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Dynamics of diameter and height increment of Norway spruce and Scots pine in southern Finland

Harri Mäkinen[1] · Tuula Jyske[1] · Pekka Nöjd[1]

Abstract
· *Key message* Onset and cessation of radial and height increment of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris L.*) in southern Finland were independent phenomena. They both contributed to the increment period duration, which was a more crucial factor defining the magnitude of annual radial and height increment.
· *Context* Phenology of diameter and height increment is a critical component of growth, also contributing to damage and survival of trees.
· *Aims* We quantified annual variation in intra-annual tracheid production and height increment of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris L.*).
· *Methods* The number of tracheids and the day of the year for the onset and cessation of tracheid production were monitored from microcores collected repeatedly during growing seasons 2001–2012 in southern Finland. Weekly height increment was also measured in an adjacent sapling stand in 2008–2012.
· *Results* The first tracheids in pine were found around mid-May and in spruce a week later. The cessation of the tracheid production occurred during the last week of August for both tree species. Increment onset and cessation were independent phenomena, both contributing to the magnitude of tracheid production via increment period duration, which appeared to be a more crucial factor defining the number of tracheids. Duration of the height increment period was also related to shoot length but the connection was less tight than the link between the duration of tracheid production and the number of tracheids. A thermal threshold around 100 d.d. (degree days) was found for the onset of radial increment. No single environmental factor triggered the cessation of tracheid production, but in some years, soil water availability appeared to play a role.
· *Conclusion* The results indicate that extending growing seasons due to the climatic warming may increase growth in the Finnish forests.

Keywords Phenology · *Picea abies* · *Pinus sylvestris* · Tracheid · Xylogenesis

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1 Introduction

The climate in boreal and temperate continental forests is characterized by high temperature fluctuation between seasons. Phenological events, in particular onset and cessation of diameter and height increment, are an adaptation to this seasonal variation in growing conditions. Onset and cessation of increment are controlled by a variety of exogenous (e.g., photoperiod, temperature, water availability, and nutrients) and endogenous (e.g., phytohormones and sugars) factors and by interaction between them (e.g., Plomion et al. 2001; Samuels et al. 2006; Aloni 2015). Timing of phenological events is also vital for assessing the impacts of future changes in environmental conditions on tree growth and frost damage (Suvanto et al. 2017).

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Increment onset indicates a holistic tree status driven by the past winter chilling, photoperiod, and thermal forcing, all translated by phytohormones into preparedness for growth (Sarvas 1972, 1974; Hänninen and Kramer 2007). Some studies (e.g., Svendsen et al. 2007; Dufour and Morin 2010; Tanino et al. 2010) have recently shown that temperature may mediate this photoperiod response in woody species. Whereas development of tree status integrates signals over longer periods, the actual onset of height and radial increment may depend on thermal thresholds (Rossi et al. 2008; Vitasse et al. 2011; Delpierre et al. 2016). In Europe, increasing temperatures since the early 1960s have already led to earlier bud burst and leaf unfolding (Häkkinen et al. 1995; Menzel et al. 2006; Cleland et al. 2007). Moreover, a combined model of night length and temperature sum described the annual cycle of trees better than photoperiod alone (Koski and Sievänen 1985). In the northern regions, the stimulus for increment cessation is considered to be primarily controlled by photoperiod (e.g., Tranquillini and Unterholzner 1968; Allona et al. 2008). Limited soil water availability may also affect the cessation of tracheid production (Gruber et al. 2010; Mäkinen et al. 2012; Delpierre et al. 2016). According to Lupi et al. (2010), timing of radial increment onset and cessation are also linked with each other and delayed increment onset results in earlier cessation of tracheid production.

Annual radial increment and tracheid production of boreal trees are mainly related to ambient temperature, especially during the middle part of the growing season. In southern parts of the boreal zone, precipitation plays a more significant role (e.g., Mäkinen et al. 2000; Helama et al. 2005). Fairly high correlations between summer precipitation and annual increment variation have been observed in southern Finland and Estonia (Henttonen et al. 2014). In the boreal forests, increment variation was also correlated with light intensity (Hari and Siren 1972; Li et al. 2014), modeled photosynthetic production (Hari and Nöjd 2009), and air humidity (Li et al.

2014). In addition to the increment rate, growing season length is an important determinant of annual tracheid production (Cuny et al. 2012; Kalliokoski et al. 2013). Both early onset and late cessation have been related to higher numbers of tracheids produced during a growing season (Rathgeber et al. 2011; Cuny et al. 2012).

The aim of the study was to quantify variation in the onset, cessation, and duration of tracheid production and height increment, and to investigate how they are related to each other. We also analyzed how the onset, cessation, and duration of increment periods are related to the number of tracheids produced and to the length of the annual height increment. We hypothesized that increment onset and cessation are independent phenomena, and that they both contribute to the extent of tracheid production and height increment via duration of increment periods.

2 Material and methods

The material consisted of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) trees growing in southern Finland (Ruotsinkylä, Tuusula, N 60° 21, E 25° 00). In 2001, five mature dominant Norway spruce trees were monitored in a stand on fertile mineral soil classified as *Oxalis-Myrtillus* forest type (Cajander 1949) (Table 1). The site and sample trees are described in detail in Mäkinen et al. (2003). In the second stand, located approximately 500 m from the first stand, tracheid production of Norway spruce was monitored in four to six trees in the years 2002–2012 and in four to five Scots pine trees in 2002–2010 (Table 1). In the second stand, the sample trees were growing in a mixed spruce-pine stand on a relatively fertile mineral soil classified as *Myrtillus* forest type (Cajander 1949). The site and sample trees of the second stand are described in Mäkinen et al. (2008) and Jyske et al. (2014).

Table 1 Mean characteristics of the sample trees (± 1 standard deviation) monitored from 2001 to 2012 (Norway spruce) or from 2002 to 2010 (Scots pine)

Variable	Scots pine	Norway spruce
Number of sample trees[a]	4–6 (22)	4–5 (23)
Age (years)	38	38
Stem diameter (at 1.3 m, cm)	20.7 (3.8)	22.6 (3.7)
Height (m)	17.8 (1.8)	20.1 (4.5)
Crown length (m)	8.6 (1.8)	16.4 (2.4)
Crown width (m)[b]	3.8 (0.77)	3.9 (0.49)
Number of saplings, monitored for height increment	10	0
Age of saplings (years)	8–12	
Height of saplings (m)	1.5–2.0	

[a] Trees monitored per year. The number of sample trees varied between the study years. The cumulative number of individual sample trees over the sampling years in parentheses

[b] Crown width was calculated as the mean of the maximum crown width and the width perpendicular direction of it

Small microcores were extracted at breast height twice a week in spring and early summer and once a week in late summer. Microcoring was started around mid-May and continued until late September. From 2001 to 2007, microcores were collected using injection needles and since 2008 using Trephor, a tool designed for microcoring (Rossi et al. 2006).

Tracheid production was measured using two methods. The microcores collected in 2001–2006 were split perpendicular to tracheid axes and the tracheids of the current-year ring were counted and their widths measured. The samples collected in 2007–2012 were dehydrated with ascending series of ethanol, cleared with Tissue-Clear (Tissue-Tek, Sakura Finetek, Tokyo, Japan), and immersed in liquid paraffin. The samples were then embedded in paraffin blocks and radial sections cut with a microtome were stained and mounted on microscopic slides. Number and widths of current-year tracheids were measured from digital images taken from the samples (for details see Kalliokoski et al. 2012, 2013; Jyske et al. 2014). The measurements based on the two methods were shown to be comparable by Jyske et al. (2012).

The onset of tracheid production was defined as the date when at least one current-year tracheid in the enlargement phase was found. Exact cessation date of tracheid production was more difficult to determine due to random variation in the number of tracheids among sampling points. Therefore, the Gompertz function was fitted to the observed number of tracheids on each tree to describe the progress of tracheid production during growing season (Zeide 1993; Rossi et al. 2003). The cessation date was defined as the time point when the fitted Gompertz function reached 95% of its maximum value.

Intra-annual height increment of ten pine trees was monitored weekly in 2008–2012 in a sapling stand adjacent to the second stand. The height of the saplings was 1.5–2.0 m. The height increments of the main stem axis were measured using a ruler from a pin attached to the top of the previous year shoot. The onset and cessation dates of height increment were defined as the time point when 5 and 95% of the total annual increment were reached.

Daily average temperature and precipitation data were obtained from a meteorological station of the Finnish Meteorological Institute located approximately 5 km from the study stands (Table 2, Fig. 1). Temperature sum at each day (degree days, d.d.) was calculated as a sum of positive differences between the daily mean air temperature and the threshold temperature + 5 °C (Arnold 1959; Sarvas 1967).

The differences in the timing (onset, cessation, duration) of tracheid production and height increment between the tree species were analyzed using mixed model analysis (the MIXED procedure in the SAS software) for repeated measurements:

$$z = S + Y + t \tag{1}$$

where, z is the dependent variable, S is the fixed tree species effect, Y is the fixed year effect, and t is the random tree effect.

The mixed model analysis was also used to quantify the share of the total variation (z_{var}) in the timing (onset, cessation, duration) of tracheid production and height increment

Table 2 Mean annual, May, June, July, and August temperature and precipitation sums for the same time periods

Year	Temperature (°C)					Precipitation (mm)				
	Annual mean	May	June	July	August	Annual sum	May	June	July	August
2001	5.6	9.9	14.3	20.5	16.4	685	18	112	56	69
2002	5.8	12.0	16.4	19.3	19.2	443	25	67	56	16
2003	5.3	10.0	13.3	20.5	16.1	504	61	51	25	68
2004	5.4	10.3	13.0	16.5	16.7	839	34	91	214	75
2005	5.9	10.3	14.2	19.2	16.2	654	33	106	36	162
2006	6.2	10.7	16.3	19.1	18.4	555	42	28	4	38
2007	6.5	11.0	15.8	17.4	17.4	756	43	44	59	66
2008	6.8	11.0	14.5	17.3	14.8	848	13	123	25	81
2009	5.6	11.6	14.2	17.2	16.2	659	34	78	104	63
2010	4.5	11.9	15.0	22.4	17.7	595	81	32	15	71
2011	6.8	10.8	17.4	20.9	16.9	716	27	42	56	87
2012	5.3	11.3	13.9	18.0	15.5	938	50	97	68	71
Mean	5.8	10.9	14.9	19.0	16.8	683	38	73	60	72
SD	0.7	0.7	1.3	1.3	1.2	147	18.9	33.1	55.6	34.2

The weather data were obtained from a meteorological station of the Finnish Meteorological Institute located about 5 km from the study stand

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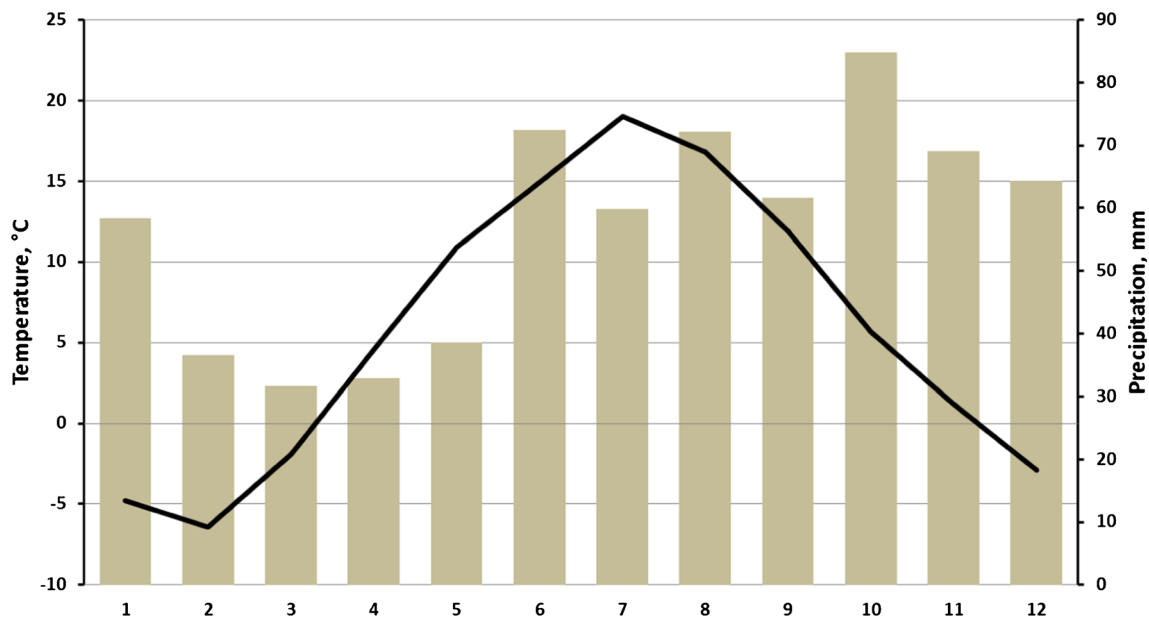
Fig. 1 Mean monthly temperature (line) and precipitation sum (bars) in 2001–2012. The weather data were obtained from a meteorological station of the Finnish Meteorological Institute located approximately 5 km from the study stands

accounted for the between-year (y), between-tree (t), and between-species (s) differences:

$$z_{var} = s + y + t \qquad (2)$$

assuming all the variables were random.

Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

3 Results

The first new tracheids in pine were found around mid-May (day of year (DoY) 137) and in spruce a week later (DoY 143) (Fig. 2a), the difference between the species being statistically significant (Table 3). Accordingly, temperature sum accumulated by the onset of tracheid production was slightly lower for pine than that for spruce, i.e., 95 and 103 d.d., respectively (Fig. 2b). The earliest onset of tracheid production for both species occurred during the first week of May in 2009 and 2011. In 2003, the onset in both species was as late as the first week of June. In 2001 with a cool May (Table 2), the onset of tracheid production in spruce was delayed close to mid-June (DoY 163) (pine was not monitored in 2001).

For pine, onset of height increment in the adjacent sapling stand occurred approximately 1 week earlier (DoY 131) than the onset of tracheid production (Fig. 2a). On average, temperature sum accumulated by the onset of the height increment was 47 d.d. (Fig. 2b).

The cessation of the tracheid production occurred during the last week of August for both tree species (Table 3), on average at DoY 242 and 238, with 1235 and 1189 d.d., for the pine and spruce, respectively (Fig. 2). The latest cessation in both species was in 2009, when the tracheid production continued until the second week of September. In pine, tracheid production ceased during the second week of September also in 2003. In both years, average temperature and precipitation sum of August were close to their averages over the 12-year study period (Table 2). The earliest cessation of tracheid production in spruce (DoY 222, August 10) took place in 2002, a year with rather low precipitation in August (Fig. 2a, Table 2). In both species, tracheid production ceased early also in 2010, which displayed average temperature and precipitation conditions in August but the warmest July during the study period. The height measurements of pine saplings indicate that height increment ceased on average during the last week of June, at a temperature sum of 399 d.d., i.e., considerably earlier than tracheid production in the mature trees (Fig. 2).

The average duration of the period when tracheids were produced was slightly longer for pine than that for spruce, i.e., 106 and 96 days, respectively (Fig. 2, Table 3). The shortest tracheid production period (63 days) occurred in 2001 due to the delayed onset of tracheid production. In contrast, 2009 had the longest tracheid production period (132 and 123 days for pine and spruce, respectively) resulting from both early onset and late cessation. The duration of height increment ranged from 43 to 56 days (the average being 46 days), which was considerably shorter than the duration of tracheid production in pine.

The onset and cessation dates of tracheid production were not significantly correlated with each other (Fig. 3a, b). As in tracheid production, the onset and cessation dates of height

Fig. 2 The tracheid production period of Scots pine (continuous lines) and Norway spruce (short-dashed lines), as well as height increment period of Scots pine (longer-dashed lines) in the study years. The lower and upper ends of each line mark the onset and cessation of the production period according to day of year (DoY) (**a**) and temperature sum accumulation (**b**)
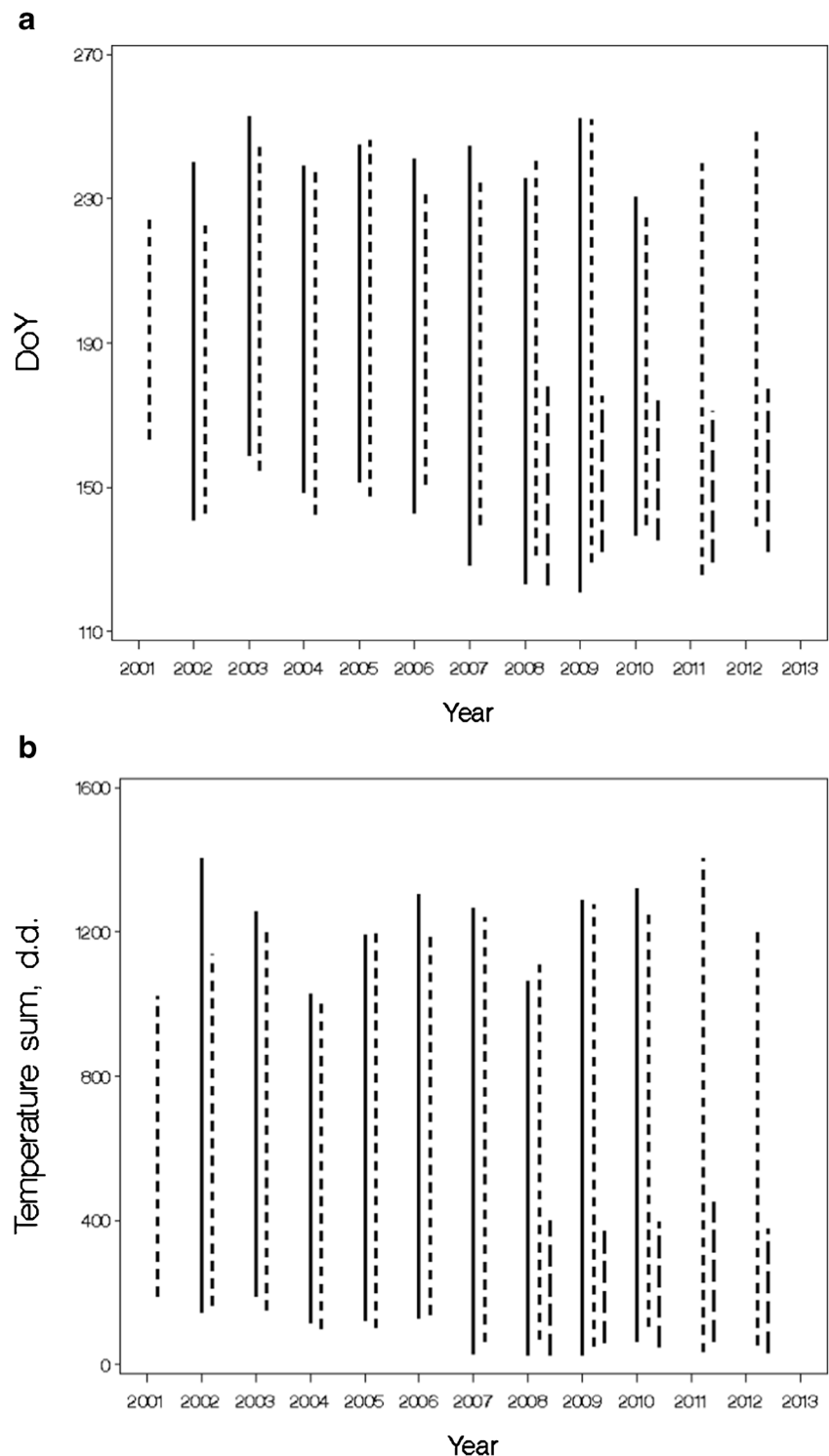
increment were not correlated with each other (Fig. 3c). However, both the onset and cessation dates were equally strongly correlated with the duration of the tracheid production period (Figs. 3 and 4), i.e., they both contributed to the duration of tracheid production period but independently from each other. The situation was similar for the duration of height increment period, but correlation with the respective cessation dates was somewhat higher than that with the onset dates (Figs 3f and 4c).

In pine, the number of tracheids produced during the growing season was equally strongly correlated with the onset and cessation dates of tracheid production. However, its correlation with the duration of the production period was even stronger (Fig. 5a–c). In contrast, in spruce, although the number of

Table 3 Mixed model analysis (Eq. 1) on the between-species and between-year difference in the onset DoY, cessation DoY, and duration of tracheid production period

Variable	Parameter	DF	F-value	P value
Onset	Species	37	4.71	0.037
	Year	37	46.37	0.001
Cessation	Species	37	1.80	0.188
	Year	37	3.40	0.001
Duration	Species	37	4.27	0.046
	Year	37	9.13	0.001

tracheids produced during the growing season was approximately equally strongly correlated with the onset date and duration of tracheid production period, the correlation with the cessation date was lower although still statistically significant (Fig. 5d–f).

The final length of the terminal shoot in the pine saplings was not significantly correlated with the onset date of height increment (Fig. 6a). However, shoot length was significantly correlated both with the cessation date and duration of the height increment period, the correlation with the cessation date being stronger (Fig. 6b, c).

In the mixed models, between-year variation accounted for the highest share of the total variation in the onset date (83%) and in the duration of the tracheid production period (51%), as well as in the onset date (75%) and in the length of the height increment period (61%) (Fig. 7). In contrast, between-tree variation accounted for the highest share of the total variation in the cessation dates of the tracheid production and height

increment periods (77 and 60%, respectively). In tracheid production, the magnitude of between-tree variation was clearly higher (14–77%) compared to that of the between-species variation (3–6%). The distribution of height increment variation was similar to the variation in tracheid production. This appeared to hold true for the magnitude of the between-tree variation in the onset and cessation dates, as well as in the duration of tracheid production (note that between-species differences were not available for height increment, which was only measured for pine).

4 3. Discussion

4.1 Tracheid production

The number of tracheids produced was related to the onset and cessation dates of increment period both in spruce and pine. Duration of increment period appeared to be a more crucial factor defining the final number of tracheids. The onset and cessation dates of tracheid production were not correlated with each other, further confirming our initial hypotheses.

The results of this study support the previous Finnish studies suggesting a thermal threshold around 100 d.d. for the actual onset of radial increment. Based on dendrometer measurements in central Finland, Mielikäinen et al. (1998) reported that approximately 100 d.d. are required for the onset of wood formation in Scots pine. Accordingly, using the pinning method, Seo et al. (2008) found that on average 104 and
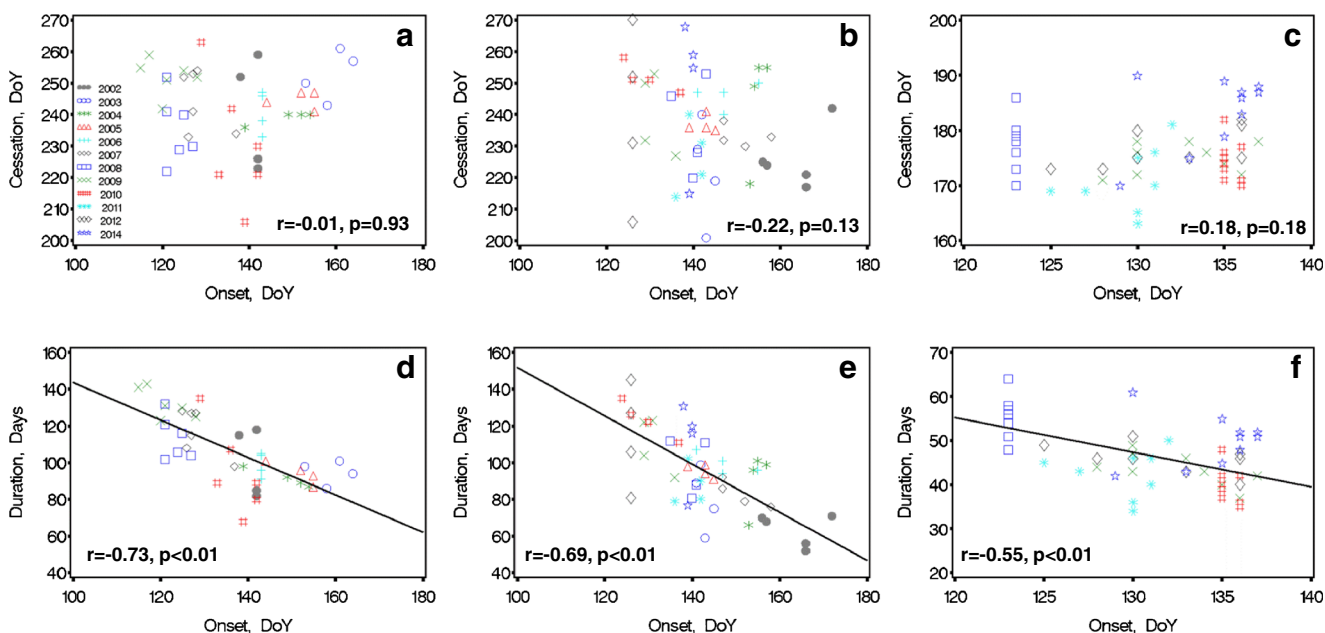
Fig. 3 The cessation dates and duration of tracheid production periods of Scots pine (**a, d**) and Norway spruce (**b, e**), as well as height increment of Scots pine saplings (**c, f**), plotted against the onset dates of tracheid production and height increment, respectively. The different symbols separate the individual study years; a linear regression line is shown when the correlation is significant
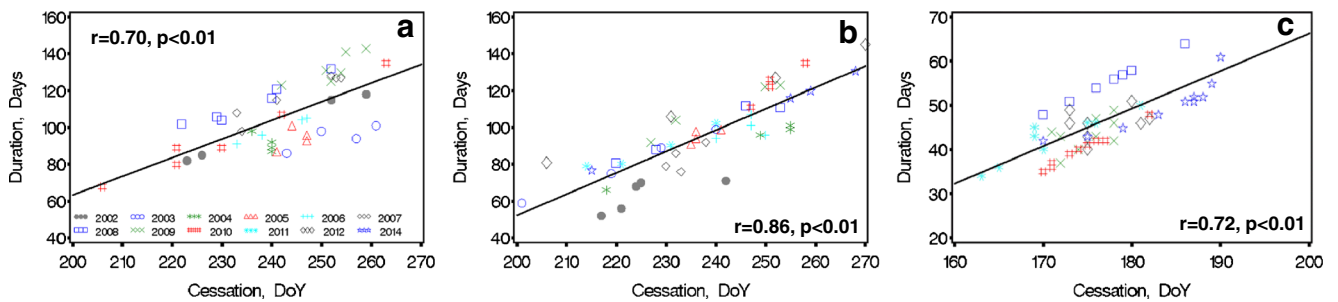
Fig. 4 The duration of tracheid production periods of Scots pine (**a**) and Norway spruce (**b**), as well as height increment of Scots pine saplings (**c**), plotted against the cessation dates of tracheid production and height increment, respectively. The different symbols separate the individual study years; a linear regression line is shown when the correlation is significant

93 d.d. were required to trigger tracheid production in two Scots pine stands in northern Finland. In a recent study, we found that the onset of tracheid production in Scots pine and Norway spruce varied from late May in southern Finland to mid-June in northern Finland (Jyske et al. 2014). No latitudinal trend was found in the temperature sum accumulated by the onset of tracheid production. Thus, the results of this study and those of the previous studies (e.g., Cleland et al. 2007; Jyske et al. 2014; Delpierre et al. 2016) indicate that cambium reactivation in spring is by temperature, but not necessarily independent of photoperiod.

The variation between years in the cessation of tracheid production indicates that other factors in addition to photoperiod affect the cessation date (cf., Rossi et al. 2008; Rathgeber et al. 2011; Kalliokoski et al. 2013). Based on our results, it is difficult to identify one single environmental factor triggering the cessation of tracheid production, but in some years, soil water availability seems to play a role, especially for spruce. In

a dendrometer study (Mäkinen et al. 2012), we found that in the exceptionally dry summer of 2006, diameter increment of spruce in central Finland ceased in early July. Likewise, in the study reported here, tracheid production of spruce was also terminated early in 2006 at DoY 233, which was the third earliest date among the study years.

Recently, Lupi et al. (2010) found that a high number of tracheids produced during a growing season postponed the cessation of tracheid formation. They also suggested that earlier onset of tracheid formation due to high temperatures will delay tracheid maturation in autumn. The discrepancy between the findings of Lupi et al. (2010) and this study may be caused, at least partly, by the different methods used for determining growth cessation, i.e., we defined it based on termination of tracheid production, while Lupi et al. (2010) measured the ending of secondary cell wall deposition.

In comparison to spruce, tracheid production in pine initiated a week earlier and ceased later (cf., Henttonen et al. 2009;
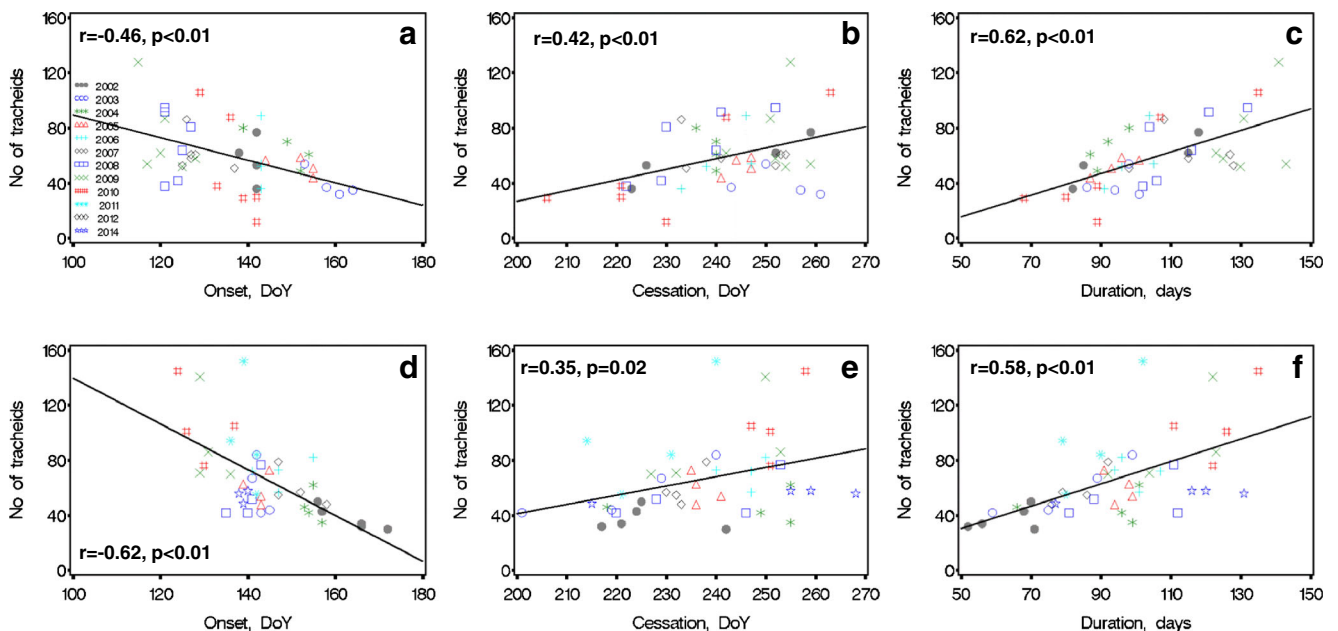
Fig. 5 The number of tracheids produced during the growing season plotted against the onset date (**a, d**), cessation date (**b, e**), and duration (**c, e**) of tracheid production periods of Scots pine (upper row) and Norway spruce (lower row). The different symbols separate the individual study years; a linear regression line is shown when the correlation is significant
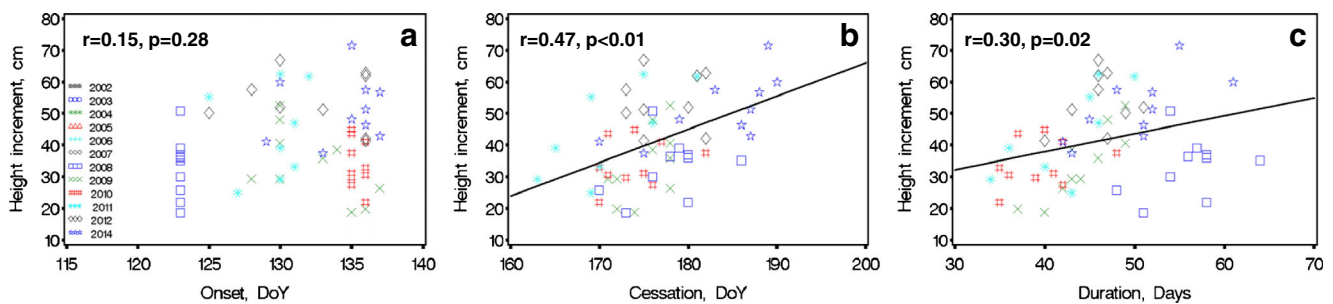
Fig. 6 Annual height increment of Scots pine saplings plotted against the onset date (**a**), cessation date (**b**), and duration (**c**) of the height increment periods. The different symbols separate the individual study years; a linear regression line is shown when the correlation is significant

Jyske et al. 2014). Accordingly, in France, the first enlarging tracheids were found 1 week earlier and tracheid formation ceased 3 weeks later in pine than in spruce (Cuny et al. 2012). Scots pine is a light-demanding pioneer tree species, while Norway spruce is a more shade-tolerant later successional species. It has been suggested that pioneer tree species have adopted more "risky" life strategies with early onset and late cessation of increment, while later successional species are associated with "safer" strategies (Körner 2006; Körner and Basler 2010; Cuny et al. 2012). Nevertheless, despite the evident differences in the timing of the tracheid production period between spruce and pine, the magnitude of the between-species difference was actually rather small compared to that of the between-year differences.

Studies on annual radial increment variation have revealed a strong link between annual increment and summer temperatures in northern Finland, but in the south, the correlation has been considerably weaker (Mäkinen et al. 2000; Helama et al. 2005). The site of this study is situated in southern Finland, which can be considered as a transitional zone between northern temperature-limited and southern moisture-limited regions (Mäkinen et al. 2002b; Henttonen et al. 2014). Moreover, the site has only a moderate water holding capacity. Thus, the strength of the contribution of different factors for the timing

and the rate of increment might probably vary from year to year.

4.2 Height increment

Regarding height increment, late cessation date and increment period duration were important components affecting final shoot length. However, in comparison to the number of tracheids produced, shoot length was less strongly correlated with height increment period duration. The height increment of Scots pine has two developmental phases, i.e., formation of a bud in the previous year, and elongation of the pre-formed stem units in the following summer (e.g., Kozlowski et al. 1973; Powell 1977). Thus, the final shoot length is affected by the conditions during bud formation, in addition to conditions during shoot elongation (Lanner 1976; Junttila and Heide 1981; Junttila 1986). For example, whereas daily shoot elongation rate of Scots pine and Norway spruce is related to daily temperature variation (Worrall 1973; Kanninen 1985), total annual height increment variation is correlated both with early summer temperature of the current year and late summer temperature of the previous year (Mäkinen 1998, 2002a; Salminen and Jalkanen 2005, 2007; Jansons et al. 2015).

Duration of shoot elongation ranged from 43 to 56 days, which is shorter than the 59-day period reported for northern Finland (Salminen and Jalkanen 2007), and well in line with the period of 43–45 days found by Seo et al. (2010) also for northern Finland. Duration of shoot elongation has been shown to depend on temperature accumulation (Huikari and Paarlahti 1967; Salminen and Jalkanen 2007). However, results on threshold values appear to differ. For example, Raulo and Leikola (1975) found that height increment of Scots pine ceased in southern Finland when 510–520 d.d. had accumulated, which is considerably higher than the temperature sum found in this study (399 d.d.). On the other hand, our result corroborates the study by Koski and Sievänen (1985) who reported that height increment of pine seedlings ceased when approximately 400 d.d. was accumulated. The longer height increment period reported by Salminen and Jalkanen (2007) for northern Finland could thus be due to slower temperature sum accumulation at the higher northern latitudes.
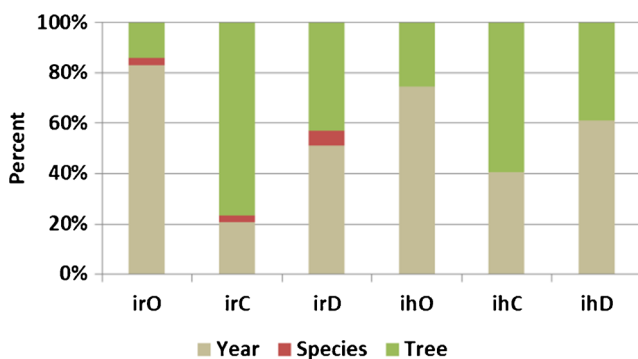
Fig. 7 Percentage of the total variation in the mixed models (Eq. 2) on the onset (O), cessation (C), and duration (D) of radial (ir) and height (ih) increment accounted for by year, tree species (Scots pine, Norway spruce), and individual trees. Note that for height increment, only Scots pines were measured

Hormones may play a role in regulating these growth processes. Auxin produced in young growing needles and transported basipetally towards the stem base participates in the reactivation of vascular cambium and in inducing tracheid production in spring (Larson 1964; Sundberg and Uggla 1998; Uggla et al. 1998). Development of buds and cambium should therefore be closely interlinked (Antonucci et al. 2015). However, earlier studies on different conifer species have reported that bud break has also occurred before and after cambium reactivation (Ladefoged 1952; O'Reilly and Owens 1989; Rensing and Owens 1994; Huang et al. 2014). In the pines observed in this study, height increment actually started 1 week earlier than the first enlarging tracheids emerged. In contrast, Cuny et al. (2012) recently found that cambial activity of Scots pine began a few days before the onset of shoot elongation. Similarly, Rossi et al. (2009) reported earlier reactivation of cambium with respect to onset of shoot increment in the Italian Alps. However, the discrepancy between the studies may, at least partly, rest with different definitions and measurement approaches for bud break (Antonucci et al. 2015). Generally, bud growth resumption begins several weeks before visible bud break (e.g., Sutinen et al. 2012).

Artificial heating of dormant conifer cambium initiates tracheid formation (Oribe et al. 2001; Gričar et al. 2006; Begum et al. 2013). Because auxin has been found in dormant cambium (Little and Wareing 1981; Sundberg et al. 1991), Rossi et al. (2009) suggested that the onset of tracheid production is related to the ability of the cambium to respond to available auxin, not solely to increasing polar transport of auxin. Hence, the potential linkage of bud break and the timing of increment onset at different heights along the stem still remains debatable.

5 Conclusions

The results of this study demonstrated that the timing of both onset and cessation of tracheid production independently contributed to annual wood production via the duration of the increment period. Duration of the height increment period also correlated to shoot length, however, less strongly than tracheid production period and number of tracheids did. The variations in the timing of tracheid production and height increment periods stress the important role of other environmental factors, in addition to photoperiod, for regulating the timing of increment.

The growth of Finnish forests increased slightly during the first half of the twentieth century, followed by rapid increases after the 1970s (Henttonen et al. 2017). About one third of the increase could be attributed to environmental drivers. Due to laborious sampling and measurements, decades-long time series on wood formation phenology do not exist. However, as advancing bud break of several tree species has been found

during the past decades, the phenological linkage between primary and secondary growths may be regarded as a good indicator that extended growing seasons have contributed to the considerable growth increase observed in the Finnish forests.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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