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Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length

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Summary

• Intra-annual radial growth rates and durations in trees are reported to differ greatly in relation to species, site and environmental conditions. However, very similar dynamics of cambial activity and wood formation are observed in temperate and boreal zones.
• Here, we compared weekly xylem cell production and variation in stem circumference in the main northern hemisphere conifer species (genera *Picea*, *Pinus*, *Abies* and *Larix*) from 1996 to 2003. Dynamics of radial growth were modeled with a Gompertz function, defining the upper asymptote (*A*), *x*-axis placement (β) and rate of change (κ).
• A strong linear relationship was found between the constants β and κ for both types of analysis. The slope of the linear regression, which corresponds to the time at which maximum growth rate occurred, appeared to converge towards the summer solstice.
• The maximum growth rate occurred around the time of maximum day length, and not during the warmest period of the year as previously suggested. The achievements of photoperiod could act as a growth constraint or a limit after which the rate of tree-ring formation tends to decrease, thus allowing plants to safely complete secondary cell wall lignification before winter.

Key words: conifers, intra-annual growth, photoperiod, temperature, wood, xylogenesis.

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Introduction

Annual tree-ring differentiation involves the production of cells through the phases of division, expansion, secondary wall thickening, lignification and programmed cell death (Savidge, 1996; Plomion *et al.*, 2001). Wood formation is a highly dynamic process: the onset, rate and duration of cell differentiation change during the growing season as the tree ring develops, creating a complex time–space system of xylogenesis (Wodzicki, 1971; Uggla *et al.*, 2001; Deslauriers *et al.*, 2003a) precisely regulated by gene expression (Hertzberg *et al.*, 2001; Schrader *et al.*, 2004), hormonal signals (Uggla *et al.*, 1998; Schrader *et al.*, 2003) and environmental factors (Denne, 1971, 1976; Savidge, 1996; Antonova & Stasova, 1997; Deslauriers & Morin, 2005).

In European and North American conifers of cold environments, tracheid production mostly occurs from May to the beginning of August (Camarero *et al.*, 1998; Horacek *et al.*, 1999; Deslauriers *et al.*, 2003a; Mäkinen *et al.*, 2003; Rossi, 2003; Schmitt *et al.*, 2004). During the growing season, a

certain variability exists in the onset and rate of growth caused by different intra-annual weather conditions. At the same site, the onset of cambium activity can vary considerably, from the beginning of May to June (Deslauriers *et al.*, 2003a; Rossi, 2003), depending on the timing of snow melt and the rise of air and soil temperature (Vaganov *et al.*, 1999). In a boreal forest of North America, it was found that equivalent numbers of cells were produced with a faster growth rate over a shorter period and with a slower growth rate over a longer period (Gregory & Wilson, 1968; Deslauriers & Morin, 2005).

Despite this variability and the wide diversity that exists amongst geographical locations and species, the annual stem growth trends observed in temperate and cold areas of the northern hemisphere are very similar: a positive exponential growing phase is followed by a phase in which growth rate decreases, resulting in an S-shaped pattern (Ford *et al.*, 1978; Horacek *et al.*, 1999; Deslauriers *et al.*, 2003b; Schmitt *et al.*, 2004). This trend is typical of all biological limiting growth processes and is fixed in ontogeny (Klingenberg, 1998). From the annual growth pattern, three important phenological traits can be determined: the onset of growth, the time of maximum growth corresponding to the moment of transition from growth acceleration to growth deceleration (analytically defined as the inflection point), and the period of growth rest. The activation of plants in spring and their entry into dormancy have been widely studied and related to temperature and photoperiod (Heide, 1993; Partanen *et al.*, 1998; Chuine & Cour, 1999; Kramer *et al.*, 2000; Partanen *et al.*, 2001), but no study has been specifically dedicated to understanding the timing and possible variability of maximum growth rate.

The assessment of this phenological trait is important for understanding the impact of delays or early onsets on the timing and duration of both exponential phases of the sigmoid pattern. A variation of the annual maximum growth rate along the time axis, because of early or late onset, would reflect the ability of the species to exploit favourable climatic conditions, for example high temperatures, during the growing season. Recently, Mäkinen *et al.* (2003) proposed that the annual maximum growth rate of *Picea abies* Karst L. in Finland was regulated by temperature, as xylem formation occurred most rapidly in the first 10 d of July, corresponding to the highest temperatures observed during the year. Several authors also observed higher wood formation rates around June to July (Deslauriers *et al.*, 2003a; McCarroll *et al.*, 2003; Schmitt *et al.*, 2004). However, independently of variation in the onset of wood formation, after the end of cell division and enlargement, all tracheids must also complete the deposition of secondary wall polysaccharides and lignification by late autumn (Gindl *et al.*, 2000; Gričar *et al.*, 2005). Therefore, the temporal variability in the signals positioning the culmination of cell division should be low and this culmination should occur early enough in the growing season to leave a safe time margin for latewood lignification.

This paper presents the first study of the timing of maximum growth rate in wood formation in the main European and North American conifers. We tested the hypothesis that maximum growth rate is invariant in time for all species and latitudes considered, by modelling annual tree growth with the Gompertz equation. This invariance is predicted because timing of maximum growth rate should be within tight limits, ensuring both optimal temperature conditions and full cell maturation. To verify this hypothesis, a very large data set was collected, unique to the type of measurement used, the period of analysis and the variety of species included. In order to cross-validate the results for annual growth patterns, both xylem cell analysis (XCA), evaluating cambium activity in terms of weekly total tracheid production (Deslauriers *et al.*, 2003a), and automatic dendrometer measurement (ADM), assessing variation in stem size (Deslauriers *et al.*, 2003b), were used.

Materials and Methods

Study areas

Data were collected from several conifer species (see Table 1 for the species used) from high-altitude environments in Italy [5 Torri 1 (abbreviated as 5T1), 5 Torri 2 (5T2), Comelico (COM), San Vito (SVT), Pollino (POL) and Val di Susa (VSS)] and from the Canadian boreal forest [Arvida (ARV), Liberal 23 (L23), Liberal 24 (L24), Simoncouche (SIM) and Mistassibi (MIS)] (Table 1). In Italy, the sites were located between 39° and 46° N and from 1000 to 2200 m above sea level (a.s.l.). Sites 5T1, 5T2, COM and SVT were located in the eastern Italian Alps. 5T1 and 5T2 were areas located close together in the timberline ecotone with southern and northern exposure, respectively, and had a mixed open structure. Sites COM and SVT were both mixed forest stands. VSS was located at a subalpine level near the upper timberline in the western Italian Alps. POL was located in a treeline area of southern Italy and contained isolated trees growing on cliffs. In Canada, the sites were located in the province of Québec between 48° and 50° N. ARV was an urban forest on the upper border of the Saguenay River (Ville de Saguenay) included in Saucier's (1999) forest zone 4e. SIM and MIS were permanent plots of black spruce in the area of Saguenay-Lake Saint-Jean, included in ecological regions 5d and 6h (Saucier, 1999), respectively. L23 and L24 were located *c.* 100 km north of Lake Saint-Jean and consisted of two permanent plots of *Abies balsamea* included in Saucier's (1999) ecological regions 6e and 6h, respectively.

Data collection

The intra-annual dynamics of tree-ring formation were studied by XCA and ADM in several species during the 1996–2003 growing seasons, assessing xylem cell production and radial growth in the stem, respectively (Table 1).

Table 1 Geographical coordinates and altitudes of each study site, species descriptions, years of observations and measurements, number of sampled trees for xylem cell analysis (XCA) and number of dendrometers used

						XCA		ADM	
Site	Latitude	Longitude	Altitude (m a.s.l.)	Species	Age (years)	Years of observations	Number of trees	Years of measurements	Number of trees
5T1	46°27′ N	12°08′ E	2085	*Larix decidua* L.	50–60	2001–2003	5	1996–2004	2[b]
				Picea abies Karst (L.)		2001–2003	5	1996–2004	2[b]
				Pinus cembra L.		2001–2003	5	1996–2004	2[b]
5T2	46°27′ N	12°08′ E	2156	*Larix decidua* L.	50–60	2002–2003	5	2002–2004	2[p]
				Picea abies Karst (L.)		2002–2003	5	2002–2004	3[p]
				Pinus cembra L.		2002–2003	1	2002–2004	1[p]
ARV	48°26′ N	71°09′ W	80	*Abies balsamea* (L.) Mill.	100–150	1999–2000	18	–	–
COM	46°39′ N	12°25′ E	1600	*Larix decidua* L.	40–50	–	–	2002–2003	2[b]
				Picea abies Karst (L.)		–	–	2002–2003	1[b]
				Pinus sylvestris L.		–	–	2002–2003	3[b]
L23	49°58′ N	72°30′ W	380	*Abies balsamea* (L.) Mill.	150–190	1998–2000	10	1998–2004[a]	10[p]
L24	49°58′ N	72°30′ W	430	*Abies balsamea* (L.) Mill.	20–30	1998–1999	10	–	–
				Abies balsamea (L.) Mill.	150–190	1999–2001	10	1998–2004[a]	10[p]
MIS	49°43′ N	71°56′ W	342	*Picea mariana* (Mill.) B.S.P.	110–130	2000–2003	10	2001–2004	10[p]
POL	39°54′ N	16°12′ E	2053	*Pinus leucodermis* Ant.	300–500	2003	10	2003–2004	3[p]
SIM	48°13′ N	71°15′ W	338	*Picea mariana* (Mill.) B.S.P.	70–110	2001–2003	10	2001–2004	10[p]
SVT	46°26′ N	12°13′ E	1020	*Larix decidua* L.	60–80	–	–	2000–2004	2[b]
				Picea abies Karst (L.)		–	–	2000–2004	2[b]
				Pinus sylvestris L.		2003	1	2000–2004	2[b]
VSS	45°03′ N	06°40′ E	2030	*Larix decidua* L.	100–150	2003	5	–	–
				Pinus cembra L.		2003	5	–	–
				Pinus uncinata Mill.		2003	5	–	–

[a]Measurements in 2000 at L24 and in 2001 at L23 are missing because of technical problems with the data-loggers.
Automatic point (p) and band (b) dendrometers are indicated.
For descriptions of sites, see text.

For XCA, wood microcores (1.2–2.4 mm in diameter) were collected around the stems at breast height (d.b.h.) (1.3 m) from May to October using surgical bone sampling needles (Deslauriers *et al.*, 2003a) or increment punchers (Forster *et al.*, 2000). The microcores were placed in ethanol (50% in water) in Eppendorf microtubes and stored at 5°C. Weekly samples were taken, except for *P. abies* at SVT and *A. balsamea* at L24 during 2001, where microcores were collected every 3–4 d and every 15 d, respectively. Samples usually contained the previous three to six tree rings and the developing annual layer with the cambial zone and adjacent phloematic tissue. Microcores were embedded in paraffin (Anderson & Bancroft, 2002) and transverse sections 8–12 μm thick were cut with a rotary microtome (Rossi *et al.*, 2006). Sections were stained with cresyl fast violet (0.05% in water) or cresyl violet acetate (0.16% in water) and observed with visible and polarized light at ×400–500 magnifications to differentiate the developing xylem cells. The cambial zone and cells in radial enlargement showed only primary walls that did not shine under polarized light compared with secondary walls. Cells in the secondary wall-thickening phase changed from light violet at the beginning of the process to deep violet near the mature cell state. Lignification was characterized by the appearance of a blue colour, starting in the middle lamella and spreading into the secondary walls of differentiating tracheids. Xylem cells were considered lignified and mature when they were completely blue. For each sample, the total xylem cell number was found by counting the number of cells in radial enlargement and in cell wall thickening and the number of mature cells in three radial rows (Abe *et al.*, 1997; Deslauriers *et al.*, 2003a), and this was averaged for each site, species and year.

For ADM, point or band dendrometers installed at d.b.h. were used to continuously monitor radial growth (Table 1). Dendrometers measure linear displacement of a sensing rod or band pressed against the bark of the stem. The operating principle is based on the use of a linear variable differential transformer (LVDT) or a potentiometer. As the stem expands and contracts, the core of the LVDT or potentiometer moves simultaneously, translating the displacement into an electrical signal. Continuous seasonal time-series of intra-annual stem growth provided by dendrometers indicate tree-ring cell division and enlargement of the xylem and the phloem (Deslauriers *et al.*, 2003b). Raw data were recorded every 15 min, and hourly averages were then calculated. Data collected by means of band dendrometers were divided by 2π, giving linear measurements of variation in stem diameter. Because of the

unequal data collection intervals, growth curves obtained by XCA and ADM included different numbers of measurements. For dendrometer measurements, weekly averages were used to harmonize the two data sets.

Fitting of growth curves

Both XCA and ADM growth data were modelled with a Gompertz function using the nonlinear regression (NLIN) procedure with the Marquardt iterative method in the SAS statistical package (SAS Institute, Cary, NC, USA) (Motulsky & Ransnas, 1987). Of the various sigmoid models available to describe limiting growth processes, the Gompertz equation is the most appropriate because of its flexibility and asymmetrical shape (Zeide, 1993). It was therefore used to fit growth data to assess the overall dynamics of radial growth (Camarero *et al.*, 1998; Deslauriers *et al.*, 2003a; Mäkinen *et al.*, 2003; Rossi *et al.*, 2003).

The Gompertz function was defined as:

$$y = A \exp(-e^{\beta-\kappa t}) \quad \text{Eqn 1}$$

[y, weekly cumulative sum of cells (XCA) or stem increment (ADM); t, time (expressed as day of the year); A, upper asymptote (maximum growth expressed as cell number or tree-ring width); β, x-axis placement parameter; κ, rate of change of shape (Rossi *et al.*, 2003).]

The residuals were regressed on the model partial derivatives with respect to the Gompertz parameters until the estimates converged. Several possible starting values were specified for each parameter, so that the NLIN procedure evaluated each combination of initial values using the interactions producing the smallest residual sums of squares. To evaluate the general goodness-of-fit of each regression, the proportion of variation accounted for (R^2), the standard errors and linearity of each parameter and the distribution of the residuals were calculated (Motulsky & Ransnas, 1987; Ratkowsky, 1990; Draper & Smith, 1998).

Timing and variability of maximum growth rates

In the Gompertz function, the inflection point corresponds to the culmination of growth rate and the maximum value achieved by the first derivative, defined as:

$$y' = A\,\kappa \exp(-e^{\beta-\kappa t})e^{\beta-\kappa t} \quad \text{Eqn 2}$$

The placement of the inflection point on the horizontal axis (t_p) occurs where the second derivative is equal to 0, that is:

$$y'' = y'\,\kappa(e^{\beta-\kappa t} - 1) = 0 \quad \text{Eqn 3}$$

and then when $t_p = \beta/\kappa$. According to the hypothesis that maximum growth rate is invariant in time, the inflection points should occur in the same period of the year and the β/κ ratio should be equal to a constant, called T_p, and so

$$\beta = \kappa\, T_p \quad \text{Eqn 4}$$

Within-species variability of specific t_p values (Tables 2 and 3) was assessed by Student's t-test for mean location.

Results

Evaluation of the fitting

Statistical evaluation of nonlinear regression on XCA and ADM was based on statistics for goodness of fit, fitting behaviour and examination of the residuals. Nonlinear regressions explained a high proportion of variation, indicated by the R^2 in Tables 2 and 3. For XCA, the R^2 varied from 0.89 to 0.99 and higher R^2 were generally found for ADM because of lower variability in the data. For XCA, values of variance ratio (or F-test) ranged from 169.3 (*P. abies* at 5T2 in 2003) to 5397.3 (*A. balsamea* at L24 in 1998) and for ADM they ranged from 318.3 (*P. cembra* at 5T1 in 1997) to 27049.4 (*L. decidua* at SVT in 2004), reaching a high level of significance, with $P < 0.0001$. Standard errors of the parameters were lower for ADM than for XCA. Tests for linearity indicated that the standard errors were normally distributed and unbiased, and represented only 3.4% and 1.6% of the parameter values of A for XCA and ADM, respectively. The standard errors of β and κ represented 15.5% of the parameter values for XCA and 8.7% for ADM. The absence of patterns in the distributions of the residuals confirmed the model quality and the goodness of fit.

Relationship between β and κ

The relationships found between the two parameters β and κ (Tables 2 and 3) are expressed as linear regressions for both types of measurement in Fig. 1. Linear regressions showed positive slopes and highly significant F-statistics for both models ($F = 952.7$, $P < 0.0001$ with 95% confidence limits of slope 153.68–175.32 for XCA and $F = 661.8$, $P < 0.0001$ with 95% confidence limits of slope 157.58–184.01 for ADM). The estimated equations of the two regressions were

$$\beta_{XCA} = 0.32 + 164.5\,\kappa_{XCA} \quad \text{Eqn 5}$$

and

$$\beta_{ADM} = -0.22 + 170.8\,\kappa_{ADM} \quad \text{Eqn 6}$$

For XCA and ADM, the ranges of values taken by the parameters β and κ were similar, from *c.* 2×10^{-2} to 8×10^{-2} for κ and from 3 to 15 for β, and there was no significant difference between the slopes (α_1) of the two regressions ($P > 0.05$).

Table 2 Parameters of the Gompertz function and R^2 for all models fitted by nonlinear regressions for xylem cell analysis (XCA) and t_p values corresponding to the times of the inflection point

			Parameter				
Site	Species	Year	*A*	β	κ (10^{-2})	R^2	t_p
5T1	*Larix decidua*	2001	44.98 (2.74)	5.43 (0.87)	3.06 (0.51)	0.95	177.6
		2002	36.36 (0.85)	8.72 (0.94)	4.93 (0.53)	0.98	176.9
		2003	50.89 (1.68)	10.51 (1.75)	6.10 (1.01)	0.96	172.4
	Picea abies	2001	75.36 (1.91)	7.82 (0.76)	4.42 (0.43)	0.98	177.0
		2002	60.82 (1.41)	8.54 (0.9)	4.85 (0.51)	0.97	176.1
		2003	70.57 (1.77)	10.27 (1.38)	6.18 (0.82)	0.97	166.1
	Pinus cembra	2001	56.50 (2.43)	5.78 (0.93)	3.57 (0.58)	0.93	162.0
		2002	49.11 (1.82)	7.01 (1.06)	4.10 (0.62)	0.95	171.1
		2003	59.71 (2.19)	9.71 (2.01)	6.13 (1.26)	0.94	158.5
5T2	*Larix decidua*	2002	31.52 (0.69)	13.02 (1.81)	7.39 (1.02)	0.97	176.1
		2003	38.50 (1.43)	11.52 (2.42)	6.84 (1.43)	0.94	168.4
	Picea abies	2002	45.42 (2.12)	10.17 (2.44)	5.71 (1.37)	0.91	178.1
		2003	56.06 (3.07)	13.11 (4.43)	7.80 (2.62)	0.89	168.0
	Pinus cembra	2002	40.57 (1.39)	9.42 (1.75)	5.62 (1.04)	0.93	167.7
		2003	49.82 (1.93)	7.97 (1.50)	5.03 (0.94)	0.94	158.6
ARV	*Abies balsamea*	1999	38.73 (0.74)	8.58 (1.09)	5.47 (0.67)	0.95	157.0
		2000	44.38 (1.25)	7.28 (0.80)	4.17 (0.46)	0.97	174.6
L23	*Abies balsamea*	1998	37.08 (0.75)	10.92 (1.25)	6.54 (0.74)	0.97	167.0
		1999	37.01 (1.15)	9.06 (1.37)	5.42 (0.81)	0.96	167.2
		2000	38.73 (1.99)	9.93 (2.19)	5.51 (1.22)	0.93	180.2
L24	*Abies balsamea*	1998[a]	51.21 (0.56)	8.95 (0.50)	5.49 (0.30)	0.99	162.9
		1999[a]	51.22 (0.90)	6.82 (0.44)	4.04 (0.26)	0.99	169.0
		1999	42.02 (0.62)	9.49 (0.68)	5.57 (0.40)	0.99	170.5
		2000	46.13 (2.00)	9.41 (1.55)	5.09 (0.84)	0.96	184.9
		2001	45.49 (2.24)	8.90 (1.96)	5.20 (1.14)	0.96	171.2
MIS	*Picea mariana*	2000	15.22 (0.55)	12.11 (1.99)	6.55 (1.08)	0.96	185.1
		2001	19.66 (0.93)	8.95 (1.86)	5.20 (1.09)	0.90	172.1
		2002	21.81 (0.70)	5.50 (0.42)	2.92 (0.23)	0.98	188.5
		2003	20.55 (0.61)	6.19 (0.57)	3.46 (0.33)	0.98	179.2
POL	*Pinus leucodermis*	2003	26.53 (1.72)	6.16 (1.33)	3.53 (0.78)	0.91	174.3
SIM	*Picea mariana*	2001	38.87 (0.87)	5.11 (0.28)	2.85 (0.16)	0.99	179.7
		2002	36.58 (0.99)	6.35 (0.53)	3.46 (0.30)	0.98	183.8
		2003	29.38 (1.03)	7.89 (1.20)	4.56 (0.69)	0.96	173.0
SVT	*Picea abies*	2003	91.10 (4.14)	6.61 (1.41)	4.17 (0.89)	0.89	158.5
VSS	*Larix decidua*	2003	21.84 (1.05)	14.27 (4.64)	8.3 (2.67)	0.89	171.9
	Pinus cembra	2003	39.72 (1.04)	10.00 (1.64)	6.45 (1.05)	0.95	155.2
	Pinus uncinata	2003	32.32 (0.70)	8.15 (0.92)	5.16 (0.57)	0.97	158.1

Values in parentheses represent the standard error of the estimated parameters.
For site descriptions, see text.
A, the upper asymptote; β, *x*-axis placement; κ, rate of change.
[a]Young trees.

Timing and variability of maximum growth rate

In Eqns 5 and 6, the intercepts (α_0) have a minimal influence on the variables β_{XCA} and β_{ADM} as the weight of α_0 on the β-values is lower than 10%. In addition, the 95% confidence limits of the intercepts (α_0) ranged between −0.25 and 0.89 for XCA and between −0.84 and 0.39 for ADM. α_0 was not significantly different from 0 ($P > 0.05$), with *F*-values of 1.28 and 0.53 for XCA and ADM, respectively. Therefore, Eqns 5 and 6 can be approximated as $\beta \sim \alpha_1 \kappa$ and, consequently, $T_p = \beta/\kappa \sim \alpha_1$ corresponding to the slope of the regressions, the placement of the inflection point on the horizontal axis and the time at which growth culmination occurs. The maximum growth rate for all the Gompertz equations modelled for XCA and ADM (Tables 2 and 3) therefore occurred in the same period of the year. Maximum growth rate occurred at 164.5 d for XCA and at 170.8 d for ADM, corresponding to 13–14 and 19–20 June, respectively. The annual growth rates for different species and years measured with both techniques are illustrated in Fig. 2(a,b). When the curves were represented as their first derivative, growth rate culmination occurred within a limited period (grey bands in

Table 3 Parameters of the Gompertz function and R^2 for all models fitted by nonlinear regressions for automatic dendrometer measurement (ADM) and t_p values corresponding to the times of the inflection point

			Parameter				
Site	Species	Year	*A*	β	κ (10^{-2})	R^2	t_p
5T1	*Larix decidua*	1996	1.47 (0.02)	10.35 (1.00)	5.89 (0.56)	0.98	175.6
		1997	1.02 (0.02)	11.34 (1.66)	6.57 (0.94)	0.97	172.7
		1998	1.84 (0.02)	8.05 (0.62)	4.60 (0.35)	0.94	175.0
		1999	1.89 (0.02)	9.04 (0.70)	5.23 (0.40)	0.95	172.9
		2000	2.25 (0.03)	9.31 (0.81)	5.61 (0.48)	0.98	165.9
		2001	2.43 (0.02)	7.04 (0.39)	4.12 (0.23)	0.89	171.2
		2002	2.05 (0.03)	9.14 (0.87)	5.29 (0.50)	0.98	172.8
		2003	1.73 (0.01)	8.91 (0.58)	5.40 (0.34)	0.98	165.1
		2004	2.19 (0.03)	7.05 (0.40)	3.97 (0.23)	0.99	177.8
	Picea abies	1996	1.31 (0.03)	7.45 (0.79)	4.03 (0.43)	0.98	184.9
		1997	1.95 (0.14)	5.63 (0.65)	2.92 (0.38)	0.98	193.3
		1998	1.54 (0.02)	6.12 (0.45)	3.76 (0.27)	0.99	162.8
		1999	1.33 (0.02)	8.40 (0.77)	5.24 (0.47)	0.98	160.6
		2000	2.08 (0.03)	8.02 (0.68)	4.76 (0.40)	0.98	168.6
		2001	2.67 (0.04)	6.29 (0.36)	3.55 (0.20)	0.96	177.4
		2002	1.22 (0.05)	5.31 (0.70)	2.92 (0.39)	0.99	181.7
		2003	2.06 (0.05)	8.49 (1.25)	5.22 (0.76)	0.99	162.8
		2004	2.10 (0.07)	5.52 (0.55)	3.04 (0.31)	0.98	181.7
	Pinus cembra	1996	0.37 (0.01)	8.16 (1.32)	4.51 (0.73)	0.98	181.0
		1997	1.37 (0.06)	9.55 (2.22)	5.27 (1.21)	0.95	181.2
		1998	2.13 (0.02)	5.93 (0.30)	3.39 (0.17)	0.82	174.7
		1999	1.91 (0.03)	7.72 (0.55)	4.20 (0.30)	0.99	183.7
		2000	1.41 (0.02)	7.60 (0.95)	5.05 (0.61)	0.95	150.7
		2001	1.89 (0.03)	5.91 (0.44)	3.77 (0.28)	0.92	156.9
		2002	0.69 (0.03)	3.13 (0.80)	2.37 (0.57)	0.99	132.2
		2003	1.07 (0.02)	7.69 (1.30)	5.18 (0.86)	0.98	148.4
		2004	1.12 (0.02)	9.71 (1.35)	5.61 (0.77)	0.96	173.2
5T2	*Larix decidua*	2002	1.84 (0.01)	10.39 (0.57)	5.95 (0.32)	0.99	174.5
		2003	1.85 (0.01)	10.34 (0.65)	6.35 (0.39)	0.97	162.8
		2004	1.75 (0.04)	9.02 (1.01)	4.82 (0.54)	0.96	187.1
	Picea abies	2002	1.52 (0.02)	9.39 (1.04)	5.63 (0.61)	0.99	167.7
		2003	1.79 (0.03)	9.41 (1.28)	5.94 (0.79)	0.96	158.4
		2004	1.91 (0.06)	7.11 (0.87)	3.99 (0.49)	0.97	178.5
	Pinus cembra	2002	1.87 (0.03)	5.88 (0.55)	3.91 (0.36)	0.98	150.5
		2003	2.14 (0.02)	7.27 (0.58)	4.93 (0.38)	0.97	147.6
		2004	2.65 (0.06)	4.66 (0.37)	2.85 (0.24)	0.98	163.8
COM	*Larix decidua*	2002	1.12 (0.01)	10.23 (0.77)	6.05 (0.45)	0.99	169.2
		2003	1.63 (0.02)	6.57 (0.40)	3.94 (0.24)	0.99	166.8
		2004	1.18 (0.01)	8.34 (0.66)	4.81 (0.38)	0.99	173.5
	Picea abies	2002	2.26 (0.01)	7.36 (0.29)	4.42 (0.17)	0.99	166.7
		2003	3.73 (0.06)	5.56 (0.39)	3.45 (0.24)	0.98	161.5
		2004	3.87 (0.03)	8.79 (0.44)	5.02 (0.25)	0.99	175.1
	Pinus sylvestris	2002	2.19 (0.02)	7.32 (0.47)	4.45 (0.28)	0.99	164.6
		2003	2.22 (0.03)	5.14 (0.30)	3.13 (0.19)	0.99	164.1
		2004	1.99 (0.03)	6.60 (0.44)	3.78 (0.26)	0.99	174.9
L23	*Abies balsamea*	1998	2.42 (0.01)	7.02 (0.30)	4.51 (0.19)	0.99	162.6
		1999	3.06 (0.19)	6.52 (0.62)	4.11 (0.43)	0.99	157.2
		2000	1.53 (0.01)	7.58 (0.34)	4.62 (0.20)	0.99	171.8
		2002	1.58 (0.02)	8.87 (0.50)	5.00 (0.28)	0.99	171.5
		2003	1.25 (0.01)	8.90 (0.58)	5.36 (0.34)	0.99	165.1
		2004	1.46 (0.01)	9.59 (0.36)	5.29 (0.20)	0.99	178.4
L24	*Abies balsamea*	1998	1.54 (0.01)	9.97 (0.52)	6.13 (0.31)	0.99	155.6
		1999	2.10 (0.02)	9.56 (0.51)	6.08 (0.32)	0.99	158.9
		2001	1.80 (0.02)	8.82 (0.58)	5.13 (0.34)	0.99	163.9
		2002	2.15 (0.03)	8.43 (0.71)	4.92 (0.42)	0.98	177.6
		2003	0.91 (0.01)	8.98 (0.64)	5.44 (0.38)	0.99	166.1
		2004	1.26 (0.01)	9.43 (0.40)	5.29 (0.23)	0.99	181.3

Table 3 *Continued*

Site	Species	Year	Parameter				
			A	β	κ (10^{-2})	R^2	t_p
MIS	*Picea mariana*	2001	1.15 (0.01)	6.69 (0.62)	4.53 (0.41)	0.97	147.6
		2002	0.98 (0.03)	7.01 (0.96)	4.12 (0.56)	0.95	170.4
		2003	0.94 (0.06)	6.76 (1.26)	4.19 (0.80)	0.94	161.4
		2004	0.70 (0.01)	9.12 (1.15)	5.39 (0.67)	0.96	169.3
POL	*Pinus leucodermis*	2003	1.09 (0.02)	7.32 (0.88)	3.90 (0.46)	0.94	187.7
		2004	0.92 (0.03)	12.37 (1.78)	6.64 (0.96)	0.97	186.4
SIM	*Picea mariana*	2001	0.90 (0.02)	8.23 (0.80)	4.74 (0.46)	0.97	173.5
		2002	1.18 (0.02)	6.71 (0.59)	3.98 (0.35)	0.98	168.7
		2003	0.93 (0.03)	6.61 (0.90)	4.11 (0.56)	0.96	160.8
		2004	1.33 (0.04)	6.89 (0.53)	4.03 (0.32)	0.99	171.2
SVT	*Larix decidua*	2000	3.15 (0.02)	6.13 (0.20)	3.81 (0.12)	0.99	160.8
		2001	3.57 (0.02)	6.03 (0.21)	3.86 (0.13)	0.99	156.5
		2002	6.30 (0.04)	7.21 (0.25)	4.63 (0.16)	0.97	155.7
		2003	3.68 (0.03)	7.97 (0.55)	5.36 (0.36)	0.99	148.6
		2004	0.56 (0.01)	7.49 (0.18)	4.63 (0.11)	0.99	162.0
	Picea abies	2000	1.49 (0.01)	6.36 (0.29)	4.38 (0.20)	0.99	145.3
		2001	2.04 (0.01)	6.36 (0.22)	4.15 (0.14)	0.99	153.3
		2002	2.62 (0.02)	6.19 (0.35)	4.06 (0.22)	0.99	152.8
		2003	1.91 (0.02)	7.06 (0.60)	4.76 (0.40)	0.99	148.6
		2004	0.25 (0.01)	5.74 (0.32)	3.57 (0.20)	0.99	160.7
	Pinus sylvestris	2000	0.68 (0.01)	7.29 (0.78)	5.59 (0.58)	0.98	130.4
		2001	1.02 (0.01)	4.83 (0.21)	3.22 (0.14)	0.98	150.0
		2002	1.43 (0.01)	3.78 (0.13)	2.60 (0.09)	0.99	145.3
		2003	1.38 (0.01)	6.00 (0.48)	4.43 (0.35)	0.99	135.5
		2004	0.10 (0.01)	4.78 (0.41)	3.10 (0.27)	0.97	154.2

Values in parentheses represent the standard error of the estimated parameters.
For site descriptions, see text.
A, the upper asymptote; β, *x*-axis placement; κ, rate of change.

Fig. 2c,d). *F*-tests revealed no significant difference ($P > 0.05$) between the slopes of the regression and the value 172 d, corresponding to the summer solstice on 21 June (Fig. 2e,f).

The specific t_p value (Tables 2 and 3) for each species, site and year suggests that the maximum range achieved in growth culmination was 62.8 d for ADM and 33.3 d for XCA. The wide range found for ADM was related to the earlier maximum growth for *P. sylvestris* (at SVT in 2000 and 2003) and *P. cembra* (at 5T1 in 2002). For most species, t_p values were distributed around the summer solstice (Student's *t*-test; $P > 0.05$), except for *P. sylvestris* (for ADM; Student's $t = -3.63$; $P < 0.01$) and *P. cembra* (for XCA and ADM; Student's $t = -3.03$; $P < 0.01$) which generally showed earlier growth culmination. For all species, the periods over which t_p values were distributed were similar for XCA and ADM, with the exception of *P. mariana*, where the t_p values for XCA were slightly delayed with respect to those for ADM.

Discussion

Achievement of maximum growth rate in the main European and North American conifer species is limited to a short period, in most cases at about the time of maximum day length. The circannual cycles of change in photoperiod throughout the year are regular enough to represent a constant signal, explaining the synchronization observed. Timing mechanisms and temporal adaptations enable the plant to alter its physiology and biochemistry in accordance with environment changes through the perception of light signals by the phytochromes (Smith, 2000). Day or night length provides information of crucial ecological value at many stages in plant development, such as flowering, dormancy release, onset of ontogenetic development and induction of bud dormancy (Heide, 1993; Partanen *et al.*, 1998, 2001; Badeck *et al.*, 2004). The synchronization observed in this study could be bounded or fixed by ontogenetic programmes (Alpert & Simm, 2002) based mainly on photoperiod.

According to Poethig (2003), coordination of organ production, such as production of leaves or flowers, is accomplished in part by a thermal clock and by signal transduction pathways that mediate the plant response to light. Given the variability observed in the timing of maximum growth rate, maximum photoperiod could act as a growth constraint or a limit after which the rate of tree-ring formation tends to decrease.

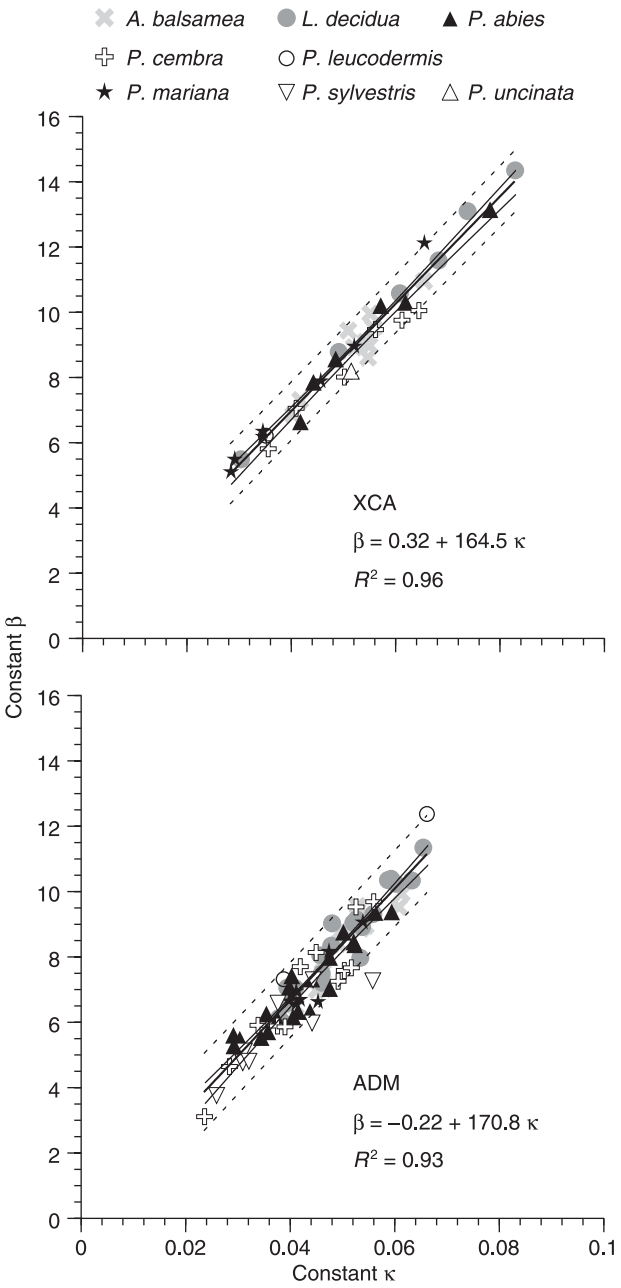

Fig. 1 Relationship between *x*-axis placement (β) and rate of change (κ) for xylem cell analysis (XCA) and automatic dendrometer measurements (ADM). Thick lines, thin lines and broken lines represent the regression line, 95% confidence limits and 95% confidence bands, respectively.

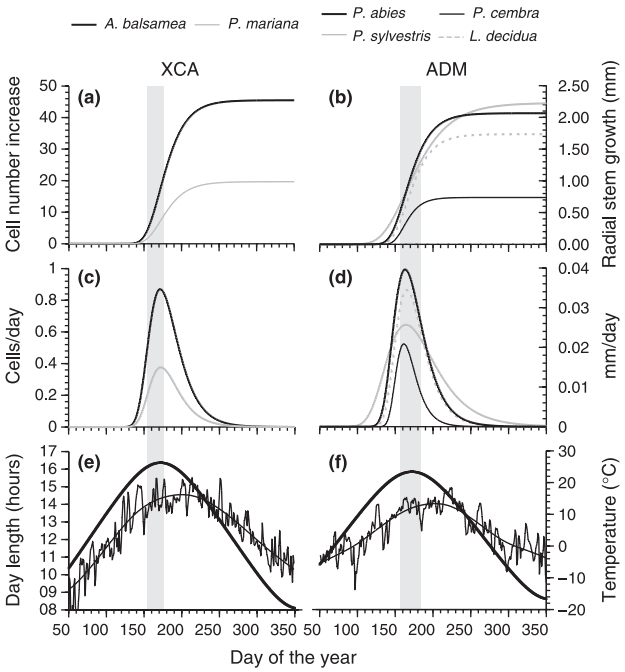

Fig. 2 Tree-ring formation assessed by xylem cell analysis (XCA) for *Abies balsamea* (L23) and *Picea mariana* (MIS) in 2001 (left side) and by automatic dendrometer measurement (ADM) for *Picea abies* (5T1), *Larix decidua* (5T1), *Pinus cembra* (5T1) and *Pinus sylvestris* (COM) in 2003 (right side). (a) Cell number increase; (b) radial stem growth (mm); (c) cell production rate (cells d^{-1}); (d) radial growth rate (mm d^{-1}); (e) day length (thick line) and mean daily temperature (°C) for the L23 site in 2001; (f) day length (thick line) and mean daily temperature (°C) for the 5T1 site in 2003. The grey bands correspond to the 95% confidence limits of the regression slopes.

By regression, the inflection point was placed slightly before the maximum photoperiod, and only nine t_p values out of 119 (7%) were at the beginning of July. Maximum growth rate occurred more frequently before than after the maximum photoperiod. Effects of other environmental factors, such as temperature, on the variation observed in the maximum growth response are not excluded and remain to be precisely evaluated for specific sites and species.

The findings of this study indicate that XCA and ADM provide similar results for the timing of the inflection point of annual stem growth, demonstrating that stem shrinking and swelling caused by water storage variation (Zweifel & Häsler, 2001) have a minimal influence. If water stress occurs in late spring or early summer, high stem radius variation could lead to major differences between XCA and ADM. However, water stress conditions were not detected during the period of highest cell production (June). Mäkinen *et al.* (2003) obtained different results with different methods for measuring the timing of growth rate culmination in a study of *P. abies* in Finland: maximum growth rate measured by dendrometer occurred in mid-June, and that measured by counting tracheid production occurred in the first two weeks of July. The paper reported that microcores were split longitudinally and the tracheids were counted with a stereo-microscope. When performing this type of analysis, all the tracheids from post-cambial enlarging cells to the mature cells have to be counted to ensure a precise assessment of tracheid production (Wodzicki, 1971). However, in order to observe cambium and enlarging cells, suitable microscope sections and magnifications have to be used (Rossi *et al.*, 2006), otherwise introduced errors will

lead to delays and misinterpretations of the timing of wood production.

The growth constraint connected with maximum photoperiod could be an adaptation to prevent a shift of tracheid production along the time axis, leaving enough time to complete cell wall formation and lignification before winter. At our study sites, xylogenesis lasted from May–June to September–October, including all processes such as cell production, enlargement, wall thickening and lignification (Deslauriers *et al.*, 2003a; Rossi *et al.*, 2003; Rossi, 2003). As a result, growth rate culmination, occurring around the summer solstice, arrives particularly early in the growing season. If, in a cold environment, tracheid production were influenced only by temperature, the persistence of warm periods in August–September could lead plants to maintain high rates of cell division in late summer. At the end of the growing period, the cambium becomes dormant, although the recently produced tracheids continue differentiating for some time (Donaldson, 1991, 2001; Gindl *et al.*, 2000; Gričar *et al.*, 2005). A latewood tracheid of *P. abies* produced in mid-August at the 5T1 site remained in the differentiation stage for 40 d, not reaching the mature stage until the end of September (Rossi, 2003). In the boreal forest also, 30–40 d are necessary to complete secondary wall formation of latewood in *A. balsamea* (Deslauriers *et al.*, 2003a). Moreover, lignification of latewood tracheids may be considerably delayed when compared with deposition of secondary wall polysaccharides (Gindl *et al.*, 2000; Gričar *et al.*, 2005). The incorporation of lignin in cell walls is the process that completes the formation of a tracheid. At lower altitude in Slovenia, lignification of *Abies alba* Mill. persists until November (Gričar *et al.*, 2005). In *P. abies*, lignin content in the secondary cell wall of the terminal latewood tracheids is positively correlated with temperature from September to the end of October (Gindl *et al.*, 2000). Unlike in temperate regions, where deposition of cell material can continue during winter or the next spring (Nix & Villiers, 1985; Donaldson, 1991, 2001), cell wall formation in conifers of colder environments was found to be finished before winter (Gričar *et al.*, 2005), sometimes resulting in incomplete development. As a consequence, delays in the timing of maximum growth rate in July, during the warmest period of the year, imply the maintenance of secondary wall synthesis and lignin deposition of latewood close to winter, when climatic conditions, especially temperature, might no longer be favourable and affect lignin content. Therefore, cell production and enlargement occurring early in the growing season, and not during the warmest period (Wang *et al.*, 2002; Mäkinen *et al.*, 2003), represent a better adaptation allowing tracheid differentiation to be completed and avoiding inadequate cell wall lignification.

The phenology of cambium and wood formation is also driven by temperature, which was also proposed as the main factor affecting growth onset (Vaganov *et al.*, 1999). For boreal and high-altitude conifer species, short-term variations of temperature were found to influence cell production (Antonova & Stasova, 1997; Rossi, 2003; Deslauriers & Morin, 2005) or stem radius increase (Downes *et al.*, 2004). Photoperiod and temperature therefore represent two crucial factors influencing xylogenesis but with different levels of interaction in growth–climate relationships. Temperature allows metabolic activities to be maintained during cell production and differentiation, while photoperiod acts as a signal regulating the timing of maximum growth rate and synchronizing radial growth at the annual level (Fig. 2). As a result of this annual growth pattern, environmental factors influencing xylogenesis can have different effects in different periods of the growing season, according to the part of the growth curves in which they occur. As growth rate tends to decrease after the summer solstice, the temperature in the first increasing part of the growth curve is expected to have a major impact on tree-ring formation and wood production.

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