Chronological Coherence between Intra-Annual Height and Radial Growth of Scots Pine (*Pinus sylvestris* L.) in the Northern Boreal Zone of Finland

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Abstract

The phenophases of Scots pine, from bud break up to the end of cambium activity, at two sites (approx. 80 and 300 km, respectively, south of the forest border) in the northern boreal zone of Finland were monitored with high time resolution during three growing seasons. Averaged over the study sites and years, bud break occurred in the first half of May. Height growth started in the second half of May and radial growth followed around end of May/beginning of June. Both processes culminated in the second half of June, clearly before the warmest period of the year. Height growth finished by end of June/early July. Lastly, radial growth was completed by end of July/mid-August. Hence, the growing season from bud break to the end of radial growth took on average 87 days. However, annual shoot length and tree-ring width were independent from the duration of height and radial growth as well as from the onset dates for height growth and cambium activity, respectively.

Key words: Scots pine, phenophases, intra-annual height and radial growth, boreal zone

Introduction

Phenology of trees is the chronology of recurring events during an annual cycle such as winter dormancy, bud break, shoot growth or cambium activity (Lieth 1974). These growth events are controlled by endogenous (e.g., Lachaud 1989, Li and Adams 1994) and exogenous factors (e.g., Antonova and Stasova 1993, Partanen et al. 1998, Rossi et al. 2006), whose intricate linkages to each other are not yet sufficiently explored (Kramer and Kozlowski 1979, Savidge 1996, Hänninen and Kramer 2007). The timing of the phenological phases within a given area is the result of a long-term process of acclimation to the prevailing environmental conditions (e.g., Sarvas 1972, Häkkinen et al. 1995, Repo et al. 2000); such acclimation is essential for the viability of a tree population (‘ecotype’) (Kimmins 1987). Badeck et al. (2004) stressed that “plant phenology might be expected to be one of the most responsive and easily observable traits in nature that change in response to climate” and outlined its relevance for agriculture and forestry.

In the boreal zone, bud swelling is the first visual phenological event of tree growth after winter dormancy. For the onset of height growth as the subsequent phenophase a certain heat-sum is needed (e.g. Sarvas 1972, Wielgolaski 1999, Salminen and Jalkanen 2007). The phenophases of height growth and radial growth are associated to each other (e.g., Worral 1970, Kanninen et al. 1982, Jayawickrama et al. 1997); however, the mechanisms controlling tree growth remain unclear yet. The same applies for the role of plant hormones in the cambial reactivation after winter dormancy (e.g., Uggla et al. 1998, Sundberg et al. 2000, Funada et al. 2002). Clear coherences between phenological processes are, therefore, desirable to further enlighten the metabolic mechanism and control of growth (Zweifel et al. 2006). Deeper insight is also urgently required to estimate tree growth under the anticipated climate warming (Dougherty et al. 1994, Badeck et al. 2004, Kullman 2007).

In the present study, therefore, we aimed at monitoring the growth phenology of Scots pine with high time resolution at two sites in the northern boreal forests of Finland during three growing seasons and comparing these data sets with each other.

Material and methods

The growth-related phenophases of Scots pine (*Pinus sylvestris* L.), 300 and 80 km, respectively, south of its northern distribution limit at Vanttauskoski (site 1) and Laanila (site 2) in the northern boreal zone of Finland (Fig. 1), were monitored during the growing seasons 2001?2003. Both sites are dry or dryish but differ as regards temperature and precipitation (Table 1).

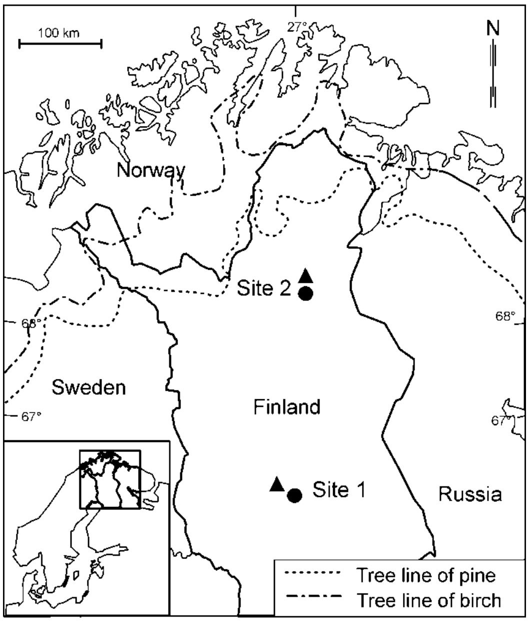

Figure 1. Study sites (●) and meteorological stations (▲); site 1: Vanttauskoski (●) / Rovaniemi (Apukka) (▲); site 2: Laanila (●) / Inari (Ivalo) (▲)

Table 1. Information on study sites and trees; prec.: precipitation, temp.: temperature, Lat.: latitude, Long.: longitude, Alt.: altitude, HG: height growth, RG: radial growth, DBH: diameter at breast height

ID	Site	Year	Vegetation type	Total annual prec. (mm)	Average annual temp. (°C)	July temp.(°C)	Location (site/weather station) Lat.(N)	Long.(E)	Alt.(m)
1	Vanttaus-koski		*Empetrum-*	613	0.3	15.8	66°22´	26°43´	150
			Vaccinium	493	0.2	16.4	/	/	/
				531	1.0	18.5	66°35´	26°01´	106
2	Laanila		*Uliginosum-*	586	-0.6	14.1	68°30´	27°30´	220
			Empetrum-	611	-0.6	15.0	/	/	/
			Myrtillus	532	0.5	17.3	68°40´	27°34´	123

ID	Year	Number of trees HG	RG	Age of trees HG	RG	Height (m) HG	RG	DBH (cm) HG	RG	Total annual HG (mm)	RG (mm)
1	2001	15	5	8 ? 20	40 ? 43	1.4 ? 2.0	11 ? 15	1.0 ? 2.0	15 ? 17	195	1.16
	2002	15	5							163	1.45
	2003	15	5							137	1.42
2	2001	5	5							114	1.12
	2002	4	5							132	1.19
	2003	5	5							76	1.18

Bud break and height growth were observed on 8–20 years old pine saplings naturally regenerated from local seeds. Bud break was noted when bud elongation had reached or exceeded 1 mm. Height growth was measured to the nearest mm once or twice a week between April and September throughout each season, according to Salminen and Jalkanen (2007). For it, a pin was permanently inserted as a reference point in the previous annual shoot of the main stem (Fig. 2A). Onset and end of height growth were defined as the point of time when shoot growth had accomplished 5 and 95%, respectively, of the total shoot length. These young trees were growing next to the stands where approx. 45-year old trees, naturally regenerated from local seeds as well, have been growing. With binoculars, we confirmed that bud break occurred in the tops of these11-15 m high, adult trees at the same time as in the up to 2 m high, young trees. Out of these adult trees, five individuals were selected for radial growth monitoring. In weekly intervals throughout the growing season their cambium was wounded by a pin to leave a timestamp in the xylem (Wolter 1968, Seo et al. 2007). This pinning technique was recently rated to be coequal to micro-coring (Mäkinen et al. 2008). After the growing seasons, the trees were felled to excise a disk including the pinning canals (Fig. 2B); for the next season, five new sample trees were selected. For microscopic observation, samples with a pinning canal, 1x1x1 cm^3 in size, were embedded in a solution of 25% polyethyleneglycol, and 18 µm thick cross-sections were cut with a sliding microtome and stained with safranine and astrablue. Then, the phenological events of radial growth, i.e. onset, early-/latewood transition and end, were microscopically determined by comparing the situation in a cross-section with the situation of the preceding pinning interval. The onset of earlywood formation was noted when new tracheids were observed next to the pinning canal between the place where the cambium zone was located at the time of pinning and the last year's tree-ring border (Fig. 2B, a+b); such tracheids were readily identifiable on the basis of their thin, unlignified walls since these tracheids died by the wounding and did not achieve maturity. The transition from early- to

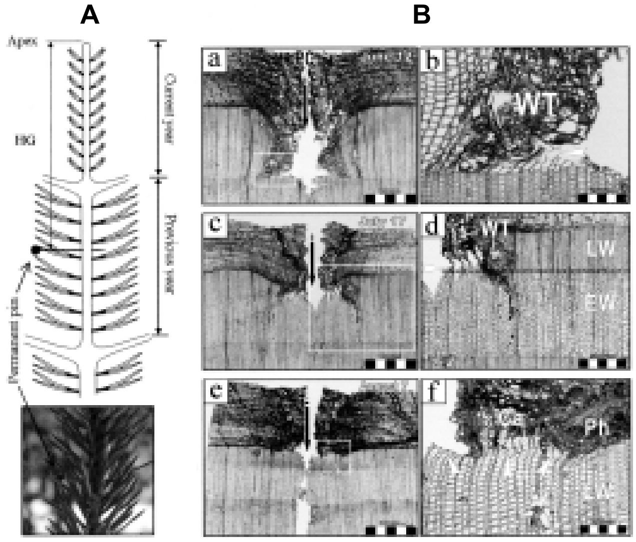

Figure 2. A: monitoring height growth (HG) of Scots pine during a vegetation period; B: determining the onset of wood formation, the transition from early- to latewood and the cessation of wood formation; on the left, overviews of transverse sections through a pinning canal; on the right, enlargements of the white-framed areas. a, b; pinning at June 12, first tracheids (white arrow head) formed after winter dormancy; c, d; pinning at July 17, tracheids (white arrow head) laid down just after the transition from early- to latewood (dotted line); e, f; pinning at August 7, tracheids formed at the end of wood formation (white arrow heads) , their secondary wall not yet completed. PC: pinning canal; WT: wound tissue; EW: earlywood; LW: latewood; Ca: cambium: Ph: phloem

latewood turned out to be rather abrupt and was therefore reliably identifiable, based on radially flattened and tick-walled tracheids (Fig. 2B, c+d). The end of radial growth was set when no new tracheids were observed at the cambium zone any longer (Fig. 2B, e+f). Between the onset and end of cambium activity, the radial increment of wood between each two pinning dates was measured and expressed as percentage of the entire tree-ring width achieved at the end of the growing season (Seo et al. 2007); these data show the intra-annual growth intensity.

The weekly meteorological situation during the three vegetation seasons at both sites, based on the nearby Rovaniemi (Apukka) and Inari (Ivalo) weather records (see Fig. 1), is illustrated as deviation of the actually measured date from their long-term mean value, calculated over the period 1961-2000 (Fig. 3). The deviations of temperature in a given year follow the same pattern at both sites; the year 2002, for example, stands out for above-average warm periods from April to mid-May and in the first half of June. In 2001, in contrast, temperature at both sites was closely fluctuating around the long-term average. Different from temperature, rainfall showed rather different patterns when compared between sites in a given year; for example, the southern site, Vanttauskoski, experienced a clear wet period from mid-June to mid-July in 2002, which was far less obvious at the northern site, Laanila.

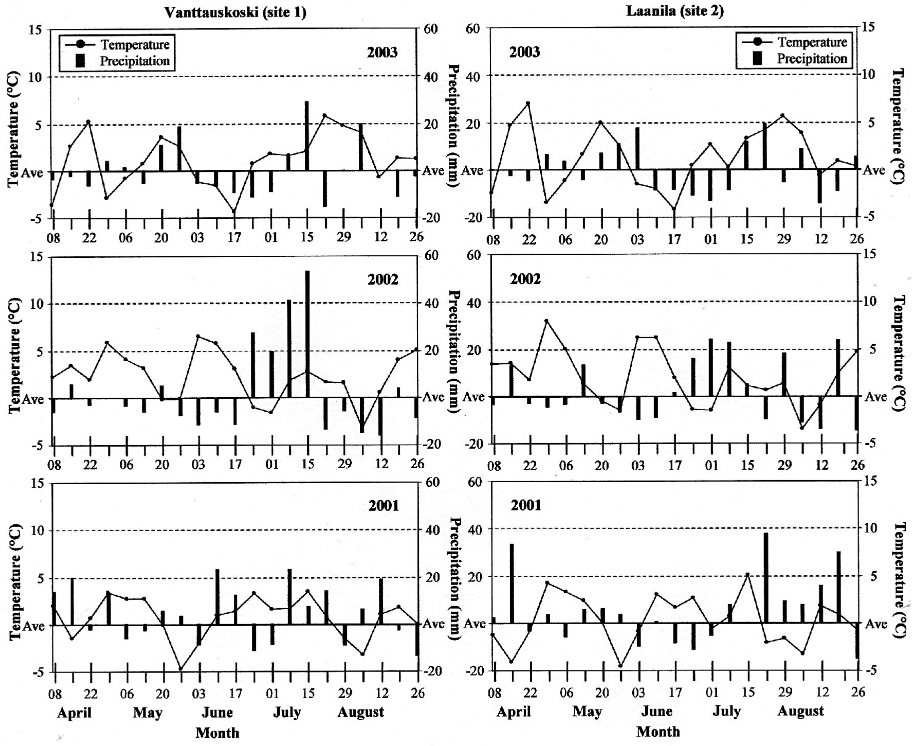

Figure 3. Deviation of weekly mean temperature and weekly sum of precipitation from the respective long-term average (Ave), calculated from 1961 to 2000

By means of the Wilcoxon rank test we checked whether there were significant differences between the phenological data sets per site or study year. Spearman's rank correlation was applied to calculate the statistical relations between the phenophases of a study year, separately for height and radial growth. Also, the total shoot lengths and tree-ring widths were correlated with the corresponding length of time for height and radial growth. Both the Wilcoxon rank test and the Spearman's rank correlation do not require normally distributed data. On the same account, we used the median for all averages and the range between the maximum and minimum values to describe the variability of data.

Results

Bud break and height-growth phenology

The dates for bud break as well as onset and end of height growth differed highly significantly between both study sites (Table 2) and also between the three study years (Table 3), except that the buds broke and height growth started in 2001 statistically at the same time as in 2003 (Fig. 4). Depending on the year, bud break took place between April 30 and May 6 (averaged over trees/year) at site 1 and about one week later (between May 2 and 16) at site 2. Height growth started on average two weeks after bud break (May 13–20 at site 1, May 19–June 2 at site 2) and culminated simultaneously at both sites in the second week of June in 2002 and in the fourth week of June in 2001 and 2003. Height growth ended in the three study years at significantly different dates, on average one week earlier at the southern site (June 24–July 6) than at the northern site (July 1–16). Onset and end of height growth depended strongly on the date of bud break (Table 4). The length of the height growth season, averaged over trees and years, was not significantly different between both sites (43 and 45 days, respectively) (Table 2), but between years (Table 3). The annual shoot length was not correlated with the length of the height growth season (Table 4).

Table 2. Wilcoxon signed-rank test to compare phenological dates between sites; bold p-values are significant on the 95% or higher confidence level

Phenology	B_B	H_O	H_E	H_D	H_L	R_O	R_E	R_D	R_W
Chi-square	10.24	11.32	6.65	0.37	10.35	3.39	6.24	15.19	1.71
n	45 / 14	45 / 14	45 / 14	45 / 14	45 / 15	15 / 15	15 / 15	15 / 15	15 / 15
p-value	**.001**	**.001**	**.009**	.544	**.002**	.065	**.012**	**.000**	**.019**

n number of study trees at the northern/southern site for each phenological variable; see also Table 1 for comparison. B_B = bud break; H_O = onset of height growth; H_E = end of height growth; H_D = duration of the height growth season; H_L = annual shoot length; R_O = onset of wood formation; R_E = end of wood formation; R_D = duration of the cambium activity season; R_W = tree-ring width.

Table 3. Wilcoxon signed-rank test to compare phenological dates between years; Y12 = between 2001 and 2002, Y13 = between 2001 and 2003, Y23 = between 2002 and 2003; bold p-values are significant on the 95% or higher confidence level

Phenology	B_B			H_O			H_E			H_D		
Year	Y_{12}	Y_{13}	Y_{23}	Y_{12}	Y_{13}	Y_{23}	Y_{12}	Y_{13}	Y_{23}	Y_{12}	Y_{13}	Y_{23}
Chi-square	19.30	1.53	29.71	13.12	1.15	5.74	9.54	15.57	23.16	2.26	13.79	22.49
n	20/19	20	19/20	20/19	20	19/20	20/19	20	19/20	20/19	20	19/20
p-value	**.000**	.216	**.000**	**.000**	.283	**.017**	**.002**	**.000**	**.000**	.105	**.000**	**.000**
Phenology	R_O			R_E			R_D					
Year	Y_{12}	Y_{13}	Y_{23}	Y_{12}	Y_{13}	Y_{23}	Y_{12}	Y_{13}	Y_{23}			
Chi-square	14.93	0.59	3.17	7.91	7.04	9.96	0.10	5.80	3.66			
n	10	10	10	10	10	10	10	10	10			
p-value	**.000**	.442	.075	**.005**	**.008**	**.002**	.756	**.016**	.056			

n number of study trees at the northern/southern site for each phenological variable; see also Table 1 for comparison. B_B = bud break; H_O = onset of height growth; H_E = end of height growth; H_D = duration of the height growth season; R_O = onset of wood formation; R_E = end of wood formation; R_D = duration of the cambium activity season.

Table 4. Spearman's rank correlation between the phenophases from 2001 to 2003, broken according to height growth and radial growth; bold p-values are significant on the 95% or higher confidence level

	B_B	H_O	H_E	H_D	H_L		R_O	R_E	R_D	R_W
B_B	1	0.51	0.66	0.15	-0.28	R_O	1	0.30	-0.34	0.01
		.000	**.000**	.272	**.034**			.104	.068	.942
H_O		1	0.45	-0.47	0.14	R_E		1	0.73	0.36
			.000	**.000**	.285				**.000**	.054
H_E			1	0.51	-0.37	R_D			1	0.22
				.000	**.004**					.248
H_D				1	-0.50	R_W				1
					.000					
H_L					1					

B_B = bud break; H_O = onset of height growth; H_E = end of height growth; H_D: duration of the height growth season; H_L: annual shoot length; R_O = onset of wood formation; R_E = end of wood formation; R_D: duration of radial growth; R_W: tree-ring width

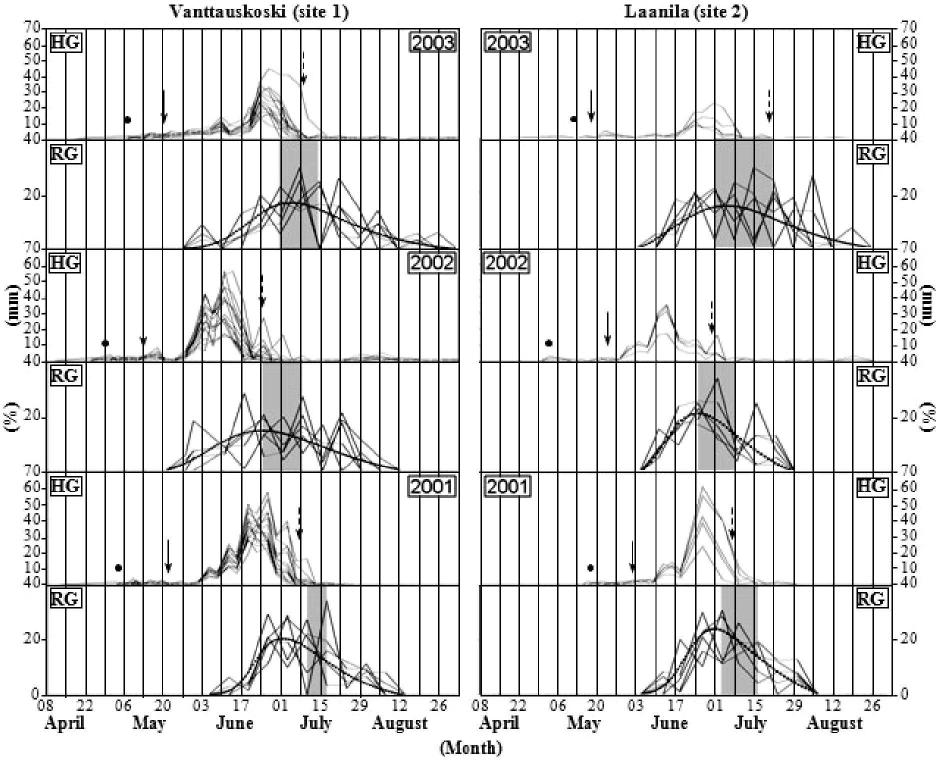

Figure 4. Overview of the intra-annual rate of height growth and radial growth of Scots pine at Vanttauskoski (site 1) and Laanila (site 2) during three growing seasons. HG: intra-annual height growth (dot: median date of bud break; arrow with a solid shaft: median date when 5% of annual shoot length were accomplished; arrow with a dotted shaft: median date when 95% of annual shoot length were accomplished); RG: radial growth in percent of the whole tree-ring width and smoothed average growth; shaded background, transition from earlywood to latewood. Statistical sample size of the phenological events corresponds to number of trees, given in Table 1.

Radial-growth phenology

The onset and end dates for radial growth differed between both sites (Table 2), even if on a low significance level (p=0.65 and 0.012, respectively). The onset dates of radial growth were significantly different between 2001 and 2002, but not between 2001 and 2003 and between 2002 and 2003 (Table 3). Depending on the study year, radial growth started between May 27 and June 11 (averaged over trees/year) at site 1 and on average one week later (June 10–16) at site 2. The beginning of latewood formation occurred statistically at the same time at both sites but not between the study years. Radial growth ended significantly differently between the study years. It ceased between July 29 and August 18 at site 1 and on average nine days earlier (July 22–August 4) at site 2 (Fig. 4). The length of the period of cambium activity was highly significantly different between both sites (62 and 47 days, respectively) (Table 2) and less significant between the study years, except between 2001 and 2002 when there was no correlation provable (Table 3). The total tree-ring width correlated neither with the onset of radial growth nor with the length of the cambium activity period (Table 4).

Chronological coincidence between bud break, height growth and radial growth (Fig. 5)

The time between bud break and the end of radial growth was on average 96 and 79 days at sites 1

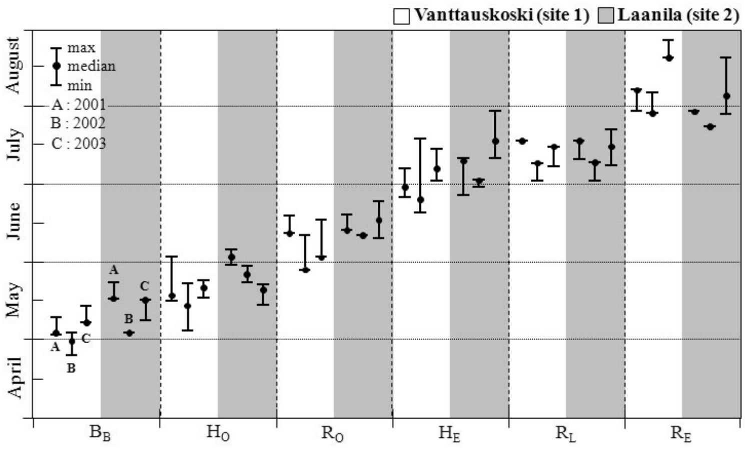

Figure 5. Chronology of the phenological events from bud break to the end of radial growth of Scots pine at Vanttauskoski (site 1) and Laanila (site 2); the phenological dates are represented by their median value and their range between maximum and minimum value. Statistical sample size of the phenological events corresponds to number of trees, given in Table 1.

and 2, respectively. Because of the shorter growing season at site 2 as compared to site 1, all phenological processes were gone through faster near tree line than farther south. From the onset of height growth (of the young trees) until the onset of radial growth (of the adult trees) on average three weeks passed at both sites. The duration between the onset of height growth and the end of radial growth (i.e., period when the trees are growing in volume) was on average 83 and 64 days at sites 1 and 2, respectively. Since the observations in this subchapter were made on different tree populations (young vs. adult trees), no correlations were calculated.

Discussion and conclusions

The phenological development of Scots pine in the northern boreal zone of Finland from bud break to the end of radial growth follows, generally speaking, a genetically fixed program, coordinated by phytohormones and modified by environmental factors (Larcher 2003). Based on a data set of the pan-European network of International Phenological Gardens (IPG), with two locations in northern Finland, Menzel (2000) revealed a lengthening of the growing season by on average 10.8 days as compared to the 1960s; this trend is consistent with observations in North America, although collected over a shorter time period (Richardson et al. 2006).

Does such an extension of the growing season explain why height growth of Scots pine in northern Finland has accelerated (Pensa et al. 2005) and volume growth has increased in the recent past (Tomppo et al. 2005)? According to Jalkanen and Tuovinen (2001) and Pensa et al. (2005), shoot length of Scots pine in northern Finland depends on July temperature of the previous summer. However, it is correlated with the rate of growth rather than with its duration (Salminen and Jalkanen 2007). In comparison, the annual tree-ring width is considerably correlated with the early summer temperature of the current year (Helama et al. 2002, Grudd 2008) and is, similar as shoot length, not correlated with the duration but with the intensity of cambium activity (e.g., Emmingham 1977, Deslauriers and Morin 2005, Vaganov et al. 2006). Our data set taken at two (climatically different) sites in three (climatically different) years deserves some confidence but intimates that the situation is not straightforward.

The onset of the phenophases of Scots pine differed between years, significantly or nearly so, thus proving a flexible and immediate response to the annually changing environment. By this capability, the trees take advantage of an early spring to improve or maintain site dominance (Bailey and Harrington 2006) and to avoid the risk of late frost damage (Hannerz 1999). Scots pine initiates cambial activity at both sites when the heat sum, in terms of degree-days, has accumulated to approximately 12.5 % of the long-term site-specific sum of degree-days (Seo et al. 2008).

The maximum rate of shoot and radial growth of our study trees occurred around or slightly later than the time of maximum day length and not during the warmest period of the year which is in the second half of July. This observation is in accordance with Rossi et al. (2006) who concluded that conifers in cold environments have adapted to a constant signal (maximum day length) to complete cell formation, including wall lignification, before early frost events may set in.

The end of all phenophases correlated with the respective onset dates, possibly due to genetic control (Oleksyn et al. 2000, Savolainen et al. 2004). Height growth ended when the heat sum, in degree days, had accumulated to approximately 41% of the site-specific, long-term heat sum (Salminen and Jalkanen 2007). The same percentage value was reported for Scots pine in southern (Raulo and Leikola 1975) and central Finland (Repo et al. 2000). Radial growth was completed when approximately 80% of the long-term heat sum had been achieved (Seo, unpubl. data); the variability of this percentage value between years is, however, higher than for the onset of radial growth, thus supporting the assumption that for growth cessation temperature is not the only trigger. A connection between growth cessation and timely frost hardening, suggested by Repo et al. (2000) for Scots pine, appears to be ecologically meaningful.

Among the study years, year 2002 was far above-average warm from April throughout July in northern Finland and the phenological cycle began (statistically highly significant) earliest at both sites as compared to 2001 and 2003. According to Häkkinen and Hari (1988), Hänninen and Pelkonen (1989) as well as Wielgolaski (1999), winter chilling and spring temperatures are the major influences for the start of the phenological cycle at high latitudes. This model-based conclusion agrees well with empirical findings (e.g. Sarvas 1972; Salminen and Jalkanen 2007). But unexpectedly, cambium activity in 2002 ended earliest as compared to 2001 and 2003, even though July was still by 1.5°C warmer than the average. Hence, the growing season in 2002 as a whole has been shifted into April by one week. For comparison, we may also consider data from the year 1996, obtained for Scots pine at the same sites and with the same technique as in the present study (Schmitt et al. 2004). The summer of 1996 was the coldest during the last 15 years; nevertheless the cambium was active from mid-June to around early to mid-August and accordingly nearly as long as in the years 2001–2003. Trees in cold environments generally synchronize their annual development with the average annual temperature cycle (e.g., Partanen et al. 1998), since an untimely onset or cessation of growth either gives rise to frost damage or results in an inadequate exploitation of resources (e.g., Heide 1985).

In agreement with Gamache and Payette (2004) as well as Kullman (2007), who referred to the heterogeneous topography and regional climate characteristics along the northern boreal vegetation zone, our phenological data set may be used as a benchmark for future monitoring activities in ecologically similar subregions.

Acknowledgements

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ХРОНОЛОГИЧЕСКАЯ СВЯЗЬ МЕЖДУ СЕЗОННЫМ ВЫСОТНЫМ И РАДИАЛЬНЫМ ПРИРОСТОМ ОБЫКНОВЕННОЙ СОСНЫ (*PINUS SYLVESTRIS* L.) В СЕВЕРНОЙ БОРЕАЛЬНОЙ ЗОНЕ ФИНЛЯНДИИ

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Резюме

Фенофазы обыкновенной сосны (*Pinus sylvestris L.),* начиная от распускания почек до конца активности камбия, были с большой временной точностью изучены в течение трех сезонов роста в двух местах (соответственно в 80 и 300 км от южной границы леса) в северной бореальной зоне Финляндии. В среднем по изученным местам и по годам распускание почек происходило в первой половине мая. Прирост в длину начался во второй половине мая, а радиальный рост последовал за этим в конце мая - в начале июня. Оба процесса достигли своего максимума во второй половине июня, отчетливо раньше самого теплого периода года. Прирост в длину закончился в конце июня - в начале июля. Наконец, радиальный прирост завершился в конце июля - в середине августа. Отсюда следует, что период роста от распускания почек до конца радиального прироста занял в среднем 87 дней. Однако длина годичного побега и ширина годичного кольца не зависели от продолжительности высотного и радиального роста, также как от начальных дат прироста в длину и активности камбия, соответственно.

Ключевые слова: обыкновенная сосна (*Pinus sylvestris* L.), фенофазы, сезонный высотный и радиальный прирост, бореальная зона