threshold of 5°C for five consecutive days. However, it does not account for winter chilling, which occurs before the onset of growing season.

4.2. Number of conduits and radial increment

None of the three phases of wood formation were directly related to the final number of conduits (N), because cells cannot divide once they enter phase I. Nevertheless, N correlated highly with wood formation

phase dynamics in both species ([Figs. 5 and 6](#)). These relationships are logical, as each phase occurs sequentially, so an acceleration or deceleration in cell division causes all subsequent phases of wood formation to be accelerated or decelerated ([Rossi et al., 2016](#)). Furthermore, the correlation of N with wood formation phase dynamics indicates that, in *P. sylvestris* and *P. abies* trees growing at latitudes of 60° and higher, conditions that are beneficial for cambial cell division also allow for an earlier onset and later cessation of each wood formation phase. A greater N under higher temperatures enables a better water supply to the branches and needles, thus facilitating subsequent growth. In both species, the radial increment (R) exhibited similar relationships with latitude, TS_{ann} , and wood formation dynamics, as N ([Figs. 7 and 8](#)). This indicates that the variability of N is crucial for the high environmental plasticity of the tree ring width.

Consequently, global warming would enable prolonged wood formation phases and increased conduit production in boreal regions.

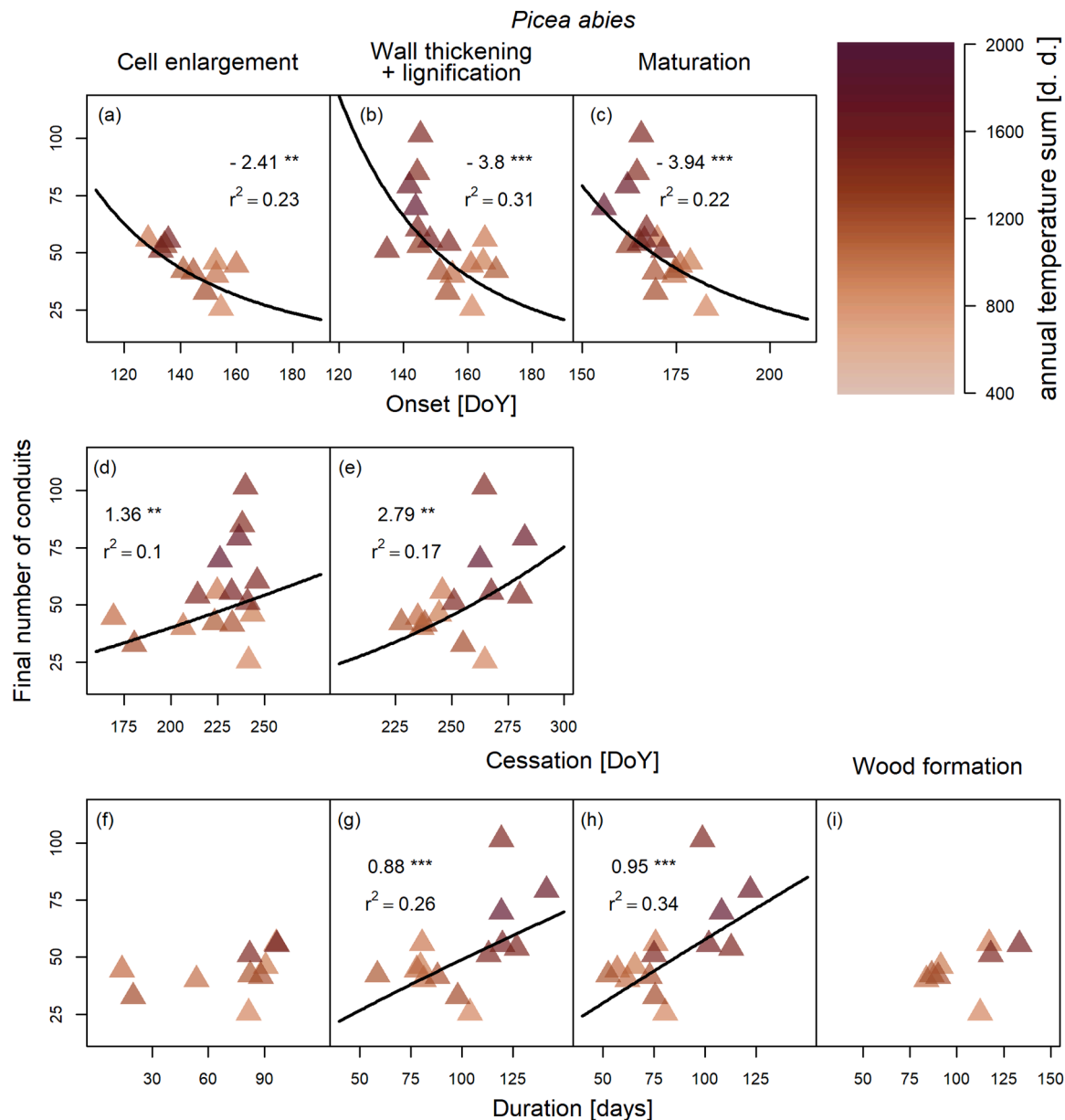


Fig. 6. Relationship of onset, cessation, and duration of wood formation and its phases (cell enlargement, wall thickening and lignification, and maturation) to the final number of conduits in one radial file in *Picea abies*. Maturation ends when no more conduits are in any previous phase, thus we defined maturation to end together with wall thickening and lignification. The lines were fitted with parameters resulting from REML models and indicate $p < 0.01$. The formulas show parameter b with its p -value ($* < 0.05$, $** < 0.01$, $*** < 0.001$) and the marginal R^2 .

However, the beneficial effect of increasing TS_{ann} on wood formation is probably finite, even in regions where low temperatures are a limiting factor. In addition to photoperiod, which limits the extension of wood formation and its phases in the boreal forest under global warming, rising temperatures may also negatively affect wood formation. Lebourgeois et al. (2010) found that warmer temperatures at the end of the growing season negatively affected the wood formation of the following growing season for *P. sylvestris* and *P. abies* growing in France. Henttonen et al. (2014) found that, for *P. sylvestris* in southern Finland, previous late summer temperatures were negatively correlated with growth, while in northern Finland, previous October temperatures had a positive effect. Prolonged wood formation phases in one growing season, particularly phase II, which requires a lot of carbon (Cuny et al., 2015), may leave fewer resources stored for the next growing season. Due to the lag between the seasonal temperature cycle and the light cycle, photosynthesis may not be able to compensate for the lower

carbon reserves. Furthermore, while our study focused on the effects of latitude and growing-season temperature on wood formation phases, other factors may become limiting to tree growth due to climate change. Even in northern Finland, low summer water availability and drought negatively affect tree growth (Henttonen et al., 2014; Mäkinen et al., 2022). In Switzerland, unfavorable summer conditions are already reducing the growth of *P. sylvestris* and *P. abies*, counteracting the earlier onset facilitated by warmer spring temperatures (Bose et al., 2025). Further studies on the effects of seasonal and monthly conditions, both within and outside the growing season, on the dynamics and rates of the wood formation phases would enable to predict more accurately the effects of climate change on wood formation at higher latitudes, where photoperiod, in addition to temperature, plays a crucial role.

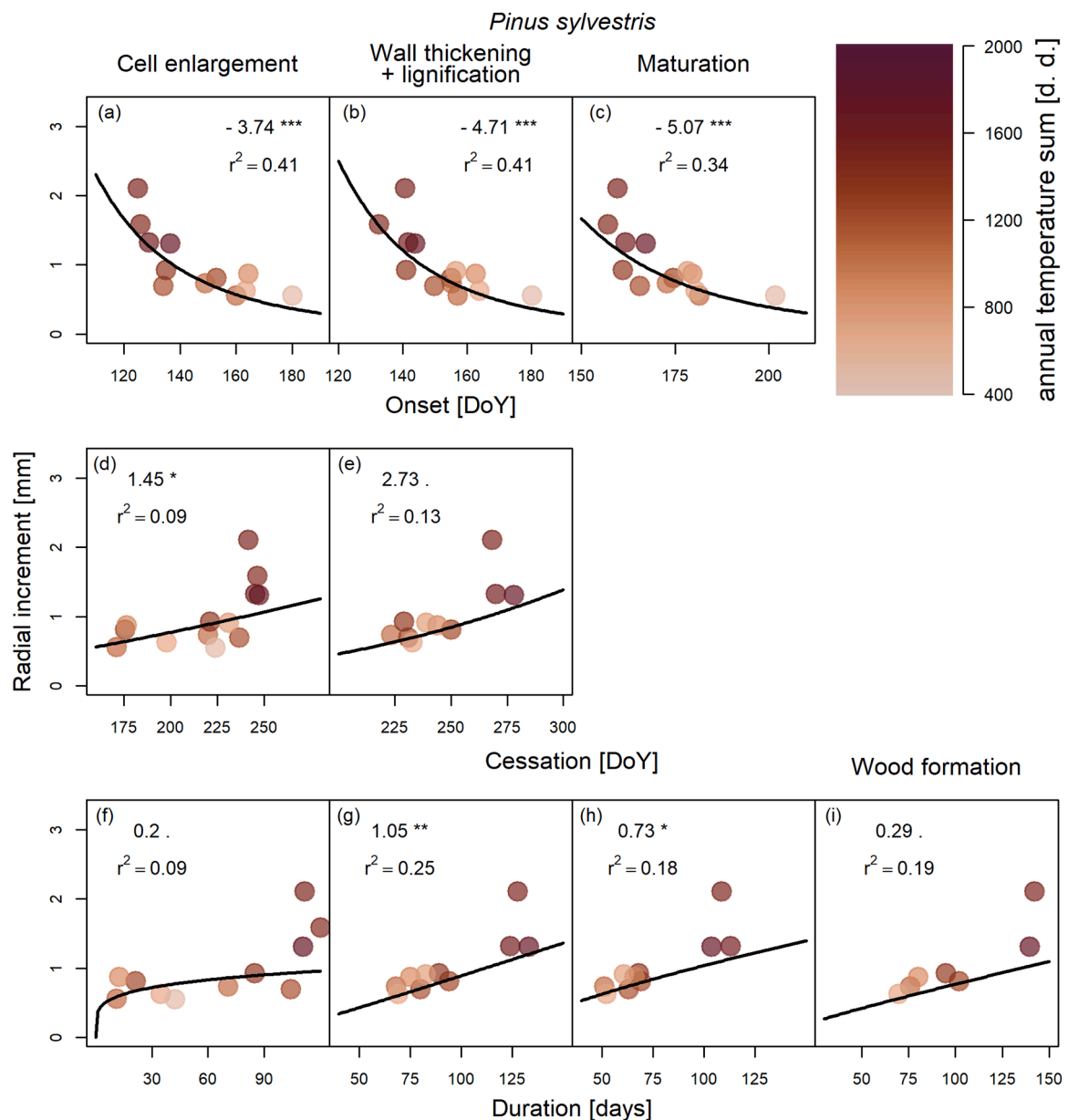


Fig. 7. Relationship of onset, cessation, and duration of wood formation and its phases (cell enlargement, wall thickening and lignification, and maturation) with radial increment in *Pinus sylvestris*. Maturation ends when no more conduits are in any previous phase, thus we defined maturation to end together with wall thickening and lignification. The lines were fitted with parameters resulting from REML models and indicate $p < 0.01$. The formulas show parameter b with its p -value ($^* < 0.05$, $^{**} < 0.01$, $^{***} < 0.001$) and the marginal R^2 .

5. Conclusions

As predicted by our first hypothesis, lower latitudes and higher annual temperature sums enabled an earlier onset and later cessation of the wood formation phases. These phases lasted longer, resulting in a higher final number of conduits and radial increment, confirming our second hypothesis. Our results indicate that years with higher temperature sums, which are expected to occur more often under global warming, may enable conifers in latitudes from 60° to 67.5° to have longer wood formation phases and higher wood production, until the annual light cycle becomes more limiting than annual temperature sum. Also, other environmental factors, like water availability winter temperatures and biotic stressors, may limit the positive effects of increasing annual temperature sums in high latitudes. Assessing the effects of multiple environmental factors on cambial activity and subsequent wood formation phases in future studies would allow to better predict

changes in wood production in boreal forests under global warming.

CRediT authorship contribution statement

Anna Lintunen: Writing – review & editing, Supervision, Conceptualization. **Tuula Jyske:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Harri Mäkinen:** Writing – review & editing, Writing – original draft, Data curation, Conceptualization. **Magdalena Held:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization.

Funding

This research was supported by the Doctoral Programme in Atmospheric Sciences (University of Helsinki) and Research Council of Finland (grants no. 115650, 124390, 250299, 355266, 337549, 357902,

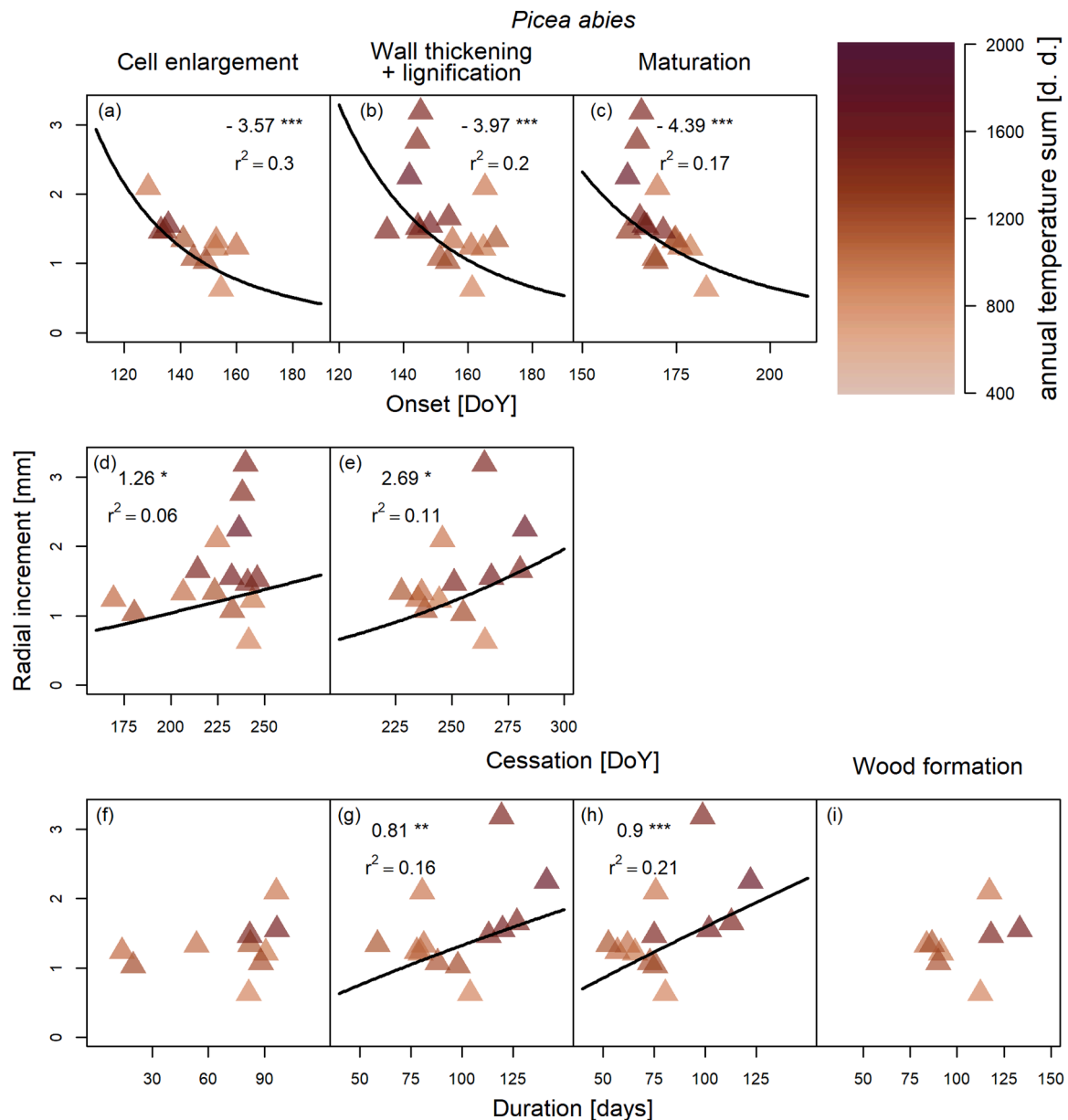


Fig. 8. Relationship of onset, cessation, and duration of wood formation and its phases (cell enlargement, wall thickening and lignification, and maturation) with radial increment in *Picea abies*. Maturation ends when no more conduits are in any previous phase, thus we defined maturation to end together with wall thickening and lignification. The lines were fitted with parameters resulting from REML models and indicate $p < 0.01$. The formulas show parameter b with its p -value ($* < 0.05$, $** < 0.01$, $*** < 0.001$) and the marginal R^2 .

355142, 359340). Open access funding provided by University of Helsinki.

Declaration of Competing Interest

Duration of wood formation phases in Scots pine and Norway spruce lengthens towards the south in the Nordic countries” by Magdalena Held, Anna Lintunen, Tuula Jyske, Harri Mäkinen

Magdalena Held: I have nothing to declare.

Anna Lintunen: I have nothing to declare.

Tuula Jyske: I have nothing to declare.

Harri Mäkinen: I have nothing to declare.

Acknowledgements

The study was conducted at the Natural Resources Institute Finland

(Luke) and the University of Helsinki. We would like to thank the laboratory staff at Luke for their dedication and expertise in the laboratory work, and to Dr. Pekka Nöjd and Dr. Tuomo Kalliokoski for their invaluable contributions to the planning and implementing the data acquisition.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dendro.2026.126534](https://doi.org/10.1016/j.dendro.2026.126534).

Data availability

Data will be made available on request.

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