Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables

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Abstract

Tracheid production of balsam fir in the Québec boreal forest (Canada) was studied by repeated cell analysis to investigate the influence of meteorological variables during the growing seasons 1998 to 2000. Wood micro-cores were extracted on a weekly basis throughout the growing season and sections were prepared in order to count the total number of cells produced. From the weekly cell number obtained, the rate of tracheid production was calculated and correlated with meteorological variables. The average total number of cells produced per year was reasonably uniform, increasing only from 36.6 in 1998, to 41.1 in 2000. However, different cell production rates were noted during the growing season. Regression analysis revealed that the cell production rate was largely dependent on minimum air and soil temperature during most of the cell production period. Mean and maximum temperature had less influence on cell production. Moreover, the influence of temperature was higher during earlywood production mainly from the end of May to mid-July. Lagging the weather data by 1 to 5 days decreased the relationship between temperature and cell production, showing the high correspondence with the same interval where cell production was measured. These results suggest a fast response of the cambium to temperature variation during tree-ring formation.

Keywords: Tracheid production, temperature, boreal forest, growing season, *Abies balsamea*,

Introduction

The boreal forest is characterized by a short growing season due to low air and soil temperatures during the spring and summer months. Seasonal temperature dynamics, which vary greatly from year to year, influence the start of the growing period and the timing of the trees' optimal growth conditions (Creber and Chaloner 1990; Zabuga and Zabuga 1990; Kirdyanov et al. 2003). Previous results have shown that balsam fir (*Abies balsamea* (L.) Mill.) growing in the boreal forest appears to be well adapted to these changing conditions and shows flexibility in the rate and duration of tree-ring development (Deslauriers et al. 2003a). When tracheid production in the tree-rings of balsam fir was compared over the period 1998 to 2000, it was found that an almost equal amount of cells (from 36.6 to 41. 1) were achieved with a faster growth rate over a shorter period or with a slower growth rate over a longer period. These results suggest that the rate of tracheid production varies with the dynamics of seasonal temperature variation or other weather parameters, such as precipitation and radiation.

Cell number and size are the two variables that define tree-ring width (Vaganov 1996). Cell number, however, compared with cell size (Richardson and Dinwoodie 1960; Denne 1971; Wodzicki 1971; Antonova and Stasova 1993, 1997; Horacek et al. 1999; Deslauriers 2003) has less frequently been used when analysing the relationship with climate (Denne 1971; Ford et al. 1978; Antonova and Stasova 1993, 1997; Wang et al. 2002). Since ring width and cell number are highly correlated tree-ring parameters (Vaganov 1996; Camarero et al. 1998), it could be expected that climate affects both parameters equally. In the boreal forest, many studies have indicated the strong influence of temperature on tree-ring width, especially during June and July, (d'Arrigo et al. 1992; Hofgaard et al. 1999; Wang et al. 2002; Kirdyanov et al. 2003; Mäkinen et al. 2003). Although synchronous variations between cell number and ring width were observed, Wang et al. (2002) found a low correlation between ring cell number and summer temperature (May-September) for black spruce located in northern Québec. However, positive correlations were found between annual tracheid production and pentad temperatures at the end of July. These results suggest that temperature might not affect tracheid production throughout the growing season. Antonova and Stasova (1993, 1997) found a positive temperature influence on the cambial activity (i.e. tracheid production) of Scots pine and Siberian larch growing in central Siberia, but only at the start of the growing season (May-June). More recently, Kirdyanov et al. (2003) found that cell size and tree-ring width of different species of larch depend on temperature during the first part of the season, from June 7 to July 11 in the Siberian Subartic. Other environmental factors were also found to influence tracheid production. Ford et al. (1978) correlated daily solar radiation and the number of cells produced by Sitka spruce over a 15-day period during the growing season**.** In a controlled experiment Denne (1974) observed an increase in cell production at higher light intensity.

The aim of this study was to understand how temperature and other meteorological factors control intra-annual tracheid production and the growing season of balsam fir in boreal forests. In order to gain a better understanding of the relationship between radial growth and weather variation, detailed analysis of tree-ring development was used. The most important period during the growing season when parameters affect cell production was also determined.

Methodology

This study was conducted in a permanent plot of balsam fir, Lib-23 (49°46'03" N; 72°34'19" W), situated around 150 km north of Lac-Saint-Jean, Québec (Morin, 1994). The plot is located near the limit of the ecological region, which makes it interesting for climate response studies. Lib-23 has a unimodal age structure with a tree establishment period ranging from 1815 to 1850 and was only slightly affected by the 1974-1988 spruce budworm outbreak (Morin, 1994). The study site has a continental climate with cold winters and warm summers. The mean temperature ranges from -22 °C in January to 24 °C in July. Mean annual temperature is –0.7 °C and mean annual precipitation is 422 cm, with 357 cm falling as snow (Environment Canada 1992).

A 10 m high meteorological station was installed in a small forest clearing to monitor weather conditions. The measured variables were air temperature (Tmean, Tmax and Tmin [°C]) and relative humidity (RH, %) at a height of 3 m above the ground. Humus temperature (Thu, °C), total rainfall (P, mm), humus water content (SW, %), and global radiation (Rad, watt/m^2) were also recorded. SW and Thu were measured at a depth of 10 cm, corresponding to half the thickness of the humus layer. Measurements were taken every 5 minutes and stored as hourly averages in a datalogger (CR10X, Cambell Scientific Corporation). From the hourly measurements, daily Tmin and Tmax were found and daily averages were computed for Tmean, RH, Thu and SW. Precipitations were computed as the daily sum and global radiation was transformed into daily sum and expressed in Mj m^{-2} d^{-1}.

Tree-ring formation was analysed on ten adult trees (mean height, 17.5 m; mean diameter at DBH, 23.7 cm) in 1998, 1999 and 2000, as described in Deslauriers et al.

(2003a). In 1998, 20 trees were sampled before the start of the growing season and 10 trees with a similar average number of cells per ring were selected in order to ensure comparable growth rates. Surgical bone sampling needles (model: DBMNI-1501) were used for the weekly extraction of small cores of wood and bark, collected in a spiral fashion up the stems at a height of around 1.3 m, from May to October. The cores were 1 mm in diameter and 15-20 mm long, containing 4 to 6 rings. Every week, one wood core per tree was taken at least 10 cm from the previous one to avoid the presence of resin ducts in the next core, as this is a common disturbance reaction with balsam fir. Microcores presenting ring development malformation, mainly caused by late frosts, were not analysed.

Wood cores were fixed in paraffin and sections (10-12 µm thickness) were prepared with a microtome. The sections were stained with cresyl fast violet (0.05% in water) and observed under normal and polarised light to differentiate the developing xylem cells. For each sample, the number of total cells n_t was counted along three radial files and the total number averaged. The number n_t included cells in the phases of radial enlargement, cell wall thickening, and the number of mature cells (Deslauriers et al. 2003a). The number of cells in the annual rings varies within the tree circumference and consequently among different samples. The number of cells was therefore counted on three radial files of the three rings formed before the developing ring and used for a cell number circumference correction of the developing ring (Rossi et al. 2003).

For each tree, the cell production rate (cell/day) was found for each tree by the weekly difference of the total cell n_t divided by 7 (equation 1) and average for each year.

[1] $\text{Cell/day} = (n_t - n_{t-1})/7$

In latewood however, negative cell fluctuations were produced when the weekly n_t was lower than that of the preceding week (figure 1). These were observed when only a small number of new cells were developing over a period of several weeks at the end of the growing season. To avoid estimation problems at the end of cell production, the period analysed each year corresponds to the period when the majority of the cells were produced during the growing season, as calculated by the Gompertz equation, removing approximately the last 3-4 latewood cells formed (equation 2 and figure 1).

The Gompertz function is defined as:

[2] $y = a \exp(-e^{(\beta - \kappa t)})$

The time required for the major period of cell formation **d** to occur is defined as:

[3] $d = 4/\kappa$

Where ***y*** is the weekly cumulative number of cells, **t** is time computed in days since the first sampling date where t=0, ***a*** is the upper asymptote of the maximum number of cells where at t_i $y \cong a$, β is the *x*-axis placement parameter, and κ is the rate of change parameter (Cheng and Gordon 2000).

Figure 1

The relationships between cell production rate and meteorological variables were found with correlations and simple regression analysis. To assess the presence of a time-lag effect, cross-correlation analysis were performed. The daily weather data were averaged for different 7-day periods: (1) the exact 7-day period between each sample day (referred to as lag 0) and (2) the 7-day period was shifted backwards from 1 to 5 days before the sampling date (referred to as lag 1 to lag 5). All weather variables were averaged as described above and, in addition, weekly Tmin and Tmax were computed to represent the lowest and highest temperature of the average 7-day period. Simple correlations (Pearson, $p<0.05$) were computed (SAS Institute Inc. 1990) between cell production rate and weather data. Linear regressions were performed (SAS Institute Inc. 1990) for the temperature related variables. A square root (sqrt) transformation was applied on the cell production rate to meet the assumptions of homogeneity of variances (homoscedasticity) when performing the correlation and regression analysis (Zar 1999).

Results

Air temperature increased from April to May and decreased only at the end of August (figure 2). The minimum temperature was generally above 0 °C after the beginning of May in 1998 and 1999, or after mid-May in 2000. The increase in humus temperature generally lagged behind the increase in minimum air temperature, but only at the beginning of May when snow is still melting. Over the three years, the main temperature differences were observed in May, with warm temperatures in 1999 and cold ones in 2000. By June, the mean temperature had generally reached 15 °C (figure 2). Precipitations were well distributed and dry periods rarely exceeded one week. The daily cell production rate, estimated from a weekly sampling, was higher in June, or in July, when the transition from earlywood to latewood was observed later in the growing season (figure 2). Cell production in May 1999 started much earlier than the other years, but a low cell production rate of less than 0.2 cell/day was observed (figure 2), so the early start did not lead to a higher tree-ring cell number (figure 1). Although air and humus temperature remain high until the end of August, cell production rate declines after mid-July, corresponding to latewood cell production. Despite the differences between years in the daily cell production rate, the total number of cells formed each year was similar in 1998 and 1999, with asymptotes (i.e. total number of cells) of 36.6 and 37.6 cells respectively. The total was slightly higher in 2000, with 41.1 cells (figure 1).

Figure 2

Cell production was influenced mainly by air and humus temperature during the week when they were produced (table 1, lag 0). Lagging the weather variables by 1 to 5 days did not improve the effects of weather variables. Positives correlations were found with Tmin, weekly Tmax, Tmean and Thu, and were higher during the 7-day period between the sampling intervals (Lag 0). However, correlations with Thu remain almost unchanged from a time lag of 1 to 5 days and are probably due to the lower daily variation of humus temperature (figure 2). Only the correlation with weekly Tmin improved with a time lag of 2 days, from r=0.35 at lag 0 to r=0.40, but still remained lower than the one found with Tmin at lag 0 (r=0.51). Positive correlations were found with P and RH with a time lag of 4 days. No significant correlations were found with Rad and SW at lag 0. These were not considered suitable for further regression analysis because when the analysis was performed for each single year, the correlations changed from positive to negative or were not considered to be significant (data not shown).

Table 1

Regression analyses with air and humus temperature were then performed with no time lag as this represents the higher correlation found. The analyses showed that the rate of cell production was positively influenced by air and humus temperature (table 2, figure 3). During the period when the majority of cells were produced, Tmin (r^2=0.26) had a greater impact on the rate of cell production than Tmean (r^2=0.15) or Tmax (r^2=0.08). Moreover, the coefficient of determination increased by 5-10% when performing the analyses solely over the period of earlywood cell production. A higher increase was observed for Tmin (r^2=0.37). The results of the regression analyses showed that cell production rate increases with Tmin distribution from 1 to 15 °C (figure 3) representing the average of the minimum temperatures of the week. The regression is lower (r^2=0.19) if considering the minimum temperature occurring during the week (table 2, figure 3), with the temperature distribution ranging from -4 to 13 °C. As the growing season started when minimum temperatures were above zero, the observations below zero were related to frost events during the cell production period usually in May or June (figure 2). Since Thu shows high inter-correlation with Tmin (figure 2), its influence on cell production is only slightly lower than Tmin, with a coefficient of determination of r^2=0.31 for earlywood. In contrast to minimum air temperature, cells were not formed at a humus temperature lower than 0 °C (figure 3). Thu is normally above 0 °C when cell production begins. However, at the start of the growing season Thu varies from year to year between 0 and 5 °C (figure 2). Cell production rate also increases positively with Tmean and weekly Tmax, but the correlations were lower than those of Tmin, showing less influence (table 2, figure 3).

Table 2
Figure 3

Discussion

Influence of weather factors on cell production

Throughout the major period of cell division, air and humus temperature positively influenced tracheid production. During earlywood formation, corresponding mainly from the end of May to mid-July, the effect of temperature was slightly greater. Since 50 to 75% of tree-ring cells were formed during this period (from 1998 to 2000), temperature variation strongly affects their rate of production. One of the primary determinants of tree growth, temperature affects both leaf and meristem activity (Kozlowski et al. 1991). Responses of cambial growth to temperature changes can be rapid, as shown by a 1-day lag effect of temperature on daily radial growth of northern oaks (Kozlowski and Pallady 1997). In our study, cell production was found to be related with temperature within the same period that cells were produced. Lagging the 7-day period by just one day decreased the correlation with Tmin from 0.51 to 0.31, showing the high correspondence with the same interval when cell production was measured. These results also suggest a fast response of the cambium to temperature variation during tree-ring formation.

These results are not surprising, as temperature was found to define cell production and differentiation at the earliest stage of cell differentiation of *Larix sibirica* Ldb. and *Pinus silvestris* L. (Wodzicki 1971; Antonova and Stasova 1993, 1997). In a northern treeline area in Québec (Canada), by using the total tracheid production of *Picea mariana* (Mill.) BSP, Wang et al. (2002) found a positive correlation with a pentad temperature of around 6-8 °C at the end of June. The results of this study are also consistent with the higher response to temperature of a tree species growing near its northern distribution (Mäkinen et al. 2003), compared with other weather variables. In effect, significant and constant influences of the other weather variables on cell production (i.e. global radiation, precipitation, humus water content and relative humidity) were not found. The main factors affecting cell production remained constant over the three years analysed suggesting one dominant factor, i.e. minimum temperature. However, a longer period of detailed analysis would be required to confirm this.

Although early summer precipitations had positive effects on annual growth of black spruce (Brooks et al. 1998; Dang and Lieffers 1989; Hofgaard et al. 1999), white cedar (Archambault and Bergeron 1992) and jack pine (Hofgaard et al. 1999), no relation was found with precipitation at lag 0. However, this is not in contrast with the result found in dendroclimatology. For balsam fir, precipitation was associated with ring width formation because of its effects on radial cell expansion (Deslauriers et al. 2003b) but not with cell production. No biologically plausible reason was found to explain the correlation with precipitation at lag 4.

The results of this study show that the lower threshold level allowing balsam fir tracheid production during the cell division period is relatively low, being almost 0 °C. In the boreal forest other physiological processes, such as photosynthesis and nutrient uptake, were also found to take place at low soil or air temperatures (close to 0 °C) for species including *Picea mariana*, *Picea glauca* and *Pinus banksiana* (Landhäuser et al. 1996; Man and Lieffers 1997). Although humus temperatures were near 0 °C at the start of cell production, a high rate of production was observed, as in May 1999. This was most likely due to unusually high air temperatures for that period. Therefore, for some years, soil temperature may not be the most suitable factor (or as good as air temperature) to explain the rate of cell production at the beginning of the growing season. Kirdyanov et al. (2003) described the importance of snow melt timing for an increase in soil temperature and growth initiation. Other studies in boreal zones, however, have reported that the timing of bud burst and the beginning of root growth were unaffected by soil temperatures (Domisch et al. 2001). From our 3-year study, the first cells showing radial enlargement were observed at a humus temperature of between 0 °C and 5 °C, and from 0 to 2 weeks after snow melt, showing high variability and rendering interpretations of cambial initiation difficult. Long-term tree-ring development analyses are still required to explain the role of air and humus temperature and radiation on the date of cambium initiation. Besides, other physiological process, such as the indole-3-acetic-acid gradient across the cambial meristem and the influence of cambium activity (Uggla et al. 1998) show complex interactions during the growing season, and not just with meteorological factors.

General pattern of tree-ring cell production and temperature

The following questions arise from the obtained results; does a higher temperature result in a greater amount of tracheids produced at the end of the growing season? and how does temperature control the rate and duration of the cell production process? From 1998 to 2000, the total number of cells was relatively similar despite differences in the general sigmoid shape and duration period (Figure 1). At the intra-annual level it was found that temperature variation influences the course of cell production, but at the end of the formation period, the total number of cells can be offset by a reduction/increase in the duration period. As a result, variations in the shape of the Gompertz sigmoid function (i.e., inflection point position, slope at the inflection point, production rate) that define the intra-annual general kinetic of tracheid production (Camarero et al. 1998;

Deslauriers et al. 2003a; Rossi et al. 2003) seem to depend on the dynamics of seasonal temperature variation but maybe not the asymptote (i.e., total number formed). Higher temperatures must occur at the correct time during the growing season (June-July) to significantly increase the total cell number. As total cell number does not depend solely on the rate of cell division but also on the number of cells in the cambial zone (Vaganov 1990), only the long-term analysis of the total number of cells, as stated by Wang et al. (2002), would allow such relationships to be found. Long-term detailed cell analyses are therefore required to assess the effect of the long-term temperature pattern on total tree-ring cell number production.

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Table 1. Cross-correlation analysis between cell formation rate (sqrt [cell/day]) and weather variables for a time-lag period from 0 to 5 days. The correlations were considered significant (Pearson $p<0.05$) over a correlation of 0.35 (n=33). Lag 0 represents the weekly weather mean for the exact period between two sampling dates. Time lag 1 to lag 5 represents the 7-day period shifted backwards from 1 to 5 days before the sampling date. The highest coefficients of correlation are highlighted in grey.

	Lag 0	**Lag 1**	**Lag 2**	**Lag 3**	**Lag 4**	**Lag 5**
Tmin	0.51	0.31	0.29	0.25	0.28	0.26
Week Tmin	0.35	0.37	0.40	0.34	0.36	0.32
Tmax	0.28	0.19	0.15	0.17	0.14	0.14
Week Tmax	0.35	0.09	0.11	0.12	0.15	0.12
Thu	0.50	0.42	0.44	0.45	0.46	0.47
Tmean	0.38	0.24	0.21	0.21	0.21	0.21
Rad	-0.24	-0.09	-0.29	-0.19	-0.26	-0.18
RH	0.33	0.23	0.35	0.36	0.43	0.39
Sw	-0.06	0.01	0.01	0.02	0.03	0.03
P	-0.01	0.13	0.22	0.12	0.38	0.30

Note: Tmean, mean temperature; Tmin, minimum temperature; Tmax, maximum temperature; Week Tmin-Tmax, minimum-maximum temperature during the 7-day period; Thu, humus temperature; Rad, global radiation; RH, relative humidity; SW, humus water content; P, precipitation.

Table 2. Linear regression equation coefficient between cell production rate (sqrt [cell/day]) and Tmean, Tmax, weekly Tmax, Tmin, weekly Tmin and Thu. Results are shown for earlywood cell production only and the period when the majority of the cells were produced.

	Tmean	**Thu**	**Tmin**	**Weekly Tmin**	**Tmax**	**Weekly Tmax**
Earlywood cell production (n=22)						
a[1]	0.3818	0.4544	0.4667	0.6941	0.4084	0.1726
b	0.0279	0.0369	0.0388	0.0222	0.0170	0.0222
R^2	0.20	0.31	0.37	0.19	0.11	0.17
p	0.03	<0.01	<0.01	0.04	0.12	0.04
Major period of cell production (n=33)						
a	0.4518	0.5083	0.5277	0.7151	0.4811	0.2847
b	0.0232	0.0285	0.0301	0.0159	0.0142	0.0187
R^2	0.15	0.25	0.26	0.12	0.08	0.13
p	0.03	<0.01	<0.01	0.04	0.12	0.04

[1] Equation coefficients are based on the linear equation: sqrt (cell/day)=a + b*[Tmean, Tmax, weekly Tmax, Tmin, weekly Tmin or Thu]

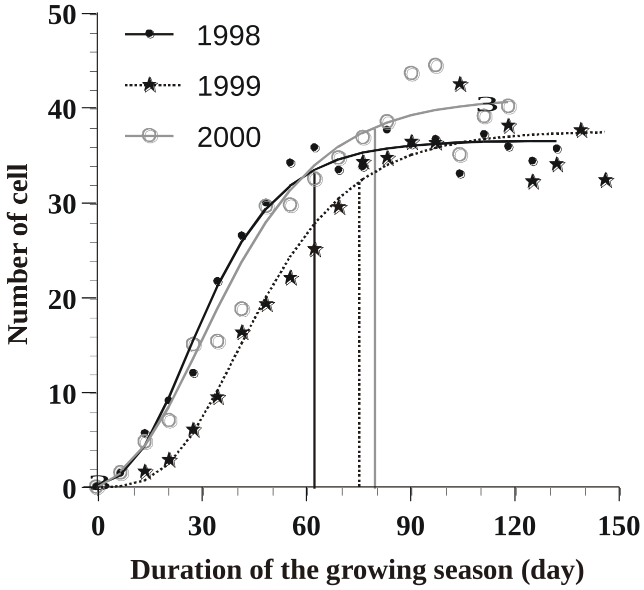

Figure 1. Cell number increase from the start of the growing season: mean total cell number of ten trees counted each week and general logistic pattern of total cell production from 1998 to 2000. The vertical lines show the limit of the total period analysed, representing the period when the majority of the cells were produced. Parameters of the Gompertz equation from Deslauriers et al. (2003a): 1998 a =36.6, β=1.66 and κ=0.065, 1999 a =37.6, β=2.09 and κ=0.052, 2000 a =41.1, β=1.51 and κ=0.05.

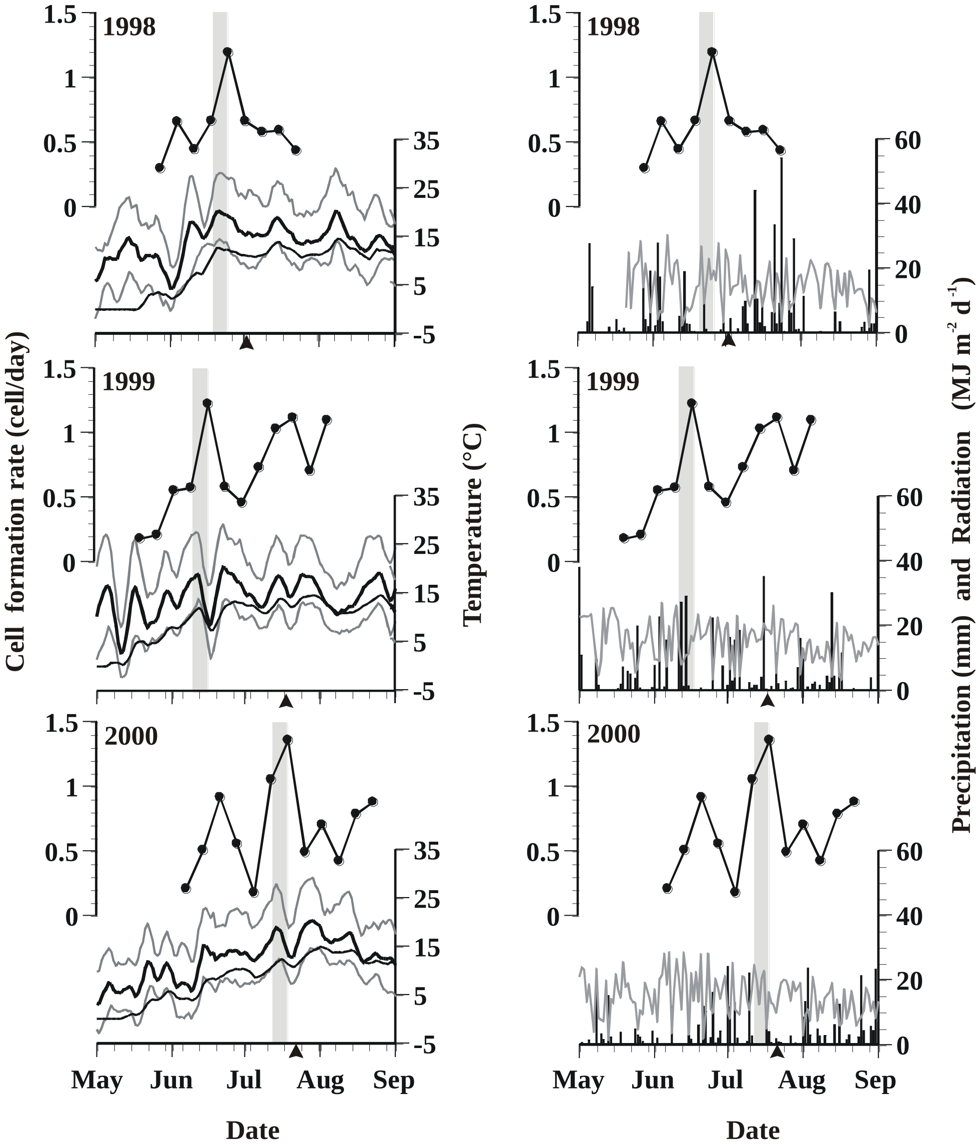

Figure 2. Cell formation rate (cell/day), temperatures, precipitation and radiation variations from May to September for 1998 to 2000. *Lower left*, mean (thick black line) maximum, minimum (grey line) and humus temperature (thin black line). *Lower right*, precipitation (black vertical lines) and radiation (grey line). Air temperature variations were smoothed for better graphic representation. The vertical grey bands highlight the 7 days weather conditions before the higher cell formation rate observed each year. The triangles indicate the earlywood to latewood transition as found in Deslauriers et al. 2003. The horizontal axis major tick marks show one month and minor tick marks one week intervals.

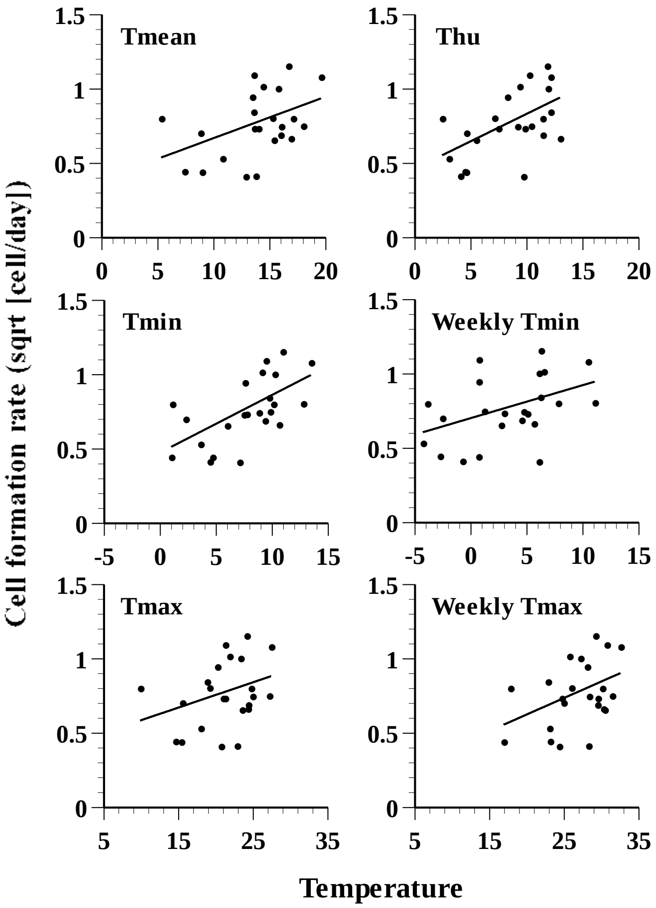

Figure 3. Relationship between square root cell formation rate (sqrt [cell/day]) and Tmean, Thu, Tmax, weekly Tmax, Tmin and weekly Tmin during earlywood cell production.