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ORIGINAL ARTICLE

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Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada)

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Abstract Daily stem radial growth of balsam fir [*Abies balsamea* (L.) Mill.] was studied between 1998 and 2001 using automated point dendrometers to investigate meteorological influence. By dividing the dendrometer day-night variation, the diurnal growth pattern was resolved into the three phases of (1) contraction, (2) expansion and (3) stem radius increment (SRI). The entire circadian cycle (4) defined by the three previous phases was considered as a fourth phase. The mean weather conditions of each phase were compared with the SRI using simple correlation and response function analysis. It was found that the weather conditions prevailing from 1600/1700 hours to 0800/0900 hours corresponding with the expansion-SRI phases had greater impact on SRI. Response function results confirmed most of the correlation analyses and explained up to 95% of the variance of the SRI series. Total rainfall in phases 2, 3 and 4 was correlated positively with SRI, and hence verifies the importance of daily water balance. The importance of water was also demonstrated by the negative effect of high vapour pressure deficit of phase 2, decreasing the possibility of cell radial expansion. The maximum temperature of phase 3 was the only temperature variable having a positive impact on SRI suggesting that night temperature was more important than day temperature in controlling radial growth. These results may influence the process of cell enlargement and reflect only the mechanical aspect of growth.

Keywords *Abies balsamea* · Dendrometer · Stem radius increments · Weather-growth relations · Response function

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Introduction

The growing season in Québec boreal forests is very short. At the latitude of about 50°N, cell division and enlargement last from the end of May to the end of July with another month being necessary to complete cell wall formation (Deslauriers et al. 2003). Therefore weather conditions from May to July are thus likely to have a great influence on tree-ring width. In north-eastern North America standard dendroclimatological analyses have generally reported low tree-ring growth sensitivity to climate (Fritts 1976; Phipps 1982). Despite that, the few studies carried out in boreal forests showed consistent effects related to precipitation but not to temperature. Early summer precipitation 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). Several studies such as D'Arrigo et al. (1992), Hofgaard et al. (1999) and Schweingruber et al. (1993), found that late spring or early summer temperatures also had a positive effect on annual growth. However, Archambault and Bergeron (1992), Brooks et al. (1998), and Dang and Lieffers (1989) have found negative effects for the same period and even conflicting results for other species (Brooks et al. 1998).

A detailed approach, based on intra-annual monitoring of tree-growth and meteorological dynamics, could considerably refine our understanding of these conflicting results. The evaluation of the relationship between climate and tree-ring growth is achieved most efficiently through taking continuous measurements of tree-growth and weather conditions on a tree located near a meteorological station by using a dendrometer or cambial markings (Schweingruber 1996). Dendrometers have the advantage of providing continuous seasonal time-series of intra-annual stem growth indicating tree-ring cell division and enlargement of the xylem and the phloem. However, considering the small amount of radial change represented by cell division on the overall process of radial variation occurring every day, cell enlargement could be considered as the major driving force for the net daily radial increase. This daily increase reflecting growth is considered as an irreversible stem reaction (Irvine and Grace 1997). In addition to irreversible stem reactions, reversible stem shrinking (day) and swelling (night) also occur due to water loss and uptake (Kozlowski and Winget 1964; Irvine and Grace 1997). The dendrometer's raw measurements do not register true radial growth but it can be estimated by removing unwanted reversible variations.

Even though dendrometers are widely used recording instruments only a small number of studies have used dendrometers to measure tree-rings development in order to understand the growth-climate relationship (Downes et al. 1999; Kozlowski and Winget 1964; Pietarinen et al. 1982; Worbes 1999). The main objective of this study was to determine the most important weather factors influencing radial growth of balsam fir in Québec boreal forests. In order to evaluate correctly the results of this study, two important aspects should be clearly defined:

1. Since true daily radial growth is linked to the reversible stem motions and is estimated by extraction methods it is more appropriate to refer to it as stem radius increment (SRI).
2. Biologically, tree growth does not react directly to meteorological events (Schweingruber 1996), but combined with synchronous SRI estimates, important information on intra-annual tree-ring dynamics may be provided.

Materials and methods

Study area

This study was conducted in two permanent plots of balsam fir, Lib-23 (49°46′03″N; 72°34′19″W) and Lib-24 (49°58′56″N; 72°30′28″W), located near the 50th parallel, about 150 km north of Lac-Saint-Jean, Québec (Morin 1994) and are included in Thibault's (1987) black spruce [*Picea mariana* (Mill.) B.S.P.] moss ecological region (no. 12b) of the boreal zone (Fig. 1). The balsam fir plots are located in the northern extreme of the ecological region's distribution, which makes it interesting for climate response studies. The two study areas, Lib-23 and Lib-24, were affected differently by the most recent spruce budworm outbreak that lasted from 1974 to 1988. Lib-23 has a unimodal age structure with a tree establishment period ranging from 1815 to 1850 and was only slightly affected by the last spruce budworm outbreak (Morin 1994). The Lib-24 study plot was severely affected by the outbreak. Most of the adult trees, established between 1875 and 1890, died during the previous outbreak and only a few are still alive. The Lib-24 stand is now mainly composed of 5- to 6-m-tall trees because of the growth release after the stand opening.

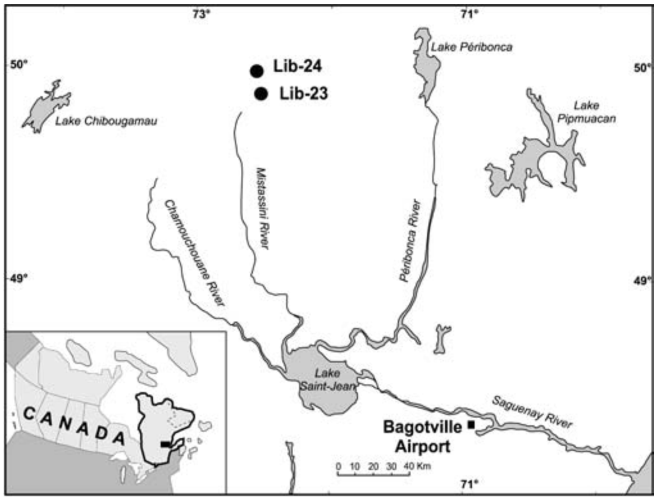

Fig. 1 Location of the study plots

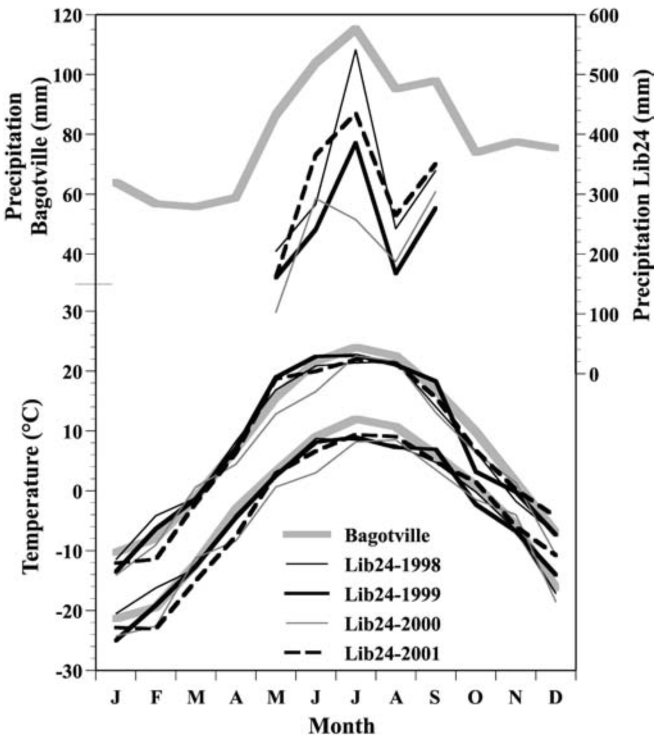

Fig. 2 Monthly maximum and minimum temperatures and total precipitation for 58 years at Bagotville airport and for each study year at Lib-24 (1998–2001)

Climate description

The climate of the study site is continental with cold winters and warm summers (Fig. 2). The mean monthly temperature ranges from −22°C in January to 24°C in July. The maximum and minimum temperature distribution at Lib-24 from 1998 to 2001 generally follows those from the weather station at Bagotville airport (48°20′N; 71°00′W). Over the 4 years study period fairly uniform summer climate conditions were observed at Lib-24 with the exception of a colder May and June in 2000. During the summer months, the total precipitation is much higher north of Lac St-Jean than near the Saguenay area. The monthly precipitation distribution

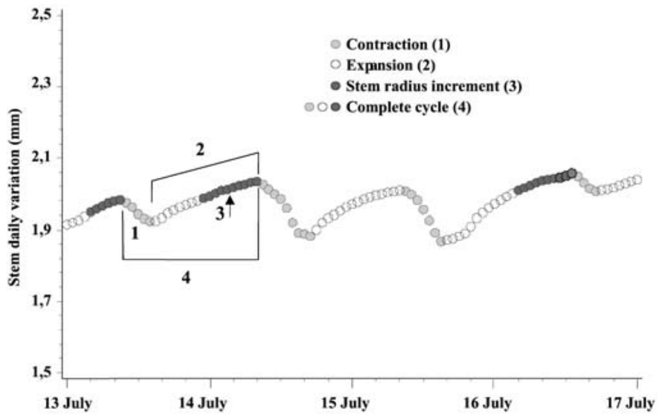

Fig. 3 The stem's circadian cycle divided into three distinct phases

at Lib-24 increases from May to July from 100 mm to more than 500 mm. The amount of snow precipitation form October to April was not registered but snow levels varied between 1 and 2 m every winter.

Data collection

Automatic point dendrometers (Agricultural Electronics, Tucson, Arizona, USA) were used for the continuous monitoring of tree growth. These instruments measure linear displacement of a sensing rod pressed against the bark of the trunk. The operating principle of the dendrometer is based on the use of a linear variable differential transformer (LVDT). Displacement can be automatically resolved to 4 μm over an unadjusted range of 15,000 μm. As the stem expands and contracts, the sensing rod is moved out and in. The core of the LVDT moves simultaneously, thereby translating the displacement to an electrical signal. The sensing rod is made of 304 stainless steel with a thermal coefficient of linear expansion of 17 μm/m/°C. Dendrometers were installed on 20 trees: 10 adult trees (19.9 m height, 27 cm DBH) were selected at Lib-23 in addition to 10 adult trees (20.7 m height, 26 cm DBH) at Lib-24. All dendrometers were mounted at a height of 1.3 m, perpendicular to the slope, on the south (Lib-24) or south-west (Lib-23) side of the trunk. The present study covered four growing seasons: 1998 to 2000 at Lib-23 and 1998–1999 and 2001 at Lib-24. Raw data were recorded every 15 min and hourly averages were calculated afterwards.

Meteorological data

One 10 m high meteorological station was installed per site in a small forest gap. Measurements were taken every 5 min, and hourly averages were calculated and stored in a datalogger (CR10X, Cambell Scientific Corporation). The variables measured were air temperature [T_{mean}, T_{max} and T_{min} (°C)] at 3 m, humus temperature (T_{hu}, °C), mineral soil temperature (T_{mn}, °C), total rain fall (P, mm), humus water content (SW, %), relative humidity (Rh, %) and radiation (R, W/m^2). SW and T_{hu} were measured at 10 cm depth at both sites and T_{mn} was measured at the humus-mineral interface, at 40 cm (Lib-23), and at 30 cm (Lib-24) depth. Vapour pressure deficit (VPD, kPa) was calculated from hourly values of T_{mean} and Rh (Jones 1983).

SRI extraction and association with the meteorological data

SRI extraction was undertaken by using the methodology described by Downes et al. (1999), which divided the "circadian cycle" into three distinct phases covering approximately 24 h (Fig. 3). The separation of the circadian cycle into distinct phases allowed the extraction of the SRI and allowed precise summaries of the meteorological data. The following phases were defined: The contraction phase (1) was defined as the period between the morning maximum and the daily minimum. The expansion phase (2) was defined as the total period from the daily minimum to the following morning maximum. This definition of the expansion phase is slightly different from the one used by Downes et al. (1999) (recovery phase) as they did not studied the whole expansion process. The SRI phase (3) was defined as that part of the expansion phase from the time when the stem radius exceeds the morning maximum until the subsequent maximum. The difference between the maximum of expansion and the beginning of the third phase represents the SRI estimate (μm). SRI was always calculated by comparing the previous cycle maximum and was considered equal to zero when the previous cycle maximum was not reached. The entire circadian cycle (4) defined by the three previous phases was considered as a fourth phase. The stem circadian cycle lasts about 24 h, starting at 0600–0900 hours, but heavy rain can cause irregular cycles of more than 24 h, due to a longer expansion phase.

Every meteorological variable was processed following the stem phase division. For each circadian cycle, four maximum temperatures (t_{max1}, t_{max2}, t_{max3} and t_{max4}), corresponding to each of the four phases, were computed and compared with the corresponding SRI. The delimitation of phases for both the meteorological and tree data series and the SRI extraction were performed by a special routine written using the SAS software package. Averages were then calculated between daily tree SRI and all meteorological data associated with each phase. To assess the need for data transformation (or standardisation), autocorrelation analyses were performed on both SRI and meteorological data series using the ARIMA procedure of the SAS software package. Since it is difficult to determine precisely the length of the growing season using the dendrometer data, particularly in spring due to high stem water content variation (Schweingruber 1996), the analysed periods were defined by cellular analysis performed on ten additional trees in each of the study plots (Deslauriers et al. 2003). The SRI extraction begins with the observation of the first cells showing radial enlargement of the growth ring at basal diameter and ends when the maximum number of cells was achieved (Deslauriers et al. 2003). The SRI time series are not continuous for Lib-24 in 1999 and Lib-23 in 2000 because of equipment problems.

Comparison between SRI and cellular growth

To evaluate the accuracy of the methodology, SRI extractions were compared with ring cellular formation. Micro-cores were extracted in October at about 20 cm above the dendrometer. Wood cores were fixed in paraffin to make transversal sections, stained with 1% water solution of safranin and permanently mounted on glass slides (Deslauriers et al. 2003). The software WinCell™ was used for cell width (μm) measurements. As these cores were taken when tree-ring growth was finished, the ring width increase (RWI), representing the cumulated cell width, had to be reconstructed for the growing season. The tree-ring cell increment pattern was determined for each site and year by using the Gompertz function (Eq. 1) calculated on the total cell number counted each week on the additional ten trees in each of the study plots (Deslauriers et al. 2003). RWI was calculated following the relative cell number increase pattern previously determined. For a given site and year, the RWI of each tree began and ended at the same time and the mean pattern was found by fitting a Gompertz function. The SRI increment pattern was also found by using a Gompertz function fitted into the daily SRI sum of each tree. The Gompertz function is defined as:

$$y = a \exp\left(-e^{(\beta-\kappa^{t})}\right) \quad (1)$$

where y is the cumulative sum of growth; t is time expressed as number of days from the start of the growing season where t=0; a is the upper asymptote of the maximum growth where at $t_i y \cong a$; β is the *x*-axis placement parameter and k is the rate of change parameter (Cheng and Gordon 2000). A biologically useful variable (r) was calculated from the fitted statistics as defined by Richards (1959) and represents the weighted mean absolute cell formation rate (μm/day, Eq. 2). Parameter ν was defined as 0.0001 since the Gompertz function is a special case of the Richards function when $\nu \cong 0$.

$$r = a\kappa/2(\nu + 2) \quad (2)$$

Growth and climate relationship

Bootstrapped response functions were calculated to estimate the climatic sensitivity of growth (Guiot 1993). The advantages of using response functions compared to other correlation or regression methods have been well demonstrated (Carrer and Urbinati 2001; Keller 1999; Zhang et al. 2000). The use of data at a resolution of less than 1 month is non-conventional, but methodologically possible in response function analysis. For instance, independent variables such monthly regressors are replaced by hourly data averaged in three daily sub-phases. The bootstrap procedure (Efron 1979) allows the testing of the significance of the regression coefficients and estimates stability in response functions generated by regression on principal components. Calculations were made using PPPBase (version 9905.1) (Guiot and Goeury 1996). Mean verification correlations were considered significant if after 1000 bootstrapped iterations their values were at least twice that of their standard deviation. Only positive SRI values were selected for further analysis. All the different models considered have seven climatic variables that represent the best and most constant results for all sites and for each year. The main parameters included in the model are T_{max3}, Rh_1, P_2, P_3, P_4, R_4 and VPD_2. These were considered significant at 95% if the ratio of the regression coefficient and standard deviation (RC/SD) was higher than 1.96. To provide a comparison with response function (Blasing et al. 1984) simple correlations (Pearson, $P<0.05$) were also computed for all weather variables. However, these values were not used to select the variables for the final response function model.

Results

SRI extraction

In general, the stem circadian cycle started with a contraction phase (1) between 0800 and 0900 hours at a standard deviation of about 2 h (Table 1). This lasted until the end of the afternoon, when the expansion phase (2) commenced at around 1600 or 1700 hours. The positive SRI phase (3) started between midnight and 0200 hours. It shows a higher standard deviation of 4–6 h. These are average cycle lengths but when rainy conditions prevailed, the increment phases continued all day until the next contraction phase. The positive value of SRI, representing the radial amplitude of phase 3, was calculated using a selected range of data corresponding to the period of growing season (Table 1, Fig. 4). No transformations (or standardisations) were performed on the series because the daily increment series were free of autocorrelation (Table 1). Defining the growing period in tree-ring analysis using a dendrometer proved to be crucial because for some years, the beginning of radial growth coincided with the stem rehydration after winter desiccation (Fig. 4). In earlywood, SRI extraction gener-

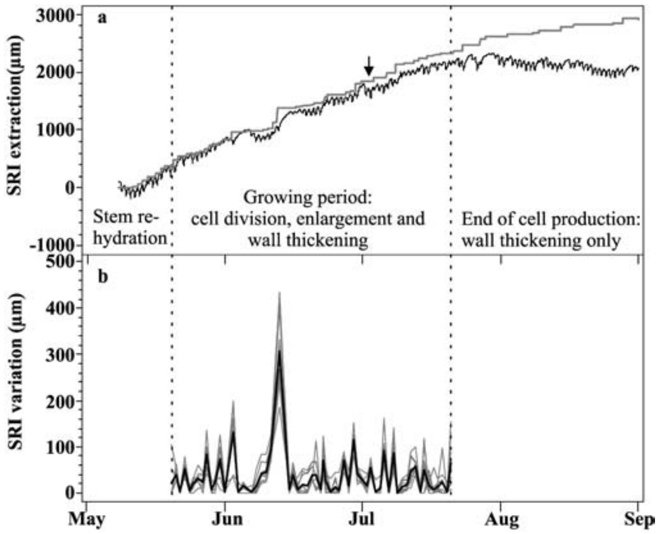

Fig. 4a, b Time series of stem radius variation from May to September at Lib-24 in 1998. **a** Daily stem radius variation (*black*) and SRI extraction (*grey*) of tree 1. **b** Daily SRI variation (μm) of 10 trees (*grey*) and the mean curve (*black*) extracted for the growing period. The *arrow* shows the earlywood and latewood transition

Table 1 General information and statistics characterising the phases and the stem radius increment (SRI) extraction for the period analysed at Lib-23 and Lib-24 from 1998 to 2001. (*No. of daily SRI* Number of positive SRI extracted during the analysis period; *Autocorr. Prob (P)* SRI probability (P) of autocorrelation until lag 6. Probability $P>0.05$ indicates no autocorrelation)

Site-year	L23-1998	L23-1999	L23-2000	L24-1998	L24-1999	L24-2001
Periods analysed	25 May–23 July	12 May–5 August	2 June–17 August	20 May–23 July	19 May–29 July	24 May–14 August
No. of trees analysed	9	8	8	10	7	8
Phase characterisation						
Beginning of phase 1	08:58±2	08:49±2	08:52±2	08:24±2	08:17±2	08:23±2
Beginning of phase 2	17:53±2	17:43±3	17:25±2	16:10±1	16:10±2	15:55±2
Beginning of phase 3	00:56±4	01:47±5	01:19±5	01:19±4	23:49±4	00:08±6
SRI extraction characterisation						
No. of daily SRI	50	76	53	59	55	63
Mean SRI (μm)	35.29	34.92	28.40	36.71	43.33	24.87
SD of SRI (μm)	50.11	43.01	38.44	47.17	46.72	24.59
Autocorr. Prob. (P)	0.773	0.870	0.655	0.491	0.685	0.583

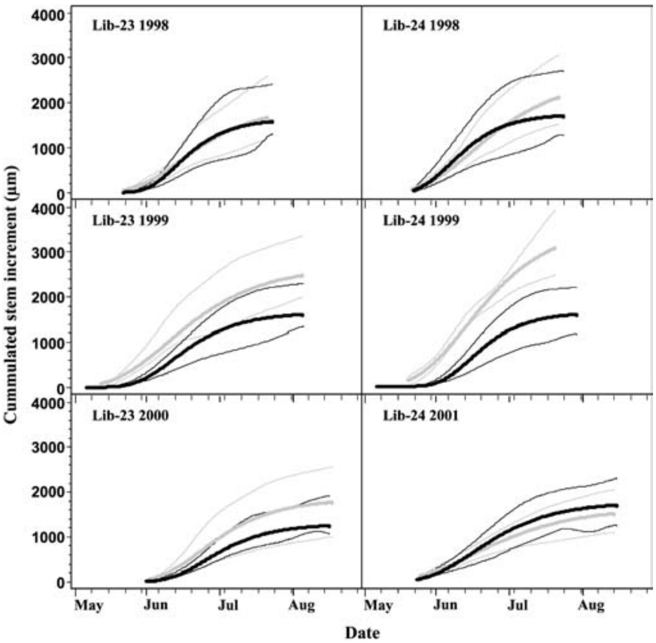

Fig. 5 Comparison between the cumulative SRI (*grey lines*) and RWI (*black lines*) during the growing season for both Lib-23 and Lib-24 study plots. The thin lines show the minimum and maximum distribution and the thick lines show the increment. On the horizontal axis the *longer tick marks* show 1 month and the *shorter tick marks* show 1 week intervals

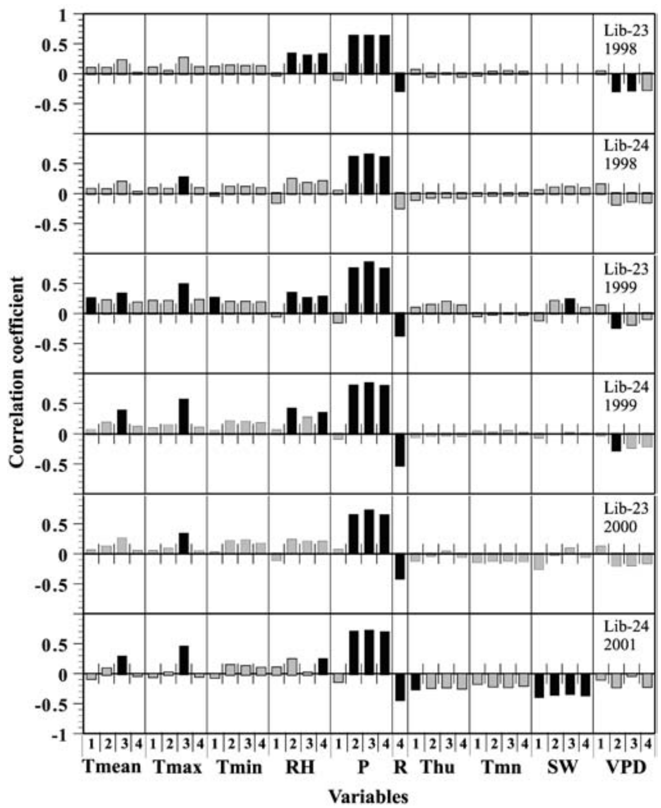

Fig. 6 Simple correlation coefficient (Pearson, $P<0.05$) between the daily SRI and meteorological variables for each phase of the circadian cycle (*1*= contraction, *2*= expansion, *3*= SRI, *4*= complete cycle). Significant results ($P<0.05$) are drawn in black

ally follows the data recorded by the dendrometer. In latewood and following cell division-enlargement, the SRI extraction value becomes higher than the dendrometer data (Fig. 4).

Individual trees show the same SRI variation pattern throughout the growing season (Fig. 4). Differences observed between trees are within the amplitude of the SRI and usually vary between 0 and 200 μm. The cumulative SRI and RWI are presented to assess the accuracy of the extraction methodology (Fig. 5). About half of the cumulative SRI are higher than the RWI. The estimated growth differences vary between year and site from almost none in 1998 and 2001, to a difference of about 1,000 μm in 1999 (Fig. 5). In most cases, the cumulative SRI does not reach its upper asymptote (a) (Table 2) since minor SRI are added due to daily differences in the water balance of stem tissues near the end of the growing season (Fig. 4). This error increased during latewood formation because smaller cells are formed.

Growth-climate relationships

The correlation analysis shows constant significant results between the different study plots and years for T_{max3}, P_2, P_3, P_4 and R_4 (Fig. 6). Most of these parameters had

Table 2 Parameters for the Gompertz function fitted for the cumulative RWI and SRI

Site-year	L23-1998	L23-1999	L23-2000	L24-1998	L24-1999	L24-2001
Cumulative RWI						
A	1,636.8	1,658.2	1,293.3	1,761.3	1,637.2	1,790.4
β	1.8530	2.3444	1.6298	1.2036	3.0735	1.2400
K	0.0823	0.0646	0.0661	0.0780	0.0783	0.0529
R^2	0.6973	0.7548	0.7598	0.6682	0.7471	0.7092
r (μm/day)	33.68	26.78	21.37	34.34	32.05	23.68
Cumulative SRI						
A	1,929.0	2,681.5	1,848.0	2,547.3	3,590.8	1,664.6
β	1.2844	1.2418	1.2406	1.2223	1.1963	0.9160
K	0.0532	0.0445	0.0573	0.0472	0.0491	0.0412
R^2	0.8251	0.8167	0.7064	0.8170	0.9576	0.8066
r (μm/day)	25.66	29.83	26.47	30.06	44.08	17.14

Table 3 Main statistics of the response functions computed for the daily SRI and a selected group of meteorological variables (T_{max3}, Rh_1, P_2, P_3, P_4, R_4 and VPD_2). (*R* Coefficient of determination, *VC* verification correlation of the response function, *SD* standard deviation of the response function

Site-year	L23-1998	L23-1999	L23-2000	L24-1998	L24-1999	L24-2001
R	0.90	0.95	0.90	0.90	0.95	0.92
VC/SD	6.68	15.82	7.03	6.16	14.86	12.22

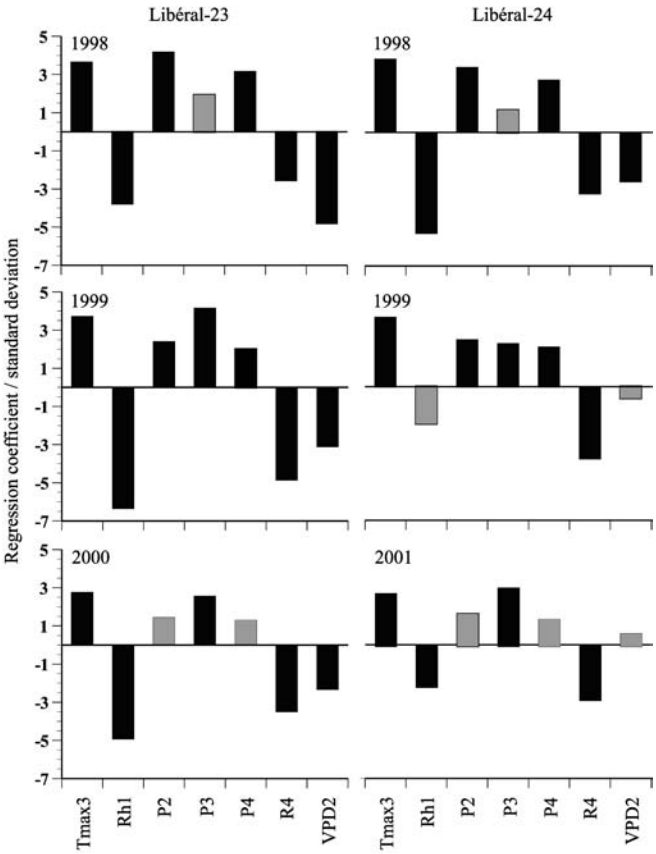

Fig. 7 Response function results for Lib-23 and Lib-24 plots from 1998 to 2001. Significant results, for a 95% level corresponding to 1.96, are drawn in black

significant positive effects on the SRI except for R_4 that had a negative one. The only non-significant results are for T_{max3} at Lib-23 1998 and R_4 at Lib-24 1998. The precipitation P_2, P_3 and P_4 have very high *R* coefficients ranging from 0.6 to 0.8. Relative humidity Rh_2, Rh_3 and Rh_4 showed a more or less constant relationship with both SRI and also VPD_2. No correlation was observed with these variables for Lib-23 in 2000 and Lib-24 in 1998 and 2000. Less consistent correlations were observed with T_{mean1} and T_{min3} and T_{min1}. The only significant correlations of soil temperature and water content were observed for Lib-24 in 2001 and had a negative effect on SRI.

The very high coefficients of determination (*R*) of response functions, ranging between 0.90 and 0.95, indicate that meteorological conditions were responsible for most of the variance existing in the SRI series (Table 3). The very high ratios between the verification correlation and their standard deviations (VC/SD), especially for both study plots in 1999, suggest that the models generated by the bootstrapped response functions are statistically reliable. The main parameters included in the model are T_{max3}, Rh_1, P_2, P_3, P_4, R_4 and VPD_2. In some cases, other variables also fitted well into the model (T_{max2}, T_{min2}, T_{min3}, VPD_3 and in some SW) but their significance was not constant throughout the different sites and years, therefore they were excluded from subsequent analyses to maintain uniformity in the model.

Response function analysis revealed that precipitation during phases 2–4 had a positive effect on SRI (Fig. 7), but unlike the correlation analysis, not all of these were significant as P_3 in 1998 and P_2–P_4 in 2000 and 2001. Response functions also revealed a positive effect of T_{max3} and a negative effect of R_4 on SRI which is also consistent with correlation analysis. The response function showed a negative effect of VPD_2 at Lib-23 but only for Lib24 in 1998, which is more or less consistent with correlation analysis. Smaller values of VPD_2 for 1999 and 2001 at Lib-24 could be a possible explanation for these results. Unlike the correlation analysis, which had weak negative or positive correlations, Rh_1 shows significant negative response in almost all analyses with values ranging from −1.9 to −6.3.

Discussion

Extraction methodology

The measurement of SRI with a dendrometer is the most direct method to obtain an estimation of daily radial growth. The daily SRI extracted during the growing period are assumed to correspond to cell division and enlargement. From June to September, intensive secondary wall formation occurs (Deslauriers et al. 2003) but this is not expressed as a radial increase because it takes place inside the enlarged cell. Because the daily stem swelling and shrinking could mask or enhance the SRI estimates, a comparison with tree-ring development was necessary. This was also crucial to selecting the appropriate period of analysis because growth initiation in the early spring may be confused with rehydration of internal tissues prior to the beginning of cambial growth (Kowzlowski and Winget 1964). Depending on the year, SRI extraction sometimes follows RWI with minor differences and sometimes an over-estimation as high as 1 mm can be observed at the end of the growing season.

The factors causing major differences observed in 1999 and 2000 are difficult to identify but we suspect they are due to diurnal pattern of stem shrinking and swelling. These daily fluctuations, mostly restricted to extensible tissues outside the cambium (Kozlowski et al. 1991; Zweifel et al. 2000), can account for a fraction of the SRI because of the increased water storage compared with the previous daily maximum. This fraction could be higher when trees are growing slowly at the beginning or at the end of the growing season. Similarly, these stem dimensional changes can also result in some days where real growth may have occurred but the stem daily maximum is lower than the previous one for several days. We suspect that a part of the high SRI overestimation in 1999 is the result of an early and slow start in May, when snow melt-out was not yet finished and stem rehydration was probably still in progress. However, when the growing season starts 2–3 weeks after the snow melt-out, SRI estimates are comparable to RWI estimates.

Growth and climate relationship

The daily cycle stratification in different phases and its association with weather data gave significant correlations. The variance explained by the response function is up to 90% in the daily SRI data series. In contrast, Downes et al. (1999) found that the average weather conditions during the increment phase (3) did not explain more increment variance in that study than average daily weather conditions. Multiple regression of daily weather variables show that they accounted for 40%–50% of the variance in the increment of *Eucalyptus nitens* and *E. globulus* trees. In this study, high coefficients were obtained using the bootstrapped response function and were used instead of regular regression analysis (Keller 1999).

Both simple correlation and response function strongly suggest that SRI can be influenced by prevailing weather conditions. More than half of the variables used for the response function analyses referred to the expansion (2) and SRI (3) phases. These results reveal the importance of the prevailing weather conditions between 1600–1700 hours and 0800–0900 hours on SRI. Dünisch and Bauch (1994), using both cell analysis and dendrometer monitoring, reported that 81% of radial cell enlargement of Norway spruce seedlings was initiated between 1800 and 0600 hours when water supply was adequate. The process of cell enlargement, estimated by SRI, is physiologically complex. It depends on many factors such as time of day and season, cell wall extensibility, water relations, energy and carbohydrate supply (Ray 1987). Even though cell enlargement takes places mostly during the night or on rainy days, intensive growth of mature pine tracheids has been shown to occur at any time of the day (Antonova et al. 1995).

Previous dendroclimatological studies on boreal forests have shown a positive effect of early summer precipitation on tree-ring growth (Archambault and Bergeron 1992; Brooks et al. 1998; Dang and Lieffers 1989; Hofgaard et al. 1999). In this study, the importance of water on the SRI is shown by four variables: P_2, P_3, P_4 and VPD_2. These strong correlations, for both analyses, could be enhanced by bark and wood swelling as heavy rain falls could lead to some over estimation of the daily SRI. However, the negative effect of high VPD in the expansion phase (2) also confirms the importance of the water component. Physiologically, the primary effect of high VPD is to inhibit cell enlargement and growth because of its indirect effect on cell turgor pressure (Major and Johnsen 2001). VPD_2 correlated better than VPD_3 probably because of its higher variation due to the relative humidity close to a 100% for VPD_3.

The only temperature variables that show constant response function results with daily SRI throughout the sites and years was T_{max3}. Downes et al. (1999) also observed a positive relationship by comparing the stem expansion rate with the average temperature during the SRI phase. Temperature (Antonova and Stasova 1993; Denne 1971) and especially night temperature (Richardson and Dinwoodie 1960) is a very important factor affecting radial cell enlargement and size. The correlation analyses suggest that maximum temperatures (12–14°C) during the expansion and SRI phases were favourable and minimum temperatures (8–9°C) had no significant result.

It seems likely that the weather conditions during the contraction phases, between 0800–0900 hours and 1600–1700 hours, did not have a great influence on the SRI. The optimum VPD for cell enlargement in black spruce is often exceeded after 0900 hours (Major and Johnsen 2001) but VPD_1 did not have a great negative influence on the following SRI. Also, the negative effect of Rh_1 and R_4 could be more associated with a reversible stem reaction than to an irreversible growth reaction. An increase in R_4 decreases the daily minimum and increases the length of the contraction phase because of a higher transpiration and evaporation demand. A better knowledge of the water tissue balance and weather variables controlling the contraction phase and SRI would improve our understanding of the impact of weather on cambial activity.

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