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DYNAMIQUE DE LA CROISSANCE RADIALE ET INFLUENCE METEOROLOGIQUE QUOTIDIENNE CHEZ LE SAPIN BAUMIER (*ABIES BALSAMEA* (L.) MILL.) EN FORET BOREALE

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RESUME

La formation du cerne de croissance du sapin de baumier (*Abies balsamea* (L.) Mill.) a été étudiée en forêt boréale dans le but de décrire son développement et de déterminer les facteurs météorologiques qui l'influencent. La croissance radiale a été mesurée à l'aide de deux techniques soit les analyses cellulaires et la dendrométrie. Des micro-carottes ont été extraites à toutes les semaines pendant les saisons de croissance de 1998 à 2000 afin d'effectuer des analyses cellulaires. Des sections ont été colorées à l'aide du *cresyl fast violet* pour dénombrer les cellules dans la phase d'élargissement radial, la phase de formation des parois secondaires et les cellules matures, permettant une reconstruction du développement du cerne. L'accroissement radial journalier a été étudié au cours des saisons de 1998 à 2001 à l'aide de dendromètres électroniques. Les analyses des cellules ont permis d'observer des variations dans le début de la croissance (7 mai–7 juin), dans la transition bois initial-bois final (2 juillet-19 juillet) et dans la fin de la lignification des parois cellulaires (20 août–20 septembre). L'élargissement radial a été de courte durée, de moins d'une semaine pour le bois initial et de 5 à 10 jours pour le bois final. Le temps requis pour l'épaississement des parois secondaires a été d'environ 20 jours et 30-35 jours pour le bois initial et le bois final respectivement. L'accroissement radial mesuré par les dendromètres a été divisé en 4 périodes suivant le cycle diurne du tronc soit (1) contraction, (2) expansion, (3) accroissement et (4) cycle total. Les conditions météorologiques moyennes de chacune des périodes ont été comparées à l'accroissement à l'aide de corrélations et de fonctions de réponse. Les conditions météorologiques prévalant de 16-17 h jusqu'à 8-9 h, correspondant aux périodes d'expansion et d'accroissement, ont eu le plus d'impact sur l'accroissement. Les fonctions de réponse étaient fortement linéaires avec une variance expliquée de 80-90 % et ont confirmé la majeure partie des résultats obtenus à l'aide des corrélations. L'accroissement a été positivement corrélé aux précipitations durant les phases 2 à 4 du cycle. Seule la température maximale de la période d'accroissement a eu un effet positif, suggérant que les températures nocturnes sont les plus importantes. Les résultats des analyses climat-croissance à l'aide des mesures cellulaires ont montré que dans le bois initial, la largeur des cellules est fortement reliée avec la température maximale, particulièrement celle du mois de juin où la majorité du cerne est formée. L'épaisseur des parois cellulaires dans le bois initial est aussi fortement reliée à la température à partir de la mi-juin jusqu'à la mi-juillet. Les résultats des analyses cellulaires montrent une flexibilité dans le développement du cerne procurant un avantage en forêt boréale où les conditions optimales de croissance changent d'années en années. La variation de la dimension des trachéides formées durant la saison de croissance est principalement affectée par la température journalière au tout début de sa différentiation. Par la suite, les processus d'élargissement cellulaire sont principalement influencés par les conditions nocturnes de précipitations et de températures.

Mot-clés : *Abies balsamea*, croissance radiale journalière, élargissement cellulaire, parois secondaires, dendromètres, température, précipitations

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CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1. Problématique

De grandes forêts à travers le monde, dont la forêt boréale, sont formées en majeure partie par des conifères. Comme il s'agit, pour bon nombre, de forêts commerciales, la compréhension de la croissance et des facteurs climatiques affectant ces écosystèmes s'avère donc très importante afin de connaître leur productivité et de bien maîtriser leur aménagement et leur exploitation. L'étude annuelle de la croissance secondaire chez les arbres permet d'expliquer la formation des cellules composant le cerne de croissance (Savidge 2001). Telle que définie ici, la croissance secondaire concerne la formation des cellules du xylème et du phloème ainsi que le maintien et l'expansion du cambium vasculaire. En connaissant la période et la durée de la formation des cellules du xylème, il est possible d'obtenir la chronologie de la formation du cerne annuel (Wodzicki 1971) qui nous renseigne sur le déroulement de la saison de croissance (Deslauriers 1999). Ces renseignements permettent ensuite d'établir précisément la relation entre la formation du bois et les variations météorologiques (Antonova and Stasova 1993, 1997; Horacek et al. 1999; Rossi et al. 2002) ou avec d'autres paramètres environnementaux (Park et Morin 2001).

À ce jour, dans le Nord Est de l'Amérique du Nord, très peu d'études sur la formation du cerne de croissance des conifères ont été publiées (Kutscha et al. 1975 ; Riding et Little 1986) et aucune ne concerne les régions écologiques boréales. L'étude détaillée du développement du cerne, accompagnée d'un suivi des conditions météorologiques journalières, permettrait de mieux comprendre la croissance annuelle des conifères et de

répondre à diverses interrogations telles : A quel moment surviennent le début et la fin de la saison de croissance ? Quels sont les facteurs climatiques qui ont le plus d'influence sur la division, l'élargissement et la lignification des cellules du cerne ? Quel est le délai de réponse de la croissance face aux variations climatiques ? Ces questions sont toujours sans réponse pour les conifères de la forêt boréale qui ont une grande importance économique dont l'épinette noire (*Picea mariana* (Mill.) BSP), le pin gris (*Pinus banksiana* (Ait.) Dumond) et le sapin baumier (*Abies balsamea* (L.) Mill.). Le développement du cerne est étudié depuis une quarantaine d'année (Antonova and Stasova 1993, 1997; Denne 1971, 1976; Horacek et al. 1999; Richardson and Dinwoodie 1960; Wodzicki 1971), mais les techniques sont encore en élaboration. Le sapin baumier est une espèce boréale qui produit, à chaque année, un nombre suffisant de cellules. Cette caractéristique est nécessaire afin d'élaborer une méthodologie appropriée pour analyser le développement du cerne et effectuer des relations journalières avec les conditions météorologiques.

Plusieurs études portant sur les relations climat-croissance ont déjà été réalisées en forêt boréale. Ces études ont d'ailleurs permis d'établir une bonne relation entre la largeur du cerne et les précipitations durant la saison de croissance (Archambault and Bergeron 1992; Brooks et al. 1998; Dang and Lieffers 1989; Hofgaard et al. 1999), mais les résultats diffèrent avec la température. Par exemple, des études ont montré un effet positif de la température sur la croissance en début de saison (d'Arrigo et al. 1992; Hofgaard et al. 1999; Schweingruber et al. 1993), alors que d'autres ont montré une corrélation négative pour la même période (Archambault and Bergeron 1992; Brooks et al. 1998; Dang and

Lieffers 1989). L'étude du développement du cerne de croissance pourrait notamment aider à l'interprétation des résultats des études dendrochronologiques ou dendroclimatologiques qui utilisent le cerne de croissance comme base d'analyse. En effet, dans une majorité d'études, les relations climat-croissance sont établies pour les mois d'avril à septembre sur la base de paramètres tels la largeur du cerne, la largeur du bois initial ou du bois final et la densité, sans tenir compte de leurs périodes de formation respectives. Cependant, le développement du cerne de croissance n'est pas un phénomène statique qui se produit au même moment année après année, car la dynamique saisonnière de la température et des précipitations est variable d'une année à l'autre (Kirdyanov et al. 2003). L'étude de l'influence du climat sur la croissance ne pourrait qu'être améliorée en connaissant *a priori* le développement du cerne et sa variabilité.

En résumé, le développement du cerne et l'influence des variations météorologiques journalières sur la croissance des cellules et sur la formation des parois composant le cerne sont toujours inconnues en forêt boréale. Une évaluation plus détaillée de la croissance journalière s'avère donc nécessaire afin d'établir de meilleures relations avec les variables météorologiques, de trouver la période de la saison de croissance où cette influence est la plus grande et de comprendre comment cette influence se reflète sur le développement du cerne de croissance.

1.2. Approche méthodologique

Alors qu'il est courant de mesurer l'accroissement annuel à l'aide des cernes de croissance, l'accroissement journalier nécessite des techniques beaucoup plus spécialisées. Deux techniques peuvent être utilisées pour suivre le développement du cerne de croissance : les analyses anatomiques et la dendrométrie. Les analyses anatomiques permettent de caractériser précisément la dynamique de la formation cellulaire du xylème durant une saison de croissance (Deslauriers 1999). La dendrométrie, soit l'utilisation des dendromètres électroniques, permet de suivre les variations radiales du tronc des arbres en temps réel et d'enregistrer les données dans des intervalles de temps très courts (Downes et al. 1999). À l'aide des dendromètres, seuls les phénomènes de divisions et d'élargissement des cellules composant le cerne en formation peuvent être enregistrés. La formation des parois cellulaires est un processus interne, se déroulant après l'élargissement cellulaire, qui ne peut donc pas être captée par les dendromètres. De plus, les mouvements journaliers réversibles de contraction et d'expansion du tronc, dus à la transpiration et à la réhydratation des tissus, masquent souvent la croissance (Kozlowski and Winget 1964; Zweifel et al. 2000). Ces processus ont une amplitude élevée en début de saison de croissance où le dégel des tissus et leur réhydratation post-hivernale masquent le début de la croissance radiale. L'utilisation des deux techniques en parallèle permettront donc de mieux utiliser les dendromètres en situant précisément le début et la fin des processus de divisions et d'élargissement des cellules.

1.3. Hypothèses et Objectifs

Selon Schweingruber (1996), la relation entre le climat et le cerne de croissance est réalisée plus efficacement par des mesures continuelles de la croissance et du climat sur un arbre situé près d'une station météorologique et en utilisant un dendromètre ou une inscription cambiale. Biologiquement, les cellules du cerne de croissance en développement ne réagissent pas directement aux événements météorologiques (Schweingruber 1996). Des recherches antérieures ont d'ailleurs supposé une influence climatique indirecte (Richardson and Dinwoodie 1960; Denne 1971, 1976), dépendant des régulateurs de croissance et de l'allocation des ressources affectant le taux et la durée de la formation de cellules. Par contre, combiné à des évaluations synchrones de croissance radiale, on s'attend à ce que des informations importantes sur la dynamique intra-annuelle soient fournies. Nous posons donc l'hypothèse qu'à l'aide de techniques d'évaluation journalière de la croissance, il est possible de mesurer un effet direct des variables météorologiques sur le développement du cerne de croissance. À cause du caractère journalier de cette recherche, le terme « variables météorologique » (ou l'anglais weather variables) remplace le terme « variables climatique ». Selon Fritts (1976), le terme climat se défini comme une expression des phénomènes météorologiques représentant la météo sur une longue période de temps. Le « climat » inclut donc une composante saisonnière représentant des variations dans tout le cycle annuel. Par opposition, « le temps (weather) » se rapporte à des variations à court terme du climat, y compris tous les phénomènes météorologiques (précipitations, températures, lumière, vent etc.) observables qui peuvent changer

abruptement dans quelques minutes et changer de jour en jour. Ce sont ces variations météorologiques qui seront reliées avec la croissance.

Cette recherche a donc pour but d'étudier la croissance radiale journalière du sapin baumier (*Abies balsamea* (L.) Mill.) en forêt boréale à l'aide de dendromètres électroniques et d'analyses anatomiques, sa relation avec les variables météorologiques et la période où cette relation est la plus forte. Les objectifs spécifiques sont (1) de décrire le développement du cerne de croissance et sa variabilité; et (2) de trouver les variables météorologiques qui influencent le plus la formation du cerne de croissance au cours de la saison.

1.4. Structure de la thèse

La thèse comprend trois chapitres principaux (II, III et IV) rédigés en anglais sous forme d'article scientifique et une conclusion générale (chapitre V). Le chapitre II porte sur la formation du cerne de croissance. La partie méthodologique de ce chapitre constitue une description détaillée des méthodologies d'analyses cellulaires pour l'étude de la formation du cerne de croissance. Les temps de formation des phases de différentiation des cellules composant le cerne de croissance, soit l'élargissement radial et l'épaississement des parois secondaires y sont décrits. Le développement du bois initial et final et sa variation temporelle selon les trois années d'échantillonnage sont discutés. Les moments importants de l'année pour le développement de chacune des parties composant le cerne de croissance

ont été mis en évidence. *Note : Ce chapitre est le fruit du travail du candidat. Hubert Morin et Yves Begin ont participé à l'élaboration des idées de base de ce chapitre.*

Le chapitre III aborde aussi la formation du cerne de croissance mais selon des mesures effectuées à partir des dendromètres électroniques. L'accroissement journalier du cerne a été extrait des données horaires mesurées par les dendromètres et différents paramètres météorologiques ont été comparés à l'aide de corrélations simples et de fonction de réponses. Les variables météorologiques influençant l'élargissement journalier des cellules ainsi que la période de la journée où cette influence est la plus grande ont été identifiées. *Note : Ce chapitre est le fruit du travail du candidat. Hubert Morin à participé l'élaboration des idées de base de ce chapitre. Carlo Urbinati et Marco Carrer ont participé à la réalisation des analyses statistiques.*

Le chapitre IV aborde aussi les relations entre le développement du cerne et les variations météorologiques mais en utilisant les mesures effectuées sur les cellules décrites au chapitre II. Afin de conserver le caractère journalier des analyses, une reconstruction journalière de la variation de la dimension de cellules (diamètre radial et épaisseur des parois) a été effectuée et comparée aux données météorologiques. Les résultats ont permis de trouver les variables météorologiques les plus importantes pour la dimension des cellules et des parois ainsi que la période de la saison de croissance où l'influence est la plus forte. Une comparaison avec les résultats obtenus au chapitre III est effectuée. *Note : Ce chapitre est le fruit du travail du candidat. Hubert Morin à participé l'élaboration des idées de base de*

ce chapitre. Sergio Rossi a participé à l'élaboration de la méthodologie d'analyse pour la relation entre la dimension des cellules et les variables météorologique.

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CHAPITRE II

CELLULAR PHENOLOGY OF ANNUAL RING FORMATION OF *ABIES BALSAMEA* IN THE QUÉBEC BOREAL FOREST (CANADA)

Annie Deslauriers, Hubert Morin et Yves Begin

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2.1. Abstract

Cell formation in growth rings of balsam fir (*Abies balsamea* (L.) Mill.) in the boreal forest was studied to describe the timing of ring formation and the development patterns of earlywood and latewood. Wood micro-cores were extracted during the growing season from 1998 to 2000. The micro-cores were stained with cresyl fast violet to facilitate counting the number of cells in the radial enlargement, wall thickening phases, and mature cell phases. The periods required to complete these various phases were then estimated. Variations in the beginning of the growing season (May 7-June 7), the earlywood-latewood transition (July 2-July 19) and the end of the growing season (Aug. 20-Sep. 20) were observed. Short cell enlargement durations, of less than a week for earlywood and 5-10 days for latewood, were observed. Time required for cell wall thickening was about 20 days for earlywood and 30-35 days for latewood. A certain flexibility was observed in the rings formation patterns and in the cells development rate, providing an advantage in the boreal forest where growth optimal conditions changes from year to year. These findings on the spatial and temporal pattern of ring development may be useful for understanding tree relationships with climate or other environmental parameters.

2.2. Résumé

La formation des cellules dans les cernes annuels du sapin de baumier (*Abies balsamea* (L.) Mill.) a été étudiée en forêt boréale pour décrire la chronologie de la formation des cernes et le développement du bois initial et final. Des micro-carottes ont été extraites pendant les saisons 1998 à 2000. Des sections ont été colorées à l'aide du *cresyl fast violet* pour faciliter le dénombrement des cellules dans les phases d'élargissement radial, de formation des parois secondaires et les cellules matures. Le temps requis pour que les cellules complètent ces phases a été estimé. Des variations dans le début de la croissance (7 mai au 7 juin), dans la transition du bois initial au bois final (2 juillet au 19 juillet) et dans la fin de la croissance (20 août au 20 septembre) ont été observées. De courtes périodes d'élargissement, de moins d'une semaine pour le bois initial et de 5-10 jours pour le bois final ont été observées. Le temps nécessaire à l'épaississement des parois secondaires était d'environ 20 jours pour le bois initial et plus de 30 à 35 jours pour le bois final respectivement. Les résultats mettent en évidence une certaine flexibilité dans le développement des cernes, ce qui procure un avantage en forêt boréale où les conditions optimales de croissance changent d'années en années. Ces résultats pourront être utiles pour mieux comprendre la relation entre les arbres et le climat ou d'autres paramètres environnementaux.

2.3. Introduction

Most dendroecological studies with balsam fir (*Abies balsamea* [L.] Mill.) in North American boreal forest are related to growth patterns caused by spruce budworm outbreaks (*Choristoneura fumiferana* [Clem.]) (Blais 1958, 1962; Morin and Laprise 1990; Morin 1994; Krause and Morin 1995). These studies provide information about the annual variation of growth but not the intra-annual variation and the period of ring development. Although research has been undertaken to understand balsam fir's reactions to massive foliage loss, basic mechanisms of tree physiology and cell development recorded in the sequence of ring widths are not well understood and need further investigation. By establishing a detailed calendar of cell division and development from wood cores taken over short time intervals, it is possible to link tree-ring development with other measured environmental parameters (Antonova and Stasova 1993,1997) or tree disturbance (Park and Morin 2001). Such a detailed approach will assist dendroclimatological and dendroecological studies by providing details on the mechanism of ring development.

In North America, few studies have been published on the seasonal formation of xylem. None of these studies were conducted in the ecological zone of the boreal forest and only a few concern the balsam fir ring formation (Kutscha et al. 1975; Riding and Little 1986). An attempt was made with balsam fir to characterize the growing season, ring development, and the influence of climate (Deslauriers 1999), but information is still lacking. The beginning of the growing period, rate of cambial activity, period of secondary cell wall development, and beginning of the dormant season, along with temporal variations

of these processes, are still unknown for balsam fir and other major conifers species in the boreal forest including black spruce (*Picea mariana* [Mill.] BSP) and jack pine (*Pinus divaricata* [Ait.] Dumond). These species are considered the most important ones with respect to forest yield and management. Balsam fir produce a higher number of cells compared with other boreal species, which makes it easier to set up a suitable methodology.

Repeated cellular analyses during the growing season is one of the best methods to understand and document the intra-annual development of growth rings. Secondary xylem production is a complex process derived from cell periclinal and cataclinal division in the vascular cambium. The differentiation of annual rings in conifers involves the formation of tracheids that go through several phases before reaching their final form. A differentiating tracheid reaches its final radial diameter during a phase of radial enlargement after it has emerged from the cambial zone (Wilson et al. 1966). The secondary wall is formed during a subsequent maturation phase (Mahmood 1971; Wodzicki 1971; Creber and Chaloner 1990).

This study contributes to the intra-annual analysis of balsam fir growth ring development by means of weekly micro-core sampling during three successive growing seasons. We had two main objectives. The first was to characterize the phase of ring development by following the development of cells from their division-radial enlargement to their maturation. This analysis provided information on the dynamics of cambium and xylem cell differentiation through the growing season. The second objective was to analyze the

period of earlywood and latewood development variation with respect to the duration of cell formation.

2.4. Material and methods

Study area

This study was conducted in two permanent plots (Lib-23, Lib-24) (Morin, 1994) located near the 50th parallel (49°58 ' N; 72°30 ' W), about 100 km north of Lac-Saint-Jean (Québec), an area located in Thibault's (1987) black spruce moss ecological region (No. 12b) of the boreal zone. The vegetation association is similar to the balsam fir – white birch (*Betula papyrifera* March.) type of the more southern balsam fir – white birch zone (Grandtner 1966). The mean annual temperature is –0,7°C and the mean annual precipitation is 422 cm, with 357 cm falling as snow (Environment Canada 1992). The balsam fir stands were located near the northern limit of the fir stands, which makes them interesting for further studies on climate-growth relationships since these trees might be more sensitive to climate. Lib-23 has a unimodal age structure with the trees establishing between 1815 and 1850. Lib-24 was severely affected by the last spruce budworm outbreak (1974 to 1988) and most of the adult trees, which established between 1875 and 1890, died in the last outbreak. The Lib-24 stand is now composed mainly of young, 5-6 meter tall trees that were released after the spruce budworm outbreak as a result of stand opening (Morin 1994).

Tree selection

One micro-core at DBH (1,3 m) was taken from each of 55 trees before the beginning of 1998 growing season for a preliminary tree selection. Cells of the last three rings formed were counted and trees with a similar average number of cells per ring were chosen to

ensure comparable growth rates. Ten adult trees (mean height, 17,5 m) were selected from Lib-23 for an analysis of ring formation in 1998, 1999 and 2000. At Lib-24, 10 adult (mean height, 18.7 m) and 10 young (mean height, 4,5 m) trees were chosen; the young trees were analyzed for the 1998-1999 growing season while the adult trees were analyzed for the 1999-2000 season.

Ring sampling

Surgical bone sampling needles DBMNI-1501 (Aiguille d'aspiration, Inter V médical, Montréal, Que.) were used for the extraction of small cores of wood and bark. The cores were1 mm in diameter and 15-20 mm long, containing 4 to 6 rings. These needles were used instead of an increment puncher (wood samples 10 mm long and 2.5 mm in diameter, Forster et al, 2000) because their smaller diameter allows repetitive sampling on small tree (dbh < 5cm) without causing significant growth disturbance. Wood cores were extracted every week for three growing seasons (1998, 1999 and 2000) from early May to October. Samples were taken following a spiral trajectory up the stem, from 30 cm below DBH to 30 cm above. Wood cores were always taken at least 10 cm apart from each other in adult trees and 5 cm apart in young trees to avoid getting resin ducts on adjacent cores, which is a common disturbance reaction in balsam fir. A total of 1410 wood cores were fixed in paraffin and transverse sections 10-12 µm thick were prepared with a microtome. Several sections from the same core were put on three to four glass slides. The sections were immersed in two baths of Histo-Clear™ for 10 minutes and two baths of alcohol (100%) for 2 minutes to remove the paraffin and dehydrate the sections, The sections were then put in

a water bath before applying stain. Two different types of analysis were conducted on each sample: ring development analysis and cell measurement.

Ring development analysis

Sections were stained with a water solution of 0,05% cresyl fast violet and kept in water to assess the ring development. This staining procedure helps differentiate the developing phloem and xylem cells (Antonova and Shebeko 1981). For each sample, the number of cells in the radial enlargement phase, cell wall thickening phase, and mature cell phase were counted along three radial files. The cells had to be kept in water and counted immediately after staining until the microscopic analysis was done as the coloration disappears after only a short period. The dormant cambium before the beginning and at the end of the growing season was easily identified by 2 to 4 radially flattened fusiform cells (Riding and Little 1984). Both cells from cambium zone and cells in radial enlargement phase (xylem) have primary pink walls. The cambial zone and cells in radial enlargement, are easily identifiable as they posses only primary walls, while both seive cells and tracheid cells have secondary walls that show strong birefringence in polarized light (Zimmermann 1964; Riding and Little 1984). Cells in the secondary wall thickening phase change from light violet in the beginning of the process to deep violet near the mature cell state. Lignification is characterized by the appearance of blue, initiating first in middle lamella and spreading into the secondary walls of differentiating tracheids. Xylem cells are considered mature or entirely lignified when they are completely blue.

Cell measurements

Sections were stained with safranin (1% in water) and permanently fixed with Permount® to asses cell measurement with the computer program Wincell™. A Polaroid camera fixed on an optical microscope and connected to a computer was used for numerical image analysis. The measured parameters were lumen area (μm^2), single cell wall thickness (μm), lumen diameter (μm) and total cell width (μm). Three radial files were measured and the average cell size (or any wood parameter measured) was computed on each section. Radial files with larger tracheids were subjectively chosen to ensure that the cell section passed through or near the limit of the middle part of their length. Because the cores were taken along a spiral, the ring width varied within the tree circumference and therefore between the different samples. Hence, the number of cells was counted on 3 radial files on the 3 rings preceeding the ring in formation and used subsequently for a cell number standardization for each sample.

Statistical analysis: ring formation

The mean cell number of the three previous years per sample and the mean of all samples per tree were computed and used for a cell number circumference standardization. The extreme values (maximum and minimum) were removed by using a stem leaf graph created by the Univariate procedure of SAS (SAS Institute Inc. 1990) to ensure a normal distribution. A ratio was obtained for each sample by dividing the mean cell number of the sample by the mean cell number of all samples per tree. The number of cells in each phase (radial enlargement, wall thickening and mature cells) was then multiplied by the ratio to

standardize the data according to the sample's relative position on the stem. Before computing the mean cell number in each phase per date of sampling, another Univariate procedure (SAS Institute Inc. 1990) was used to remove the extreme values.

The approximate date of entrance and the number of days spent in the differentiation phases (enlargement and wall thickening) of each consecutive tracheid formed during the growing season were found following Wodzicki (1971). The methodology is based on differences between (1) total cells number (radial elongation+wall thickening+mature cells), (2) wall thickening+mature cells and (3) mature cells, at a 7 day sampling interval. The calculations were done with fitted data using NLIN (NonLINear regression, Marquardt iterative option) of the SAS statistical package as the number of cells fluctuates near the end of the season. This method regresses the residuals onto the model partial derivatives with respect to the Gompertz parameters until the estimates converge (SAS Institute Inc. 1990). The examination of the R^2, the asymptotic t-statistic for the parameters, and the plots of the residual showed that the Gompertz function was appropriate to describe growth and time relationships (Zeide 1993; Huang et al.1992). The Gompertz equation has been used to model tree-ring growth (Camarero et al. 1998). The equation was fitted to establish the cell increase profile of each total described.

The Gompertz function is defined as:

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

Where y is the weekly cumulative sum of growth (expressed in 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). Two biologically useful variables were calculated from the fitted statistics, both defined by Richards (1959). A weighted mean absolute cell formation rate **r** can be obtained by equation 2, and the time required for the major portion of cell formation **d** to occur can be obtained by equation 3. Parameter ν was fixed to 0.0001 since Gompertz function is a special case of the Richards function when $\nu \cong 0$.

[2] $r = a.\kappa / 2(\nu+2)$

[3] $d = 2(\nu+2) / \kappa$

Statistical analysis: cell measurement

Curves of cell size variation in radial files of xylem, called tracheidograms, were constructed following Vaganov (1990). Standardization is required to compare tree ring structures as different rings have different numbers of cells of varying dimensions. The standardization method decreases or increases the initial tracheidogram along the abscissa leaving the ordinate unchanged (Vaganov 1990). The average number of mature cells was used to calculate the number of cells to standardize for each sampling date. Classification of cells into latewood were conducted using Mork's formula described in Denne (1988):

[4] single cell wall thickness x 4 $\geq$ tracheid lumen

2.5. Results

Tree ring characterization

The weekly averages of differentiating cells and mature cells, during the growing season from 1998 to 2000, are presented in figure 2.1. An important variation was observed between the starting and ending periods of the growing seasons (table 2.1). The starting periods vary from May 7, observed in Lib-23 1999, to June 7, observed at both sites in 2000.

The mean number of cells counted each week varied from 1 to 3 in the radial enlargement phase (figure 2.1). The highest values (four to five cells) counted on some samples in the second and the third week after the start, might reflect an active cell division at the beginning. However, the cambium zone during the first weeks of the growing season was easily ruptured and a few radially enlarging xylem cells could have been missed. The first cell in the wall thickening phase was observed between one and three weeks after the start of the growing season (table 2.1). After increasing regularly, they reached a plateau of around 10 cells for a month and a half (figure 2.1). The low variation during this long period indicates a constant flow of cells going in and out of the wall-thickening phase. Close to the end of the growing season these number decreased rapidly indicating that less cells were entering the wall thickening phase and that cell division was coming to an end.

In all cases, the total number of cells regularly increases until a mean maximum number defined as the upper asymptote, is reached. After this point, cell numbers start to fluctuate

because samples were taken at different positions on the trees. The upper asymptote, representing the fitted mean total maximum number of cells or a plateau, is reached at different dates in July or August (table 2.1, figure 2.1) and seemed to arrive earlier when the earlywood-latewood transition was earlier. However, even if this number is reached, it does not mean that it is the end of cell division. Cell division could be masked by differences in the ring width around the trunk of the trees even if standardization was done to make it more regular. The end of cell division in ring development was the hardest variable to determine because the cessation of tracheid production varies within and between trees (Sundberg et al. 1987).

Growth model

Cell increase fitted well with the Gompertz equation as shown by the R^2 variation between 73.9% and 96.5% (table 2.2). The cell formation rate (r) varied between sites and between the young and adult trees. For the total cell number, the values varied from 0,49 to 0,70 cell/day and in general, the cell formation rate decreased with a longer period of cell division. The shortest length and the highest rate were observed in 1998 when the upper asymptote was reached near July 23 at both sites. The mature cell formation rate, representing the rate at which the cells enter into a mature state, is normally lower than that of the total number of cells because it excludes the radially enlarging and wall thickening cells. The mature cell formation rate also lasts longer because its upper asymptote (*a*) is reached later in the growing season.

Earlywood and latewood formation period

The separation of ring development into two parts, earlywood and latewood formation period, was determined from weekly cell measurements. The cell classification was conducted using only mature cells to avoid the comparison of non-mature cells with mature ones. In figure 2.2, cells that are still in differentiation phases (radial enlargement or cell wall thickening) are shown to illustrate more precisely the transition between earlywood and latewood. At the end of the growing season, when the number of cells starts to fluctuate, the number of cells was standardized at mature cell fitted values corresponding to the last sampling date.

Earlywood growth was observed to be a fast process with cell division taking between 1-2 months from the start of the growing season to the transition time (table 2.1). The earlywood formation length is almost the same for 1998 and 2000 (6 to 7 weeks) but it is longer for 1999 (9-10 weeks) because of a very early growing season. Thus, most of the ring width, 65-75% earlywood for mature trees and 80% for young trees, is formed in a very short period of time. The time at which we observed the first mature earlywood cells was constant at 3 to 4 weeks after the beginning of the growing season. This gives a good indication of the time required for the complete formation of an earlywood cell which is independent of the beginning of the growing season. Complete earlywood formation, including the time necessary for cell wall thickening, took 10-12 weeks in 1998-2000, and 13-14 weeks in 1999. Variation in the transition time does not seem to be related to the start of the growing season. In fact, even if the 1999 growing season started sooner, its

earlywood-latewood shift was two weeks later than that observed in 1998, and was close to that observed in 2000 (table 2.1, figure 2.2). Total latewood formation (including the cell wall thickening) lasted 9 weeks in 1998 and 2000, and 6 to 7 weeks in 1999, which is less than for earlywood. Latewood has less cells than earlywood, but more time is required to complete single cell formation because of the longer duration of the cell wall thickening phase.

Single cell formation period

Fitted sums of data (table 2.2) were used to interpolate between sampling dates and to set an approximate period of formation for each cell during the growing season (figures 2.3, 2.4 and 2.5). These estimates can be considered quite reliable for most of the earlywood cells since the earlywood-latewood transition date is approximately the same as the actual date observed (table 2.1). For latewood, the estimation of the end of the wall thickening phase, including the last 1-3 cells, is estimated later than the one graphically observed (figure 2.2) in 1998 and 1999 in both site. This problem is due to the difference between the convergence of the upper asymptote of the total cells and that of mature cells, which causes a bias for the last cell (table 2.2).

The duration of the radial cell enlargement phase might not have a strong influence on the final, mature cell width as there is a non-relevant difference between the wide earlywood cells and the narrow latewood cells (figure 2.3, 2.4 and 2.5). Radial enlargement was relatively uniform between study sites and years as shown by the values of less than a

week. Normally these values vary from 2-6 days for earlywood with a slight increase at 5 to 10 days for latewood. Only a small difference was observed for the year 2000 where the lengths were slightly longer for both study plots. Times spent in radial enlargement are also quite similar between young and adult trees. However, wall thickening varied between earlywood and latewood with older trees spending a greater amount of time in the wall formation stage. The duration of earlywood wall thickening exhibited a constant increase during the growing season from 10 to 20-25 days before the earlywood –latewood transition. Latewood wall thickening then varied from 20-25 to 30-35 days depending on tree age (young or adult) and the year.

Pattern of ring formation

Interesting patterns of ring development were observed for the different study years and specific study plots. First, the overall growing season may almost be of the same length (based the beginning and end dates) but may possess different progressions into the cell division rates and cell wall thickening periods. Young trees at Lib-24 started their 1998 and 1999 growth season on May 20-21 (table 2.1), but the transition between earlywood and latewood occurred later in 1999 because of a slower cell division rate (table 2.2 and figure 2.4). This delay cannot be attributed to significant difference in radial enlargement, consequently the cell division rate and the cell development phase seem independent of each other. A second pattern showed that when a delay was present at the beginning of the growing season, its effects could be maintained through to the end of the growing season. In fact, the whole ring pattern of development throughout the 2000 growing season was

delayed. The year 2000 cell division rate was also slower (0,515 cell per day for Lib-23, table 2.2), and the time spent in radial enlargement was longer, making it difficult for the ring development to catch up. Similar situations were also observed when comparing the years 1999 and 2000 at Lib-23 and Lib-24. Delays of about 3 weeks to a month were observed at the beginning and at the end of wall thickening phase but not at the earlywood-latewood transition.

2.6. Discussion

Earlywood growth

A month of difference was observed for the beginning of tracheid formation, from May 7 to June 7, which is a long delay. However, these delays are commonly observed because the beginning of the growing season varies considerably, depending mostly on climate variation (Creber and Chaloner 1984, 1990; Zabuga and Zabuga 1990; Vaganov et al. 1994). For Scots pine in Russia, the start of the growing season (1978-1982) varied between the first 10 days of May to the second 10 days of June, with temperature being the main factor that influenced the initiation of tracheid formation (Zabuga and Zabuga, 1990). The temperature around 25 °C or higher at the beginning of May 1999 could explain the very early initiation of tracheid formation at Lib-23. In spite of this, detailed growth-climate analysis must be undertaken to fully understand the influence of climatic factors.

As reported for red pine (Whitmore and Zahner 1966) and Norway spruce (Horäcek 1994), the number of cells in the radial enlargement and wall thickening phases was relatively constant during most of the active growing period of earlywood following a sharp increase at the beginning. However, in our study few cells in radial enlargement (maximum of 5) were counted every week. Other studies, including those of balsam fir, have found many more cells in this phase, especially in very active cambia (Whitmore and Zahner 1966; Sundberg et al. 1987; Horäcek 1994). Even if some radially enlarging xylem were overlooked because of a rupture of the cambium zone, cell numbers remain low compared

with that of other studies, resulting in a quite short estimated enlargement time of less than a week for earlywood and 5-10 days for latewood. By comparison, in Siberia, the growth of pine tracheid primary walls lasts 3-7 days (Antonova et al. 1995).

Between 65-80% of ring width was produced in less than 2 months, from the end of May to mid-July, with June being the most important month for ring development. The short period needed for earlywood growth might be an adaptation to the cold climatic conditions of the boreal forest where cells require a very short time for their radial growth and start their wall thickening rapidly. This situation could leave a certain safety margin at the end of the growing season used to complete the lignification before frosts occur. Antonova et *al.* (1995) found that tracheid radial growth depends more on the rate of development, especially at the beginning of tracheid growth when the rate is higher, than on the duration of the process. Therefore, local and daily weather conditions at the beginning of cell enlargement should be crucial for determining both cell width and consequent ring width, because of the influence of weather on the enlargement rate. As the rate and period of earlywood development changes from year to year, the understanding of the growth mechanism could improve significantly our comprehension of the growth and climate relationship. For example, ring width is a parameter poorly correlated with monthly climatic average in Eastern North-America (Conkey 1986; D'Arrigo et al. 1992; Schweingruber et al. 1993). Monthly climatic averages may not be precise enough to characterize the short but crucial moment at the beginning of cell enlargement.

Latewood growth

Latewood initiation time is very important because it marks the end of the wide earlywood cell enlargement phase that largely defines ring width and marks the close end of cell division. The earlywood-latewood transition varies in time depending on the start of the growing season (early or late) and on the cell formation rate. The same transition date between study plots for a given year might reflect a climatic "signal" that affects a wide area. In our studies, it had varied from July 2 to July 19, a range of two weeks. Zabuga and Zabuga (1990) have observed a variation as long as a month with Scots pine in Siberia.

Latewood formation, that involves a reduction in radial expansion and an increase in wall thickening was strongly influenced by the increase in the duration of the cell wall thickening phase, which was about 10 days longer than earlywood. Other investigations have also observed that it is the duration and not the rate of wall material deposition that causes the thicker cell walls (Wodzicki 1971; Denne 1974, 1976). In addition, Uggla et al. (2001) recently concluded that latewood formation is under developmental, rather than metabolic, control. Moreover, year-to-year climatic variations, such as a decrease in soil moisture (Conkey 1986; Zabuga and Zabuga 1990), was found to explain the variations in earlywood-latewood transition time.

Several studies have found strong correlations with maximum tree-ring wood density and August temperatures (mean-max) (D'Arrigo et al. 1992; Schweingruber et al. 1993; Splechtna et al. 2000). However, the period to obtain the best correlation can vary from

mid-July to mid-August, as found in 1998 and 1999 or from mid-August to mid-September in 2000 (figure 2.3, 2.4 and 2.5). Our results suggest that July and September, can also have a significant effect on latewood density. The growing season starting date (early-late) and the earlywood-latewood transition date could both have had an influence on the end of the cell wall thickening phase. However, climatic conditions at the end of the process may be involved in explaining the variation. Lignin deposition in latewood cells still persists after the end of the cell wall thickening phases (Gindl et al. 2000), therefore complete ring density was probably attained before the period observed, from August 20 to September 20, which is the end of lignin deposition in cell wall.

Control of the growing season length: duration of rate ?

Some questions arise from the observation of the growing season process. First, does a delay in the beginning of growing season shorten the growing season and result in fewer cells produced? For example, Vaganov et al. (1994) found that in severely limited temperature conditions a narrower ring is formed when a delay is observed in the beginning of the growing season. They attributed the narrow ring to a growth suppression in the middle of June because of decreasing temperature and light. By comparing 1998-1999 with 2000, it seems that the "conditions" needed for radial growth can be delayed without strong negative effects as long as they eventually occur. Conversely, Lib-23 1999 shows that if the "conditions" or some kind of "climatic signal" are present very early in spring, trees will slowly start growing even if some snow patches are still present and frost can still occur. The growing season was longer for that site/year because of a very early start but

did not necessarily end sooner as shown by the latewood initiation date and the end of the cell wall thickening period and did not result in a greater number of cells produced nor in a wider ring. The results obtained show that the cell division rate is also very important in the progress of the growing season. Our results suggest that climate can have an effect on both the rate and the duration of the cell differentiation process, independent of the beginning of the growing season. Thus, a certain flexibility exists in the growing process, which is an advantage in boreal forests where optimal growth conditions change from year to year.

2.7. Conclusion

Repeated cellular analyses during the growing season is one of the best methods to understand the mechanism of growth ring development but it requires meticulous methodological work. On the other hand, wood growth estimation on a daily scale will make it possible to carry out precise relationships with climate, or to understand the effect of a perturbation such as insect defoliation. The data obtained by this approach will also help to understand which environmental parameters are responsible for the formation of the ring and the ring width, thus improving our prediction of forest productivity, and consequently improving forest management planning.

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Table 2.1. Date of the principal events of the growing season. The values show the date to which 50% of the sample trees had the specified characteristics.

Observation	1998		1999			2000	
	Lib-23	**Lib-24y**	**Lib-23**	**Lib-24y**	**Lib-24a**	**Lib-23**	**Lib-24a**
Start - radial enlargement	May 28	May21	May 7	May 20	May 20	June 7	June 7
Start – cell wall thickening	June 11	June 11	May 27	Mai 27	June 3	June 14	June 21
Earlywood-latewood transition	July 2	July 2	July 15	July 15	July 15	July 19	July 19
Cell number reaching the upper asymptote	July 23	July 23	Aug. 5	Aug. 12	Jul. 29	Aug. 23	Aug. 9
Dormant cambium	Aug. 20	Aug. 27	Aug.26	Sep. 2	Sep. 2	Sep.13	Sep.13
End - cell wall thickening	Aug. 20	Aug. 27	Sep. 2	Sep. 2	Sep. 2	Sep. 20	Sep. 20

Note: Lib-24y, young trees; Lib24a, adult trees.

Table 2.2. Parameters for the Gompertz function fitted for every site and year for 3 distinct cell sums.

	1998		1999			2000	
	Lib-23	**Lib24 y**	**Lib-23**	**Lib24 y**	**Lib24 a**	**Lib-23**	**Lib24 a**
Total cells (radial elongation+wall thickening+mature cells)							
R^2 (%)	75,7	90,7	75,9	91,8	89,5	74,8	79,9
a	36,58	49,19	37,61	48,20	41,35	41,12	44,89
β	1,66	1,18	2,09	1,80	2,61	1,51	1,74
κ	0,065	0,063	0,052	0,046	0,061	0,050	0,056
r (cell/day)	0,593	0,70	0,49	0,555	0,627	0,515	0,624
d (day)	61,7	63,9	76,6	86,8	65,9	79,8	71,9
Mature cell							
R^2 (%)	80,3	96,5	85,9	95,2	92,2	82,0	88,3
a	38,08	47,82	36,83	48,99	41,20	43,30	38,91
β	2,17	1,88	2,65	2,17	2,70	1,84	2,65
κ	0,045	0,051	0,040	0,037	0,042	0,033	0,055
r (cell/day)	0,430	0,613	0,369	0,449	0,433	0,353	0,534
d (day)	88,5	78,1	99,7	109,1	95,1	122,8	72,9
Wall thickening + mature cells							
R^2 (%)	73,9	93,4	79,0	93,2	90,2	78,2	84,7
a	36,1	48,37	36,79	47,67	40,64	40,20	42,3
β	1,82	1,39	2,28	1,91	2,72	1,77	2,00
κ	0,067	0,063	0,053	0,046	0,060	0,050	0,059

Note: ***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; **κ** is the rate of change parameter; **r** is the rate of cell formation by day; **d** is the total time required to complete the cell increase process, in days.

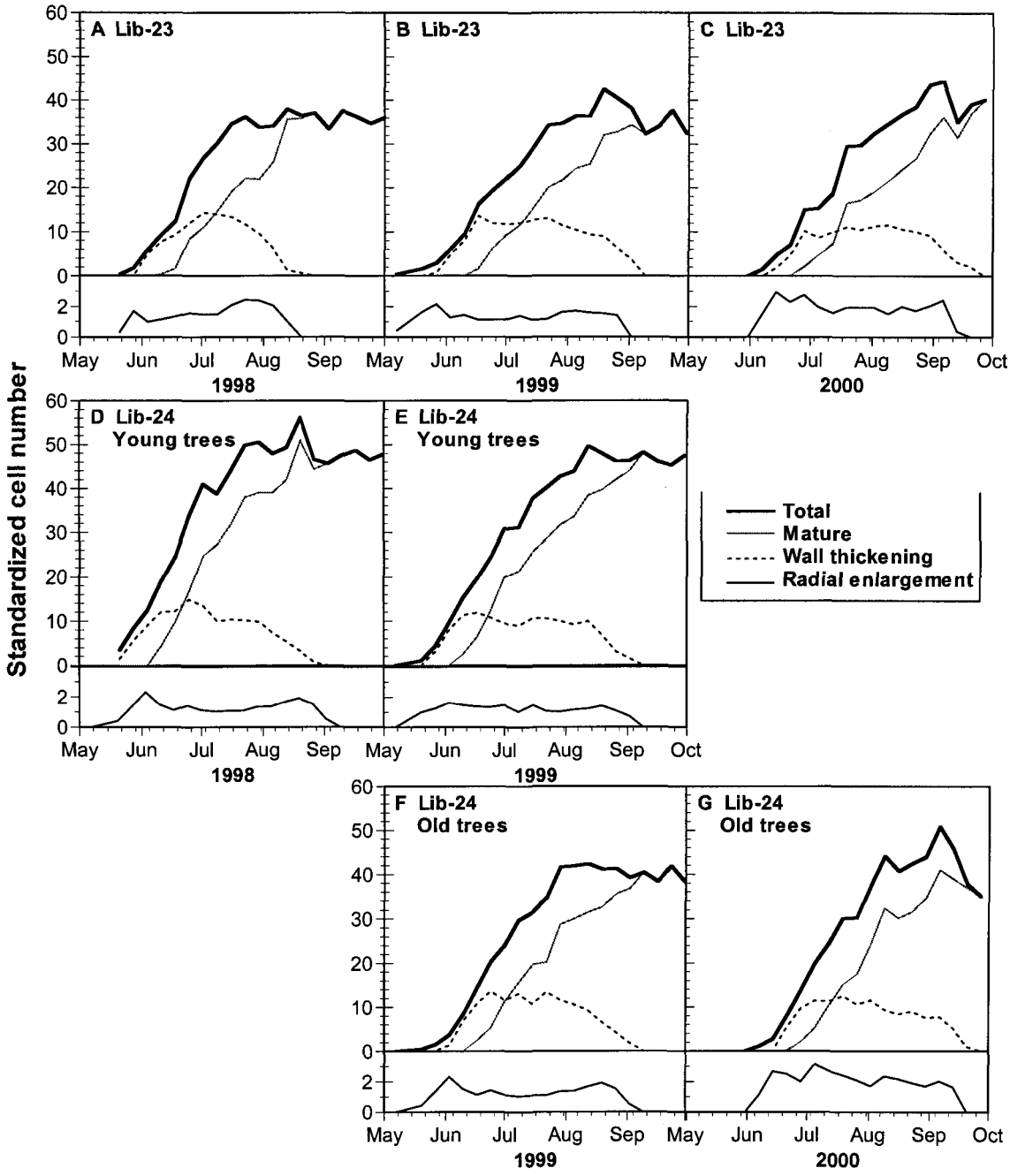

Figure 2.1. Number of cells in radial enlargement phase, wall thickening phase, mature cells and total number at Lib-23 and Lib-24 in 1998, 1999 and 2000. The horizontal axis major ticks marks show one month and minor tick marks show one week intervals.

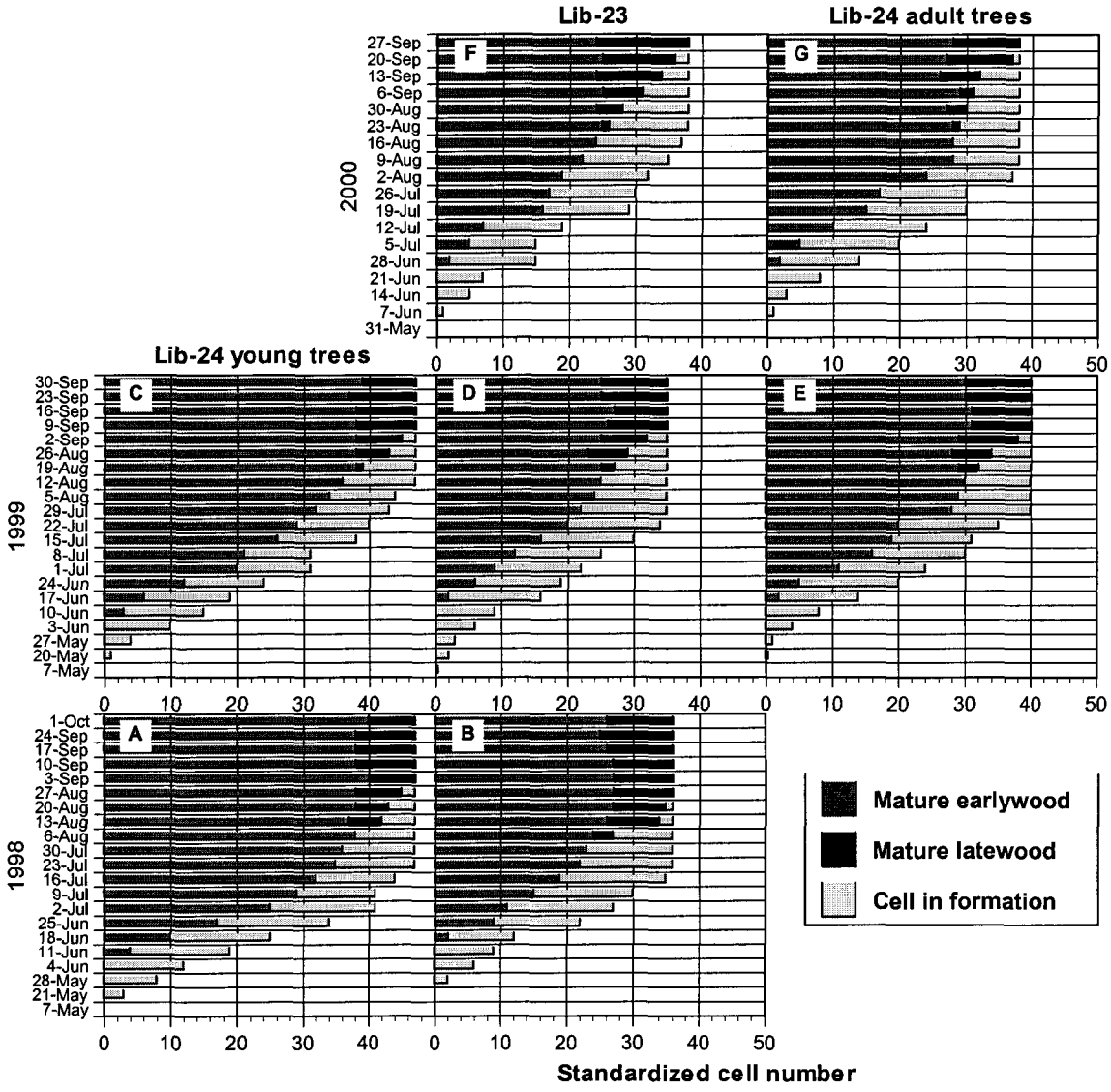

Figure 2.2. Number of mature earlywood and latewood cells and number of cells in formation (radial enlargement and wall thickening) for each sampling date from 1998 to 2000 for adult and young trees at Lib-23 and Lib-24 sites.

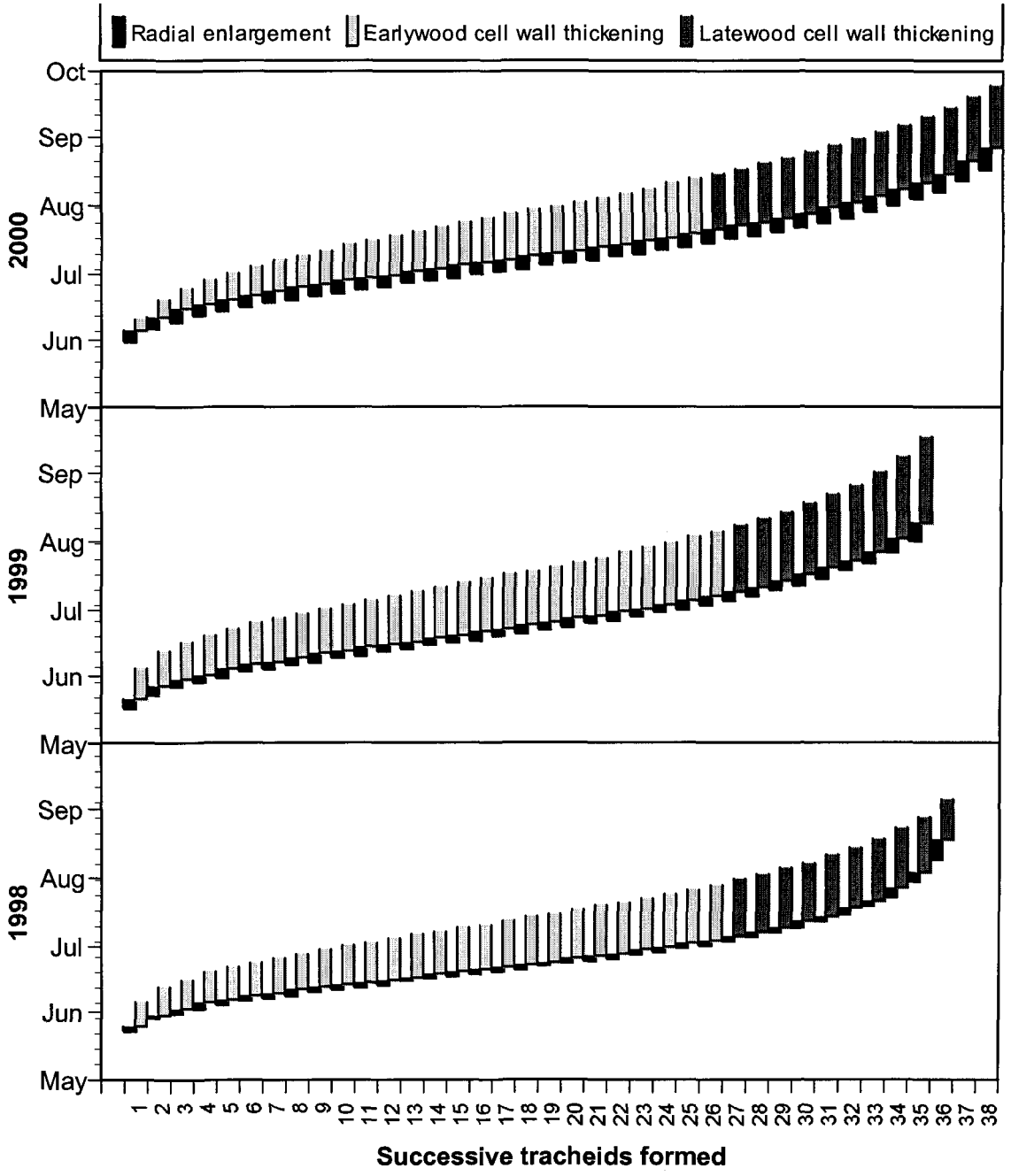

Figure 2.3. Duration of radial cell enlargement and cell wall thickening phases for adult trees at Lib-23 plot. The vertical axis major tick marks show one month intervals and minor tick marks show one week intervals.

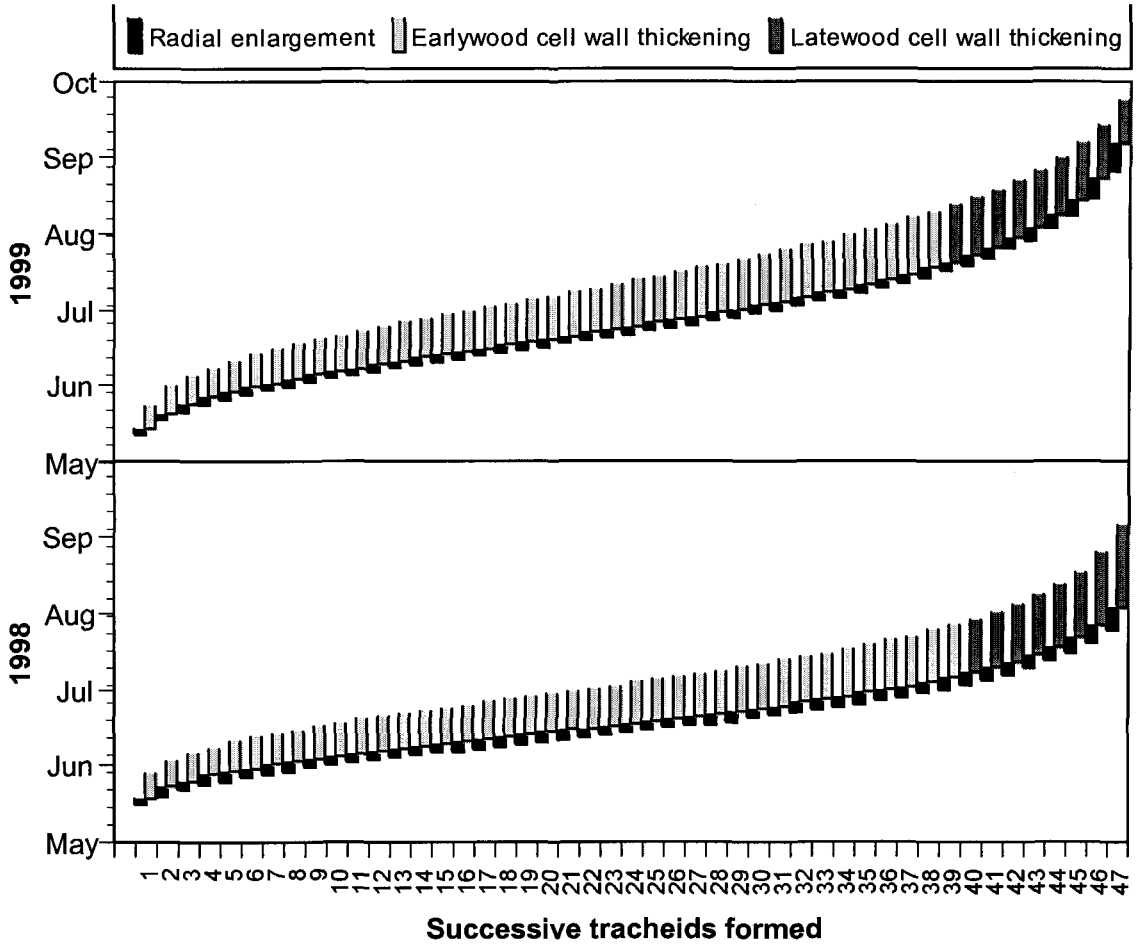

Figure 2.4. Duration of radial cell enlargement and cell wall thickening phases for young trees at Lib-24 plot. The vertical axis major tick marks show one month intervals and minor tick marks show one week intervals.

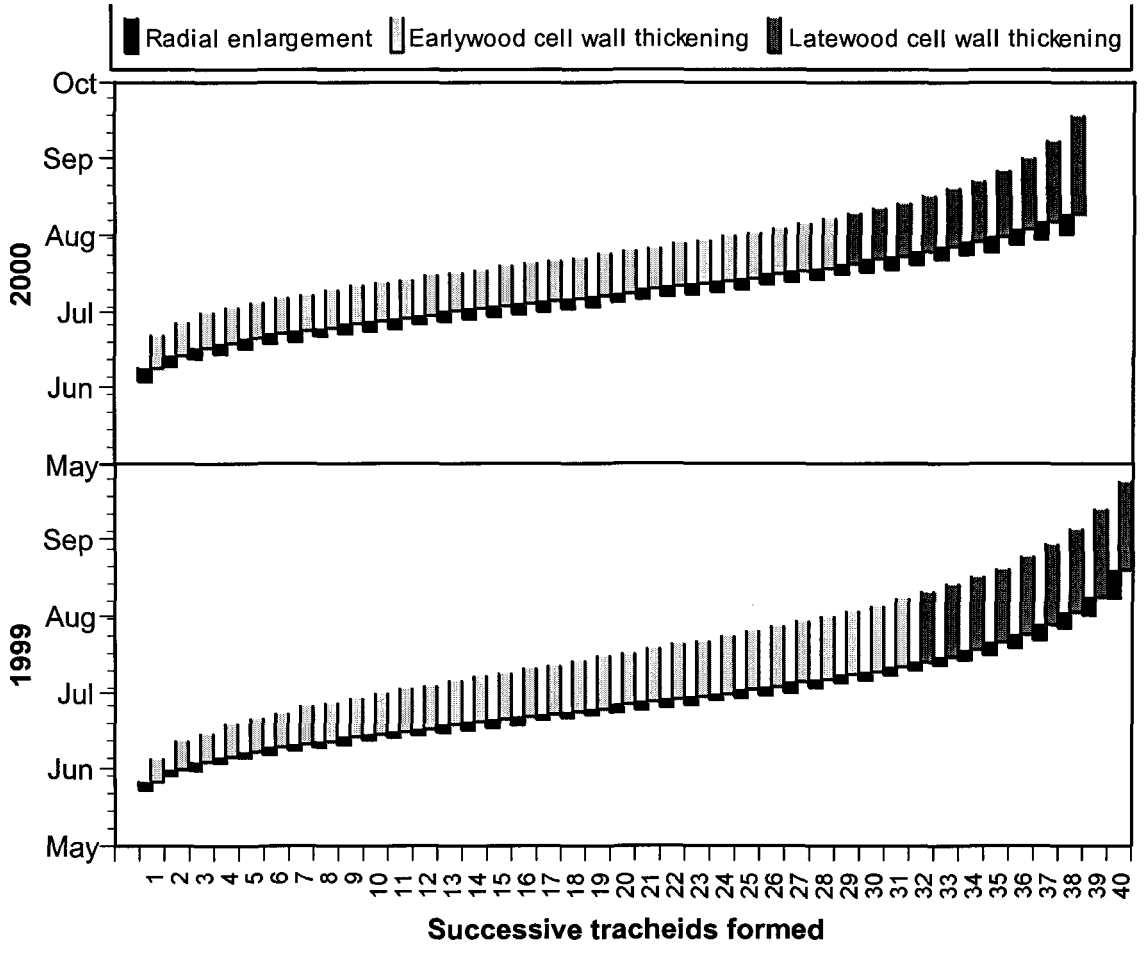

Figure 2.5. Duration of radial cell enlargement and cell wall thickening phases for adult trees at Lib-24 plot. The vertical axis major tick marks show one month intervals and minor tick marks show one week intervals.

CHAPITRE III

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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3.1. 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 influences. 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, were highly linear and explained up to 95% of the variance of the SRI series. Total rainfall in phases 2, 3 and 4 were correlated positively with SRI, and hence verify 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 would reflect only the mechanical aspect of growth.

3.2. Résumé

L'accroissement radial journalier du tronc du sapin baumier a été étudié au cours des saisons 1998-2001 à l'aide de dendromètres électroniques dans le but de déterminer l'influence des facteurs météorologiques. L'extraction de l'accroissement a été divisée en 4 périodes suivant le cycle jour-nuit des dendromètres : (1) contraction, (2) extension, (3) accroissement, (4) cycle total. Les conditions climatiques moyennes des périodes ont été comparées avec l'accroissement à l'aide de corrélations et de fonctions de réponse. Les conditions climatiques prévalant de 16-17 h jusqu'à 8-9 h correspondant aux périodes d'extension et d'accroissement ont eu le plus d'impact sur l'accroissement. Les fonctions de réponse étaient fortement linéaires avec une variance expliquée de 80-90 % et ont confirmé la plupart des résultats obtenus à l'aide des corrélations. Les résultats ont démontré que l'accroissement est positivement corrélé avec les précipitations durant les phases 2 à 4 du cycle. L'importance de l'eau a aussi été démontrée par la réponse négative du déficit de pression de vapeur au cours de l'extension affectant l'élargissement radial des cellules. Seule la température maximale de la période d'accroissement a eu un effet positif, suggérant que les températures nocturnes sont les plus importantes. Ces résultats devraient influencer le processus d'élargissement cellulaire et refléter seulement les aspects mécaniques de la croissance.

3.3. Introduction

The growing season in Québec boreal forests is very short. At the latitude of about 50° North, cell division and enlargement lasts 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 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 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). Several studies such as d'Arrigo et al. (1992), Hofgaard et al. (1999), 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 (Clark et al. 2000), only a small number of studies have used dendrometers to measure tree-ring 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. i) 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). ii) 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.

3.4. Methodology

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 (figure 3.1). 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 - 6 m tall trees because of the growth release of advanced growth after the stand opening.

Climate description

The climate of the study site is continental with cold winters and warm summers (figure 3.2). 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 four year 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 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 1-2 meters every winter.

Data collection

Automatic point dendrometers (Agricultural Electronics Corporation, 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, respectively. 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 micrometer/meter/degree centigrade. Dendrometers were installed on 20 trees: ten adult trees (19.9 m height, 27 cm DBH) were selected at Lib-23 in addition to10 adult trees (20.7 m height, 26 cm DBH) at Lib-24. All dendrometers were mounted at a height of 1.3 meters, 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 minutes 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 minutes, hourly average were calculated and stored in a datalogger (CR10X, Cambell Scientific Corporation). The variables measured were air temperature (Tmean, Tmax and Tmin [°C]) at 3 meters, humus temperature (Thu, °C), mineral soil temperature (Tmn, °C), total rain fall (P, mm), humus water content (SW, %), relative humidity (RH, %) and radiation (R, watt/m^2). SW and Thu were measured at 10 cm depth at both sites and Tmn 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 Tmean 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 hrs (figure 3.3). 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 stem radius increment (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 hours, starting at 0600 - 0900 h, but heavy rain can cause irregular cycles of more than 24 hours, due to a longer expansion phase.

Every meteorological variable was processed following the stem phase division. For each circadian cycle, four maximum temperatures (tmax1, tmax2, tmax3 and tmax4), 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's 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 10 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 (equation 1) calculated on the total cell number counted each week on the additional 10 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 (Cheng and Gordon 2000):

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

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, equation 2). Parameter ν was defined as 0.0001 since the Gompertz function is a special case of the Richards function when $\nu \cong 0$.

[2] $$\mathbf{r} = a.\kappa / 2(\nu+2)$$

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 one 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 3 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 7 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 Tmax3, Rh1, P2, P3, P4, R4 and VPD2. 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 models

3.5. Results

SRI extraction

In general, the stem circadian cycle started with a contraction phase (1) between 0800 and 0900 h. at a standard deviation of about two hours (table 3.1). This lasted until the end of the afternoon, when the expansion phase (2) commenced at around 1600 or 1700 h. The positive SRI phase (3) started between midnight and 0200 h. It shows a higher standard deviation of 4 to 6 hours. These are average cycles length 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 3.1 and figure 3.4). No transformations (or standardisations) were performed on the series because the daily increment series were free of autocorrelation (table 3.1). Defining the growing period in tree-ring analysis using a dendrometer proved to be crucial because for some years, the beginning of radial growth was coincided with the stem rehydration after winter desiccation (figure 3.4). In earlywood, SRI extraction generally follows the data recorded by the dendrometer. In latewood and following cell division-enlargement, the SRI extraction value becomes higher than the dendrometer data (figure 3.4).

Individual trees show the same SRI variation pattern throughout the growing season (figure 3.4). 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 (figure 3.5). 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 1000 μm in 1999 (figure 3.5). In most cases, the cumulative SRI does not reach its upper asymptote (*a*) (table 3.2) since minor SRI are added due to daily differences in the water balance of stem tissues near the end of the growing season (figure 3.4). This error increase 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 Tmax3, P2, P3, P4 and R4 (figure 3.6). Most of these parameters had significant positive effects on the SRI except for R4 that had a negative one. The only non-significant results are for Tmax3 at Lib-23 1998 and R4 at Lib-24 1998. The precipitation P2, P3 and P4 have very high R coefficients ranging from 0.6 to 0.8. Relative humidity Rh2, Rh3 and Rh4 showed a more or less constant relationship with both SRI and also VPD2. 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 Tmean 1 and 3 and Tmin 1. The only significant correlation of soil temperature and water content were observed for Lib-24 in 2001 and had a negative effect on SRI.

The very high coefficient 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 3.3). 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 Tmax3, Rh1, P2, P3, P4, R4 and VPD2. In some cases, other variables also fitted well into the model (Tmax2, Tmin2, Tmin3, VPD3 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 2-3-4 had a positive effect on SRI (figure 3.7), but unlike the correlation analysis, not all of these were significant as P3 in 1998 and P2-P4 in 2000 and 2001. Response functions also revealed a positive effect of TMAX3 and a negative effect of R4 on SRI which is also consistent with correlation analysis. The response function showed a negative effect of VPD2 at Lib-23 but only for Lib24 in 1998, which is more or less consistent with correlation analysis. Smaller values of VPD2 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, Rh1 shows significant negative response in almost all analyses with values ranging from -1.9 to -6.3.

3.6. 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 week 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 Eucalyptus 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 h and 0800-0900 h 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 h 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 place 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: P2, P3, P4 and VPD2. 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). VPD2 correlated better than VPD3 probably because of its higher variation due to the relative humidity close to a 100% for VPD3.

The only temperature variables that show constant response function results with daily SRI throughout the sites and years was Tmax3. 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 h and 1600-1700 h, did not have a great influence on the SRI. The optimum VPD for cell enlargement in black spruce is often exceeded after 0900 h (Major and Johnsen, 2001) but VPD1 did not have a great negative influence on the following SRI. Also, the negative effect of Rh1 and R4 could be more associated with a reversible stem reaction than to an irreversible growth reaction. An increase in R4 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.

3.7. Acknowledgements

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Table 3.1. 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.

Site-Year	L23-1998	L23-1999	L23-2000	L24-1998	L24-1999	L24-2001
Periods analysed	May 25-July 23	May 12-Aug. 5	June 2-Aug. 17	May 20-July 23	May 19-July 29	May 24-August 14
No. of trees analysed	9	8	8	10	7	8
Phase characterization (hour):						
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
Stem radius increment extraction characterization:						
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	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

Note: Phase 1, contraction phase; Phase 2, expansion phase; Phase 3, SRI phase; No. of daily SRI, number of positive SRI extracted during the analysis period; SD of SRI, standard deviation of SRI; Autocorr. Prob (*p*), SRC probability (*p*) of autocorrelation until 6 days lag. Probability $p>0.05$ indicates no autocorrelation.

Table 3.2. Parameters for the Gompertz function fitted for ring width (RWI) and stem radius (SRI) increase.

Site-Year	L23-1998	L23-1999	L23-2000	L24-1998	L24-1999	L24-2001
RWI increase						
a	1636.8	1658.2	1293.3	1761.3	1637.2	1790.4
β	1.8530	2.3444	1.6298	1.2036	3.0735	1.2400
κ	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
SRI increase						
a	1929.0	2681.5	1848.0	2547.3	3590.8	1664.6
β	1.2844	1.2418	1.2406	1.2223	1.1963	0.9160
κ	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 3.3. Main statistics of the response functions computed for the daily stem radius increment (SRI) and a selected group of meteorological variables (Tmax3, Rh1, P2, P3, P4, R4 and VPD2).

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

Note: R, coefficient of determination of the model; VC, verification correlation of the response function; SD, standard deviation of the response function.

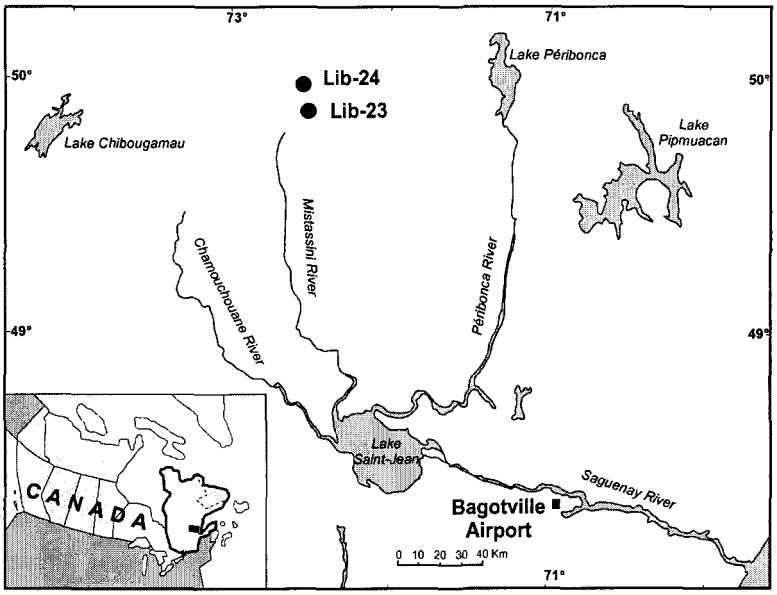

Figure 3.1. Location of the study plots.

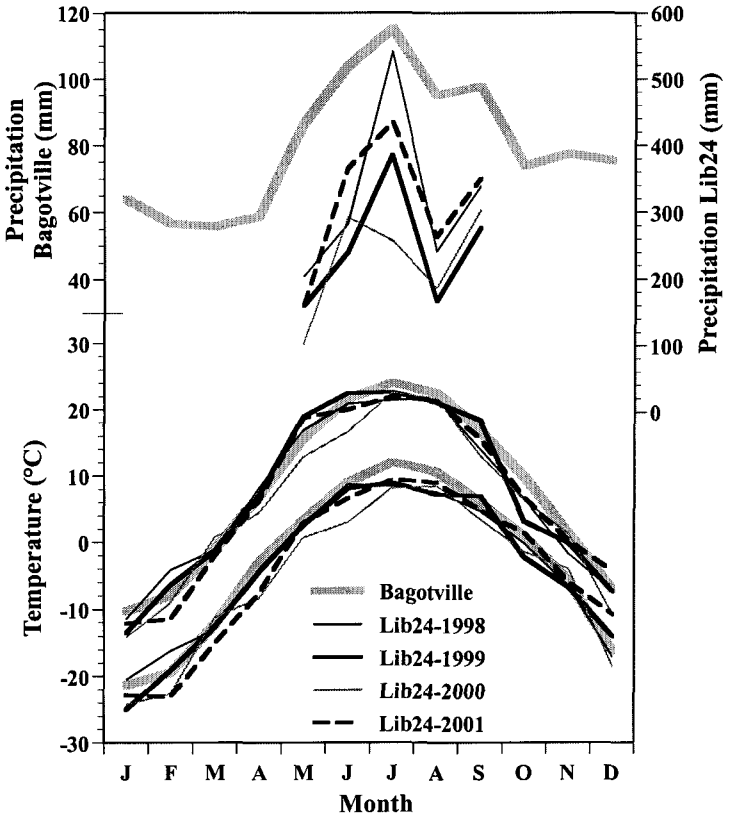

Figure 3.2. Monthly maximum and minimum temperatures and total precipitation for 58 years at Bagotville airport (the nearest station around) and for each study year at Lib-24 (1998 to 2001).

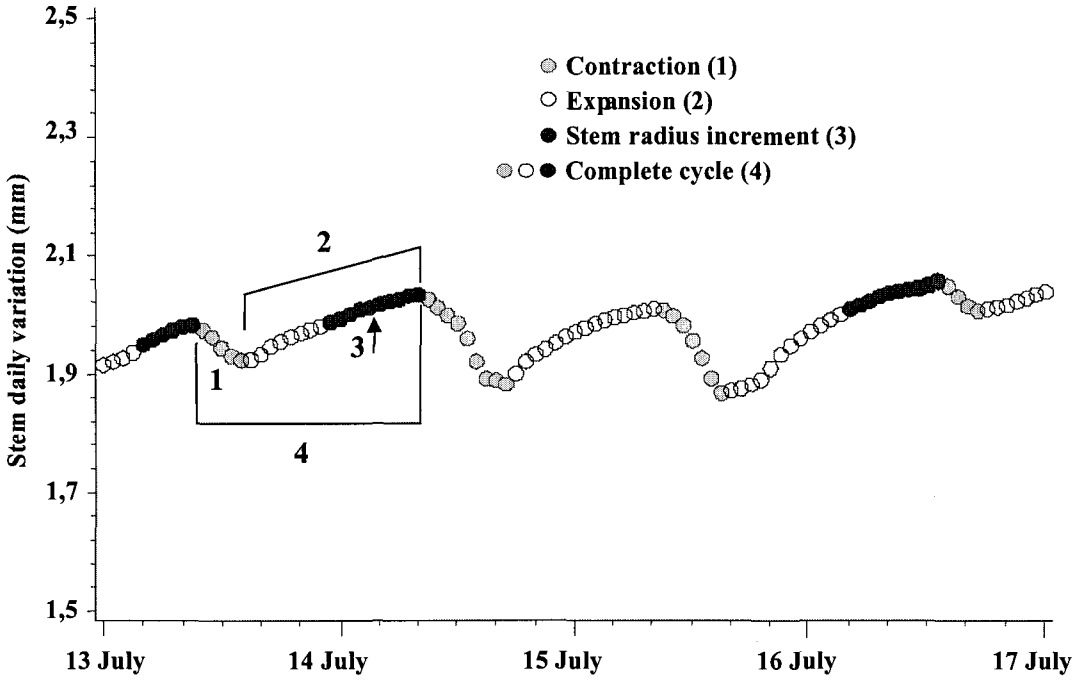

Figure 3.3. The stem's circadian cycle divided into three distinct phases.

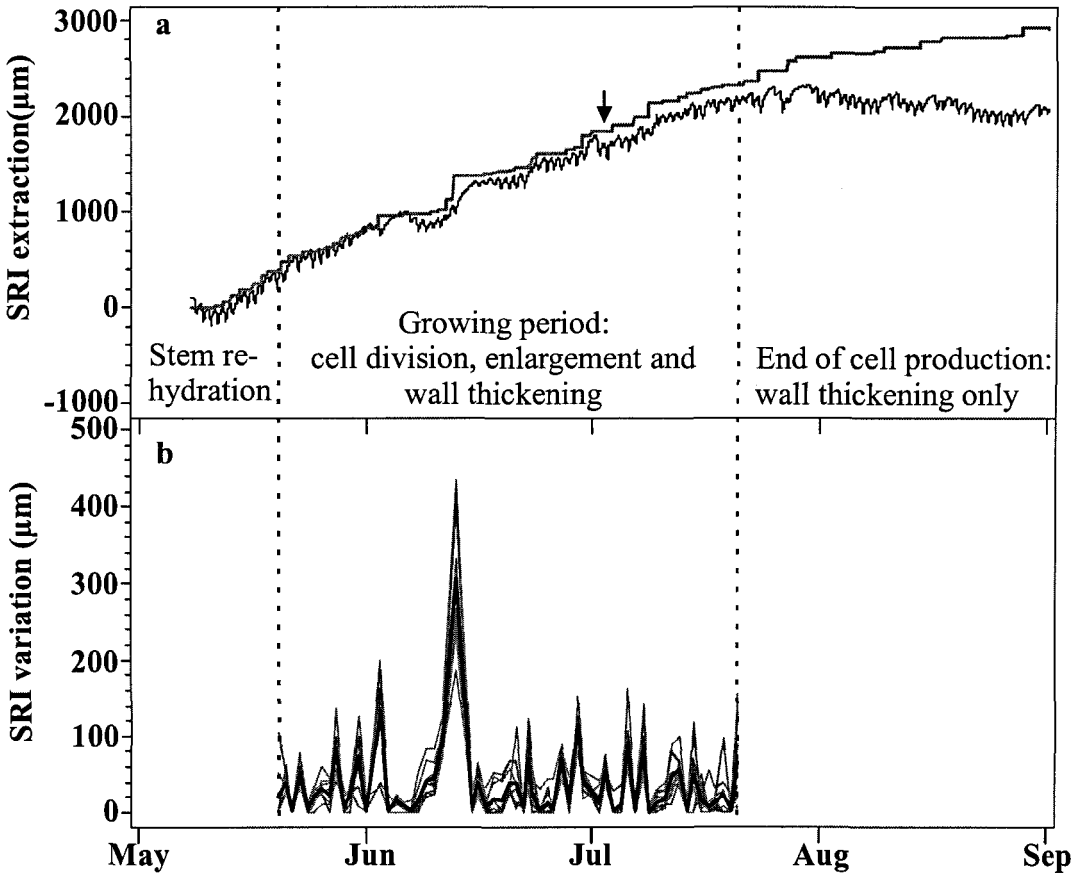

Figure 3.4. Time series of stem radius variation from May to September at Lib-24 in 1998. **a.** Daily stem radius variation (black) and SRI extraction (grey) of tree 1. **b.** Daily SRI variation (µm) of 10 trees (grey) and the mean curve (black) extracted for the growing period. The arrow shows the earlywood and latewood transition

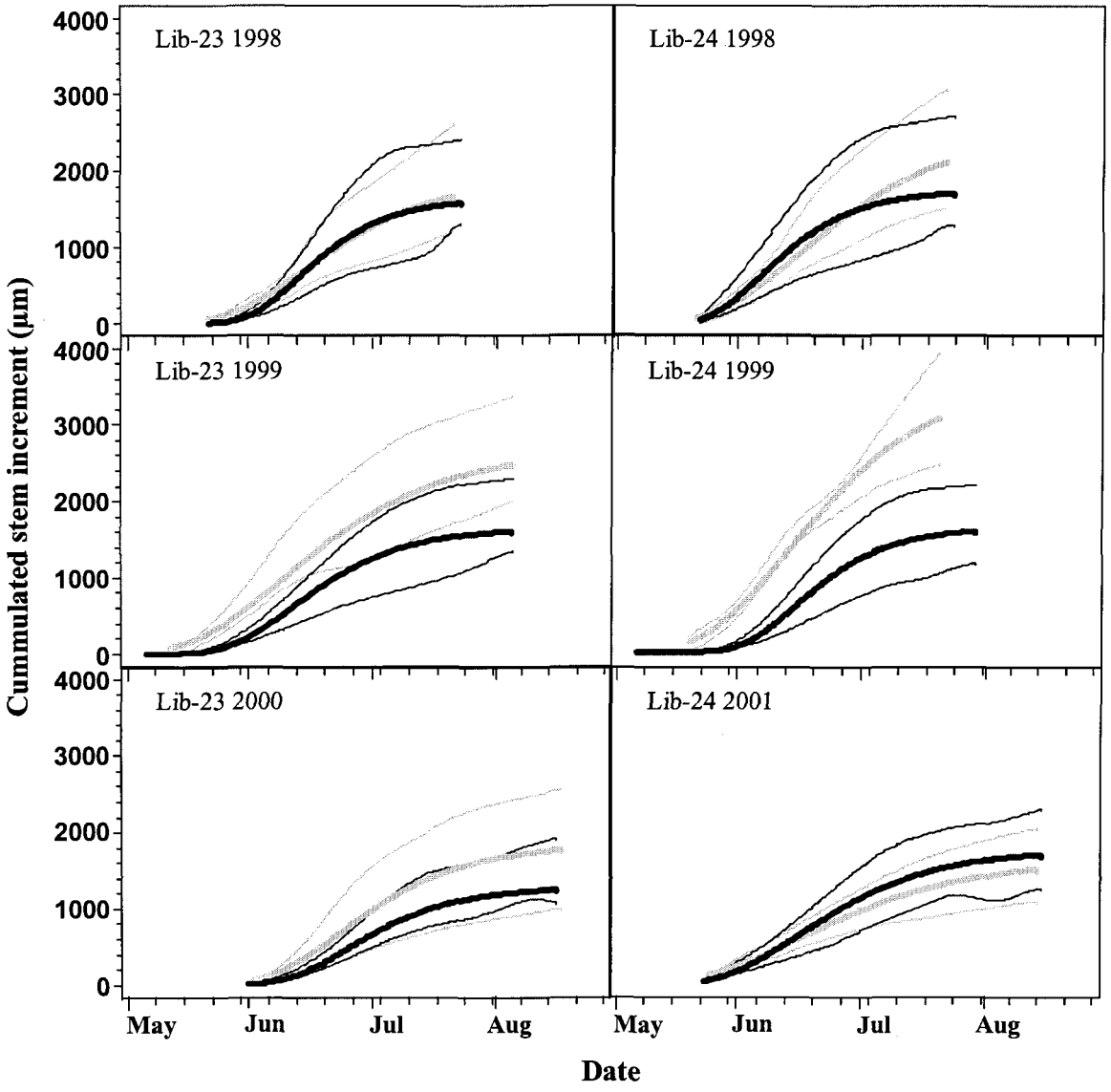

Figure 3.5. Comparison between SRI (grey lines) and RWI (black lines) during the growing season for both Lib-23 and Lib-24 study plots. The thin lines show the minimum and maximum distribution and the thick lines show the increment. On the horizontal axis the longer tick marks show one month and the shorter tick marks show one week intervals.

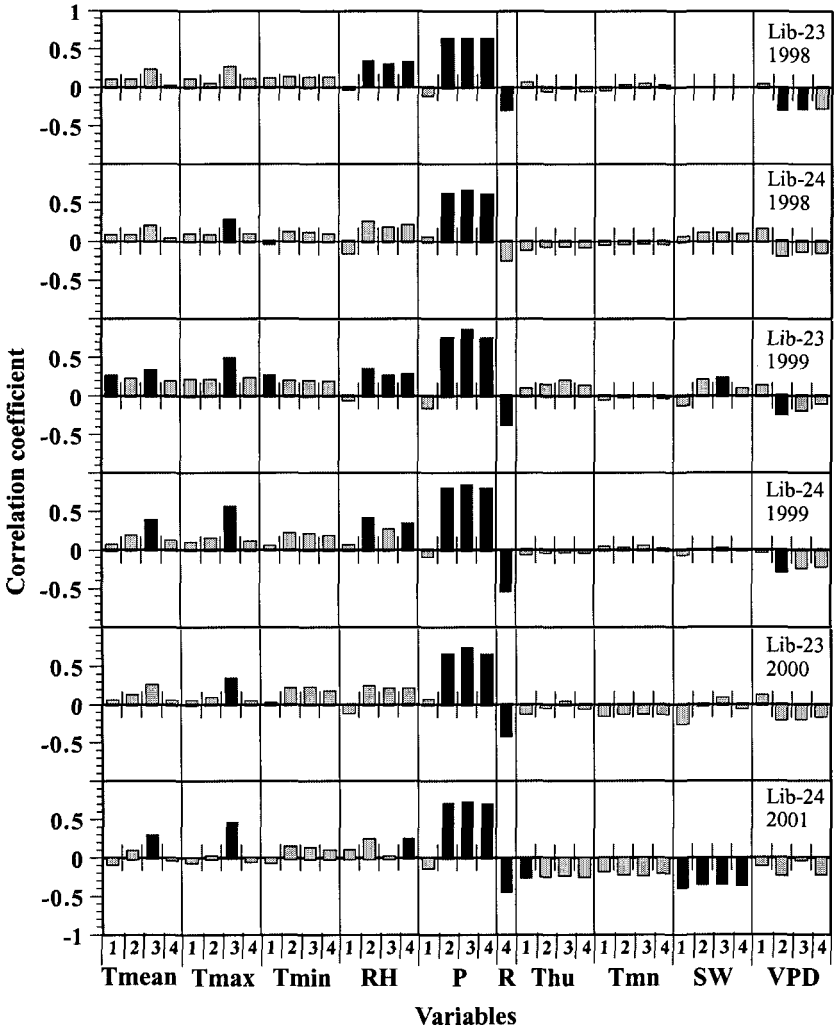

Figure 3.6. Simple correlation coefficient (Pearson, p<0,05) between the daily SRI and meteorological variables for each phase of the circadian cycle (1=contraction, 2=expansion, 3=SRI, 4=complete cycle). Significant results (p<0.05) are draw in black.

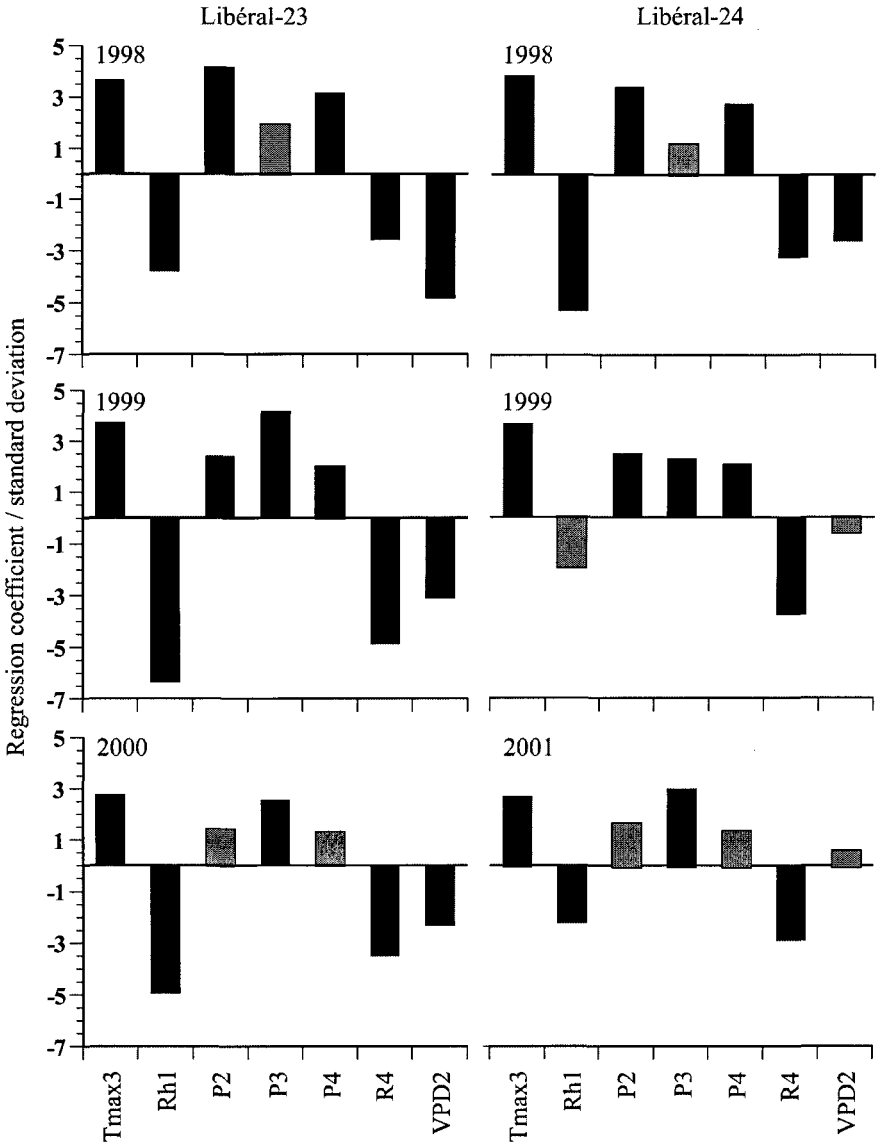

Figure 3.7. Response function results for Lib-23 and Lib-24 plots from 1998 to 2001. Significant results, for a 95% level corresponding to 1.96, are drawn in black.

CHAPITRE IV

DYNAMICS OF RADIAL GROWTH AND DAILY WEATHER RESPONSE OF *ABIES BALSAMEA* (L.) MILL. IN THE QUÉBEC BOREAL FOREST

Annie Deslauriers, Hubert Morin and Sergio Rossi

(À soumettre au Journal Canadien de la Recherche Forestière)

4.1. Abstract

The meteorological influence on the daily variation of cell dimension in balsam fir was studied between 1998 and 2000. Wood micro-cores were extracted on a weekly basis throughout the growing season and thin sections were prepared. Both the number of cells within the differentiation phases (radial enlargement and cell wall thickening) and the total amount of mature cells were counted in order to assess the duration of cell development. To match the cell dimension tracheidogram with weather, the tree-ring formation was reconstructed daily for each phases. Similar variations in cell dimensions were found between different trees during the growing season when the daily reconstruction was performed, thus indicating a clear weather signal independent of the cambial activity. In earlywood, the variation in cell dimensions indicated a strong correlation with daily maximum temperature, particularly in June for cell radial diameter and from mid-June to mid-July for cell wall thickness. Tree-ring width development is a rapid process in the boreal forest and therefore the correlation between tree-ring characteristics and the weather should be studied during the tree-ring formation period. A change in temperature greatly affects the cell's dimensions suggesting that they could be determined by the current year's weather patterns.

4.2. Résumé

L'effet des variables météorologiques sur la variation journalière des dimensions cellulaires du cerne du sapin baumier a été mesuré entre 1998-2000. Des micro-carottes ont été extraites hebdomadairement durant la saison de croissance et des sections minces ont été préparées. Le nombre de cellules dans les phases d'élargissement radial, de formation des parois secondaires et les cellules matures ont été dénombrées pour en déterminer la durée de développement. Pour chacune des phases, le développement du cerne de croissance a été reconstruit quotidiennement et corrélé avec les variables météorologiques. Des variations journalières similaires dans la dimension des cellules ont été observées entre les arbres indiquant que le signal météorologique est enregistré indépendamment du niveau d'activité cambiale. Dans le bois initial, les variations des dimensions cellulaires ont été influencées par la température maximale, notamment celle du mois de juin pour le diamètre des cellules et celle de la mi-juin à la mi-juillet pour l'épaisseur des parois cellulaires. Le développement du cerne de croissance est rapide en forêt boréale et les corrélations avec les variables météorologiques devraient être cherchées pendant sa formation. Un changement de température affecte rapidement la dimension des cellules suggérant un effet direct des conditions météorologiques courantes.

4.3. Introduction

Wood growth estimation on a daily scale is undertaken in order to study in detail the relationship between the environment and the individual tree by providing information on the dynamics of cambium and xylem cell differentiation throughout the growing season (Antonova and Stasova 1993, 1997; Horacek et al. 1999; Park and Morin 2001; Rossi et al. 2002). The differentiation of annual rings in conifers involves the formation of tracheids that go through several phases before reaching their final form. A differentiating tracheid reaches its final radial diameter during a phase of radial enlargement after it has emerged from the cambial zone (Wilson et al. 1966). The secondary wall is formed during a subsequent maturation phase (Mahmood 1971; Wodzicki 1971; Creber and Chaloner 1990). The mechanism of balsam fir (*Abies balsamea* (L.) Mill.) growth ring formation has been previously described in detail (Deslauriers et al. 2003a), where information regarding the timing of cell differentiation and a new insight into the meteorological influence was provided. As balsam fir produces a higher number of cells compared to other boreal species, it is easier to set up an adequate methodology.

In the boreal forest, the ring width of balsam fir is produced from the mid-end of May to the mid-end of July, with June being the most important month for earlywood development (Deslauriers et al 2003a). The weather conditions during this short period are therefore crucial. The role of water supply and temperature during the formation of the annual growth rings in the boreal forest has been demonstrated by many researchers, who either found a positive relationship mainly in June (Hofgaard et al. 1999; Schweingruber et al.

1993; D'Arrigo et al. 1992) or throughout the whole growing season (Brooks et al. 1998; Dang and Lieffers 1989). By using automated point dendrometers, daily stem radius increment of balsam fir was found to be correlated principally with precipitation and temperature occurring during the expansion period between 1600 hours and 0800 hours (Deslauriers et al. 2003b). This was discovered by very fine monitoring of daily tree increment. However, the impact of meteorological variables have to be investigated further on the tracheid size and wall thickness.

As it is generally recognise that the weather conditions during cell enlargement and cell wall thickening are related to the cell dimension and wall thickness, many studies have showed the influence of the mean weather conditions during the development stages of tracheids (Antonova and Stasova 1993, 1997; Horacek et al. 1999). However, these studies do not provide information regarding the influence of short weather variations and give only average results when the period of cell development is long. How the process of xylem differentiation is controlled by the weather is difficult to understand because at any particular moment during the growing season there are cells in different phases of development and in different stages of these phases (Vaganov, 1996). This concept of tree-ring formation suggests that a daily reconstruction of cell diameter and cell wall thickness variation, by using the information regarding the timing of cell differentiation, would be more appropriate. To understand further the meteorological influence, and to find which period of the growing season weather conditions mostly affect tracheid development, daily analysis is required. In this study, the daily variations of cell radial diameter and cell wall

thickness of balsam fir have been investigated in order to evaluate the meteorological influence.

4.4. Methodology

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. The floristic composition is that of the typical balsam fir – white birch (*Betula papyrifera* March.) association, which characterize the southern balsam fir – white birch forest zone (Grandtner 1966). The balsam fir plots are located in the north of the ecological region's distribution, which makes it interesting for weather response studies. The two study areas, Lib-23 and Lib-24, were affected differently by the most recent spruce budworm outbreak (1974 to 1988). The Lib-23 has a unimodal age structure with a tree establishment period ranging from 1815 and 1850 and was only slightly affected by the most recent spruce budworm outbreak (Morin, 1994). However, the Lib-24 study plot was severely affected by the outbreak. Most of the adult trees, established between 1875 and 1890, died during the last outbreak. The Lib-24 stand is now mainly composed of 5 - 6 m tall trees because of the growth release of advanced growth after the stand opening.

Several transformations were needed to assess the effect of weather on tracheid dimensions. The first part of the methodology concerned the tree-ring cell development: the cell development time t_e and t_w were found (figure 4.1) and the cells were measured. The second part concerned the transformation (standardisation) of the measured cells: to assess

the weather effect, the seasonal trend found in cell dimension was removed (figure 4.2). A mean curve for each tree of cell wall thickness and cell radial diameter variations was found by standardising and averaging several sampling dates. Then, the cell dimension variation of each tree were reconstructed for each day by using the information previously gained regarding cell development time (table 4.1). Finally, the effect of weather on cell dimension variation was assessed by correlations.

Tree-ring cell development

Tree-ring formation was analysed by counting the number of cells in the radial enlargement and wall thickening phases and the number of mature cells and by measuring the mature cells (Deslauriers et al. 2003a). These measurements were undertaken in 1998, 1999 and 2000 on ten adult trees (mean height, 17.5 m) selected from Lib-23 plot. At Lib-24, 10 adult (mean height, 18.7 m) and 10 young (mean height, 4.5 m) trees were selected; the young trees were analysed in the 1998-1999 growing season and the adult trees were analysed in the 1999-2000 season. Surgical bone sampling needles (model: DBMNI-1501) were used for the weekly extraction of small cores of wood and bark from May to October. The cores were 1 mm in diameter and 15-20 mm long, containing 4 to 6 rings. The small diameter of the needle allowed repetitive sampling also on small trees (DBH < 5cm) without causing significant growth disturbance. Samples were taken following a spiral trajectory up the stem, from 30 cm below DBH to 30 cm above. A total of 1410 wood cores

were fixed in paraffin and several sections (10-12 μm thickness) of the same cores were prepared with a microtome and placed on glass slides (Deslauriers et al. 2003a).

The first series of sections were stained with safranin (1% in water) and permanently fixed with Permount® to allow the measurement of the mature cells by using the Wincell™ software package. The measured parameters were the lumen area (μm^2), single cell wall thickness (μm), lumen diameter (μm) and total cell width (μm). The obtained data was processed by following the procedure detailed by Deslauriers et al. 2003a. A further series of the same sections were stained with cresyl fast violet (0.05 % in water) and observed with polarised light to differentiate the developing xylem cells. For each sample, the amount of cells in the phases of radial enlargement (n_e) and cell wall thickening (n_w), and the number of mature cells (n_m), were counted along three radial files (Antonova and Shebeko 1981; Deslauriers et al. 2003a).

Assessment of the xylem development requires a positive weekly increase in the number of cells. However, it is difficult to obtain a positive increase when the sampling is undertaken on the entire stem circumference and when only a small amount of new cells are developing over a period of several weeks at the end of the growing season (figure 4.1). For this reason, a function fitting the biological growth trend was used, ensuring the adjustment of cell numbers in different samplings and a proper estimation of xylem development (Rossi and Deslauriers 2003). The Gompertz equation (Cheng and Gordon 2000) was used for a fitting of the cell number using NLIN (NonLINear regression, SAS Institute 1990).

The cell number increases are (1) total cell n_t (n_e+ n_w+ n_m), (2) n_{wm} (n_w + n_m) and (3) mature cell n_m (Deslauriers et al 2003a; Rossi and Deslauriers 2003). For each tree, the number of days spent in the differentiation phases, the radial cell enlargement (t_e) and cell wall thickening (t_w) of each consecutive tracheid formed during the growing season was estimated by Rossi and Deslauriers (2003). The methodology is based on differences between n_t and n_{wm} to find t_e and on differences between n_{wm} and n_m to find t_w (figure 4.1). In figure 4.1, a schematic representation of the date of entrance and the time spent in each of the phases of radial cell enlargement (t_e) and cell wall thickening (t_w) is shown for cell number 28.

Standardisation

Because tree-ring samples have different numbers of cells, standardisation was required in order to compare cell dimensions when averaging several tracheidograms. For each tree, a relative standardisation (Pj) was performed on the weekly obtained samples j to position the number of mature cells according to the number found at the end of the growing season (formula 1). To ensure a positive increase each week, weekly n_m and total number of cell N at the end of the growing season, found with the Gompertz equation, were used for cell standardisation. The standardised cell numbers obtained were rounded-down and the dimension of the cells rounded-down to the same number were averaged.

[1] $$Pj=\left(\frac{n_i}{N}\right)*n_m$$

$n_i = j$ measured number of cells

N = fitted total number of cells

$n_m = j$ fitted number of mature cells

Trend removing

Within the year, the intra-seasonal changes determined by weather variation are partially masked by seasonal trends (Djanseitov et al. 2000) such as decrease in cell radial diameter or increase in cell wall thickness (figure 4.2a and c). Indexing was performed to eliminate the trend by fitting smoothing splines with ARSTAN (Cook 1985). A cubic smoothing spline of half the length of each cell-series was performed. The growth trend removal allowed the residuals to be averaged by adjusting the series for differential growth rates due to different positions on the stem (figure 4.2b and d). For each tree, a mean tracheidogram of cell dimension was found by averaging 5 to 6 tracheidograms (figure 4.2b and d) chosen according to the core position on the stem (similar angle) and to the similarity in cell dimension variations ensuring a reliable and comparable mean between trees (figure 4.2e).

Daily reconstruction of cell size variation

To match the tree mean tracheidograms with the weather series, the tree-ring development of each tree was reconstructed on a daily basis for each development phase (radial enlargement and cell wall thickening) (table 4.1). The principle idea behind the daily reconstruction is that in each given day of the growing season, there are many cells in differentiation. Therefore, each cell dimension d_i was copied for each day that it remains in

a given development phase t_e or t_w (table 4.1). Then for each day j_i of the growing season, a mean cell dimension dj_i was found by averaging each cell that was differentiating on that day. For each tree, the reconstructions were performed on two cell parameters, cell diameter and cell wall thickness, representing the result of two development processes: t_e was used to reconstruct the cell diameter variations and t_w was used to reconstruct the cell wall thickness variations. The average daily cell dimension variation between trees was found using a spline function (TRANSREG, Smooth of 20, SAS Institute 1990) . The spline function eliminates the high-frequency oscillations in cell sizes and maintains a maximum of cell size variation caused by external conditions (Djanseitov et al. 2000).

Meteorological data

One 10 m high meteorological station was installed per site in a small forest gap. Measurements were taken every 5 minutes, hourly average were calculated and stored in a datalogger (CR10X, Cambell Scientific Corporation). The variables measured were air temperature (Tmean, Tmax and Tmin [°C]) at 3 meters, humus temperature (Thu, °C), total rain fall (P, mm), humus water content (SW, %), and global radiation (Rad, watt/m^2). SW and Tshu were measured at 10 cm depth at both sites. As the seasonal trend were removed into the cell dimension, the temperature seasonal trend was removed also to analysed only the residual (variations). The weather series was indexed for eliminating the seasonal trend by fitting a 2-order polynomial. Then, the weather residual series was smoothed by using a five-day moving average filter to removed the high-frequency variation.

Statistical analysis

Simple correlations (Pearson, $p<0.05$) were computed between weather series and reconstructed cell dimension series to assess the meteorological effect. To assess the changes in the correlation over the whole growing period, a 15-days correlation window was used and performed with Tmean, Tmax, Tmin and P. This was performed by incrementing a 15-days correlation (Pearson, $p<0.05$) by one day producing an array of coefficients indicating the changing strength of the relationship. Therefore, one correlation coefficient was found for a given date, representing the mid-point of the 15 days windows.

4.5. Results

Daily variation in cell size

Similar variations in cell dimension were found between individual trees during the growing season when performing the daily reconstruction (figures 4.3 to 4.6). For one given day of the growing season, the reconstruction represents an average cell dimension (cell diameter or cell wall thickness) of the cells that were developing on that day. The span of the reconstructed cell dimension variation begins and ends following the estimated development time t_e and t_w of the cell (table 4.2). Cell dimension reconstruction was performed by using the mean residual series found for each tree by averaging several residual series ensuring that the cell variations were the result of a common weather effect registered in the tracheids by each tree (figure 4.2).

Since cell production is higher in earlywood, cell dimension variations were made-up of a higher number of cells, resulting in a better synchronisation between the residual of the different sampling date (figure 4.2) and therefore a more similar pattern between trees when performing the reconstruction (figures 4.3 to 4.6). In latewood, the higher standard deviation of the reconstruction indicates a lower synchronisation between trees (figures 4.3 to 4.6), as a result of a poorer synchronisation of the residual selected series (figure 4.2). Regarding cell wall thickness, the residual of the last latewood tracheids were frequently over and under evaluated by the spline function (figure 4.2) and these generated a similar

pattern when performing the daily reconstruction (figures 4.3 to 4.6). Moreover, the long latewood cell wall thickening phase of more then 25 days increased this pattern.

Even if the trees did not have the same number of cells, due to different cambial activity, developing rings were synchronised in time when expressed on a daily basis (figures 4.3 to 4.6). The cell dimension variations were composed of a greater number of cells in a tree with a higher cell production and vice versa. The reconstructions of cell dimension variation for each tree were similar because the development time t_e and t_w of each cell that made up the growth-ring was considered. This was also illustrated by comparing the cell dimension variations of the adult and young trees of Lib-24 in 1999; similar patterns were observed even though the growth-rings of younger trees produced a higher number of cells (figure 4.5).

Effect of weather

Simple correlations were used to test the effect of several meteorological variables on the cell dimension reconstructions (figure 4.7). All of these variables were assumed to act directly on the reconstructed series. These correlations were computed with the entire chronology for cell radial diameter. Air temperature (Tmean, Tmax and Tmin) showed a significant positive correlation with both cell radial diameter. Correlations with cell radial diameter, for the young trees at Lib-24, were lower then the one observed for adult trees, especially in 1998 where Tmean, Tmax and Tmin were not significant. No explicit pattern of positive or negative correlations were observed with the other variables (figure 4.7).

However, for some site and years Rad and Tshu had a certain positive effect. Precipitations were regularly distributed throughout the growing season (figures 4.3 to 4.6) rendering it difficult to find any effect on radial cell diameter. Correlations were computed with earlywood only for cell wall thickness (figure 4.7). The pattern created by the reconstruction (figures 4.3 to 4.6) unables to performed correlations in latewood. For all sites and years, Tmean, Tmin and Tmax had a positive influence on cell wall thickness variations. In earlywood, temperature variations were generally well synchronised in time with those of cell wall thickness (figures 4.3 to 4.6). Unlike cell radial diameter, the positive effect of temperature on cell wall thickness for the young trees at Lib-24, were comparable as the ones observed for adult trees (figure 4.7). Rad and Tshu had a rather positive effect but correlations were not always significant. No explicit pattern of positive or negative correlations were observed with P and SW despite some strong correlation observed.

A fifteen days correlation window was used to illustrate the pattern of change in the correlation between the daily cell dimension variations and air temperatures (Tmean, Tmax and Tmin) and precipitation (figure 4.8). In earlywood, a correlation of greater significance was shown between the maximum temperature and cell radial diameter than with other temperature parameters, with June being the month where the response was higher. However, these correlations varied over time and were not always positive, especially in latewood. The first 10-15 days of the growing season also showed non-significant or negative correlations. The correlation window between cell radial diameter and

precipitation did not allow the finding of any new response than the simple correlation analysis. The correlation with precipitation is normally negative when the correlation with temperature is positive. However, some positive responses were observed for short periods in June (1999) or July (1998-2000) for the adult trees in both Lib-23 and Lib-24. For the young trees in 1998 and 1999, the correlation with precipitation was not significant during most of the period of ring development.

The correlation between temperature and cell wall thickness also varied over time. At Lib-23 for the first 20 to 25 days of wall formation, thickness was found to be more affected by minimum temperature, while mean and maximum temperature were more influential at Lib-24. However, the high correlations observed at the beginning of the wall formation decreased after 10 to 15 days until 20 to 25 days where negative correlations were observed. For the second half of the earlywood wall formation period, corresponding approximately to mid-June to mid-July, stronger correlations were observed especially with maximum temperature. For the final 10 days of earlywood and all latewood wall formation unstable correlations were generally found due to the reconstructed pattern that increased independently of the temperature variations.

4.6. Discussion

The reconstructions of the daily variations in cell dimensions reveal that short-term (i.e. weekly) weather variations can induce a change in tracheid radial diameter and in cell wall thickness. The final size of the tracheids depends on the kinetic characteristics during the season which change in fast and slow growing trees identically and simultaneously (Vaganov 1990). Despite substantial anatomical variations among different trees, including cell number, cell radial diameter and cell wall thickness, resulting from different cambial activities, the developing growth-rings showed comparable responses to meteorological effects. These responses were clearer in earlywood than in latewood where small differences in cell size were more difficult to analyse.

Meteorological effects: cell radial diameter

Throughout the growing season, temperature was the major variable influencing cell radial diameter variations. Many studies using cell analysis (Antonova and Stasova 1993, 1997) or the entire growth-ring (Schweingruber et al. 1993; D'Arrigo et al. 1992; Wang et al. 2002) also showed a positive effect of temperature on growth. Temperature regulates cambial growth by influencing many processes such as the time of seasonal initiation of division as well as the subsequent rate of the cell development. Early researchers supposed that the influence of temperature on tracheid growth was not direct (Richardson and Dinwoodie 1960; Denne 1971, 1976) and depended on growth regulator and substrate availability that influenced the rate and duration of the process. However, the primary cell

walls occupy 7-8 % of the volume of all cell biomass (Grozdits and Ifju 1984) and do not require a large substrate supply, making a fast response possible. Moreover, responses of cambial growth to temperature changes can be rather rapid, as shown by a 1-day lag effect of temperature on daily radial growth of northern oak trees (Kozlowski and Pallady 1997). Vaganov (1996) attributed the final size of tracheids to an external effect determined at the earliest stage of cell differentiation. The results of this present research show a strong daily correlation with maximum temperature, especially in June where most of the growth-ring , from 50 to 75 % depending of the year, is formed.

The daily influence of water is much more complex to identify within the tracheid radial diameter than the influence of temperature. The results of this research showed no clear correlation despite the daily relationships found between night-time precipitation and balsam fir stem radius increment as measured by a dendrometer (Deslauriers et al. 2003b). Other studies have shown that a uniform relationship is more apparent in cell diameter only for dry habitats (Vysotskaya and Vaganov 1985). In wet sites, the dependence of the growth increment upon moisture supply is more complex (Wodzicki 1971). Within the higher and lower temperature variations that result in similar cell radial diameter patterns, one or several events of precipitation occurred, possibly allowing an adequate turgor pressure for cell enlargement. However, both methods seem to be complementary. The dendrometer measurements tracked every small event of nocturnal cell enlargement of probably several cells at a time, related with precipitation, vapour pressure deficit and maximum temperature (Deslauriers et al. 2003b). Conversely, the cell radial diameter

reconstruction was undertaken with the final result of each of these events making it difficult to find a precise relationship with water. However, the variation in cell radial diameter suggests that maximum temperature is the most important parameter controlling the radial diameter of the tracheids, as long as nocturnal precipitation and vapour pressure deficit are adequate. The rapid variations observed suggest that temperature can affect cell radial diameter very early at the beginning of the cell enlargement phase (Vaganov 1996, 1990).

Meteorological effects: cell wall thickness

The correlations between the earlywood cell wall variations and temperature clearly indicate that cell wall thickness increases with rising temperature. The correlation window has showed that this relationship was more pronounced from mid-June to mid-July or until the transition zone between earlywood and latewood was reached. The increase in cell wall thickness throughout the growing season is known to be subject to developmental control rather then metabolic (Uggla et al. 2001) and is mainly influenced by the duration of the process (Deslauriers et al. 2003a; Horacek et al. 1999; Wodzicki 1971). Early researchers concluded that a rise in temperature increases the wall thickness (Denne 1971) and the rate of wall thickening (Wodzicki 1971) but also reduces its duration (Denne 1971). However, more recently Horacek et al. (1999) found also an increase in the duration of maturation with diurnal temperature.

The results of this present study show that when the seasonal trend of cell wall thickness increase is removed, wall thickness variations are positively correlated with temperature. This study has demonstrated the importance of removing the tendency when a daily relationship is performed because this could lead to an inverse relationship (Antonova and Stasova 1993, 1997). Indeed, the temperatures are generally higher during the formation of earlywood in June and July and lower in August and September during the formation of latewood. Even if the correlation could not be realised in latewood, temperature probably affects cell wall thickness as it does in earlywood. The relationship between densitometric characteristics and temperature has clearly showed that the maximum or latewood density expresses the mean summer temperature from May to September (Wang et al. 2001 2002; D'Arrigo et al. 1992; Schweingruber et al. 1993). However, the relationship found between earlywood mean density and temperature is normally weak (Wang et al. 2001, 2002). With minimum density, non significant (Wang 2001) or negative relationships in June and July (Schweingruber et al. 1993) were found because of the relatively short period when correlations are significant.

Other meteorological parameters did not show a constant relationship with cell wall thickness variation. Cell wall development depends on precipitation and radiation considerably less than on temperature as shown by the weak positive or even negative correlation obtained. Generally, precipitation is not correlated with cell wall thickness (Wodzicki 1971) although other authors have found a positive influence (Antonova and Stasova 1993). Global radiation was positively correlated in 1999 at two sites but not for

the other years. Light intensity was found to have no effect on wall thickness (Denne 1976), except for the last few cells of the latewood (Denne, 1974).

4.7. Conclusion

This investigation has shown that intra-annual studies are useful to identify the influence of weather on wood parameters. Similar variations in tracheid dimensions was revealed between different trees when their tracheidograms were expressed on a daily basis resulting from similar meteorological influences. The tree-ring width development is a rapid process in the boreal forest and the correlation between tree-ring characteristics and weather conditions should be studied during this period of formation. A strong correlation with temperature was found in June where more than half of the cell divisions and enlargements occurred. A change in temperature greatly affects the cell size, suggesting that cells size is determined by the current year's climate.

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Table 4.1. Representation of the cell reconstruction by day.

		Julian day	j_1	j_2	j_3	j_4	j_5	j_6	j_7	j_8	j_9	j_{10}
Cell	**Cell dimension**	**Mean daily cell dimension**	dj_1	dj_2	dj_3	dj_4	dj_5	dj_6	dj_7	dj_8	dj_9	dj_{10}
1	d_1		d_1	d_1	d_1							
2	d_2			d_2	d_2	d_2	d_2					
3	d_3				d_3	d_3	d_3	d_3				
4	d_4					d_4	d_4	d_4				
5	d_5						d_5	d_5	d_5	d_5		
6	d_6							d_6	d_6	d_6	d_6	
7	d_7								d_7	d_7	d_7	
8	d_8									d_8	d_8	d_8

Table 4.2. Summary of daily reconstructed cell-series for radial cell diameter and cell wall thickness.

Year	Site	Number of tree (n)	Span of reconstructed daily variation	
			Cell diameter	Wall thickness
1998	Lib-23	8	May 24 - Aug. 12	May 27 - Sep. 6
	Lib-24 young	10	May 19 - Aug. 11	May 23 - Sep. 11
1999	Lib-23	10	May 13 - Aug. 11	May 25 - Sep. 3
	Lib-24 young	9	May 10 - Aug. 22	May 12 - Sep. 12
	Lib-24 adult	10	May 12-Aug. 11	May 20-Sep. 11
2000	Lib-23	9	May 27 - Aug. 30	Jun. 2 - Sep. 26
	Lib-24 adult	8	Jun. 2 - Aug. 30	Jun. 5 - Sep. 26

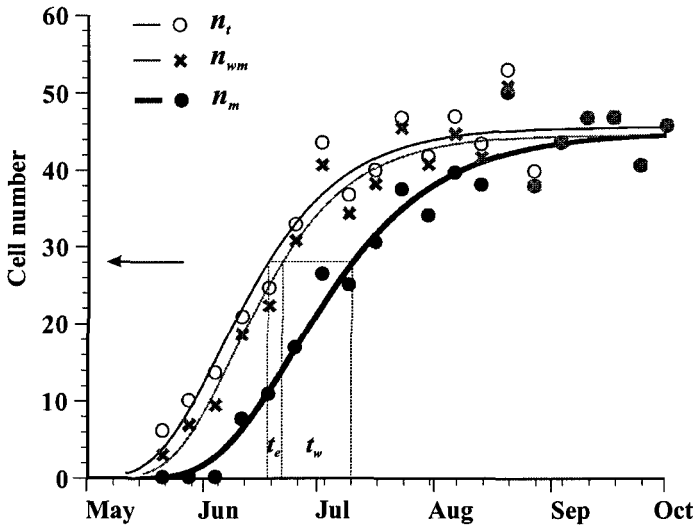

Figure 4.1. Cell number increase of one young balsam fir in 1998, n_t, n_{wm} and n_m, counted during the growing season and represented with the Gompertz equation. A schematic representation of the date of entrance and the time spent in the phases of radial cell enlargement (t_e) and cell wall thickening (t_w) is shown for cell number 28.

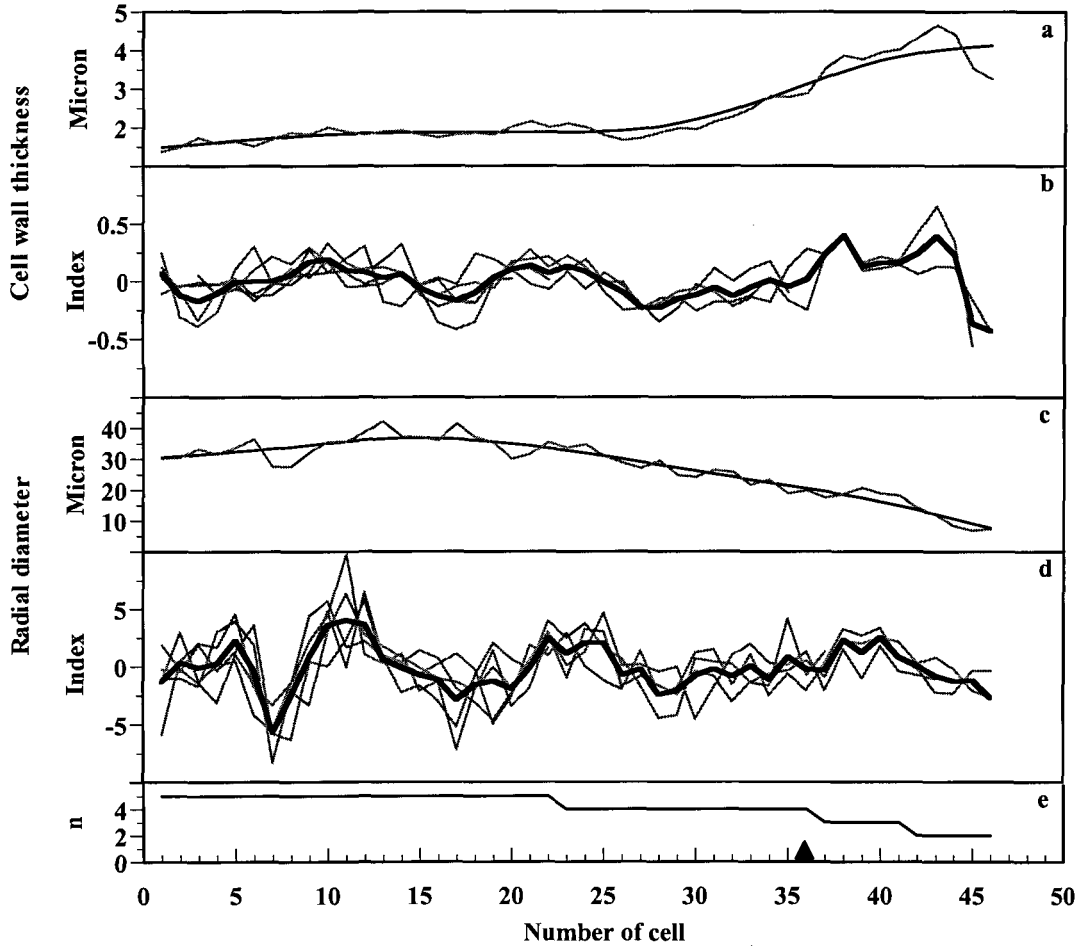

Figure 4.2. Two examples of the typical seasonal growth trend (in grey) that can be found in cell wall thickness (a) and cell radial diameter (c) that was removed by fitting smoothing splines (in black). Mean residual of cell wall thickness (b) and cell radial diameter (d) (black, thick lines) found by averaging 5 sampling date (grey, thin lines) at different positions on the stem for one young balsam fir. Samples were taken at different angle and included (e) the number: (5) July 2, 320°; (4) July 23, 2°; (3) August 13, 70°; (2) September 17, 350°; (1) October 1, 160° where North is at 0°. The triangle represents the limit between earlywood and latewood.

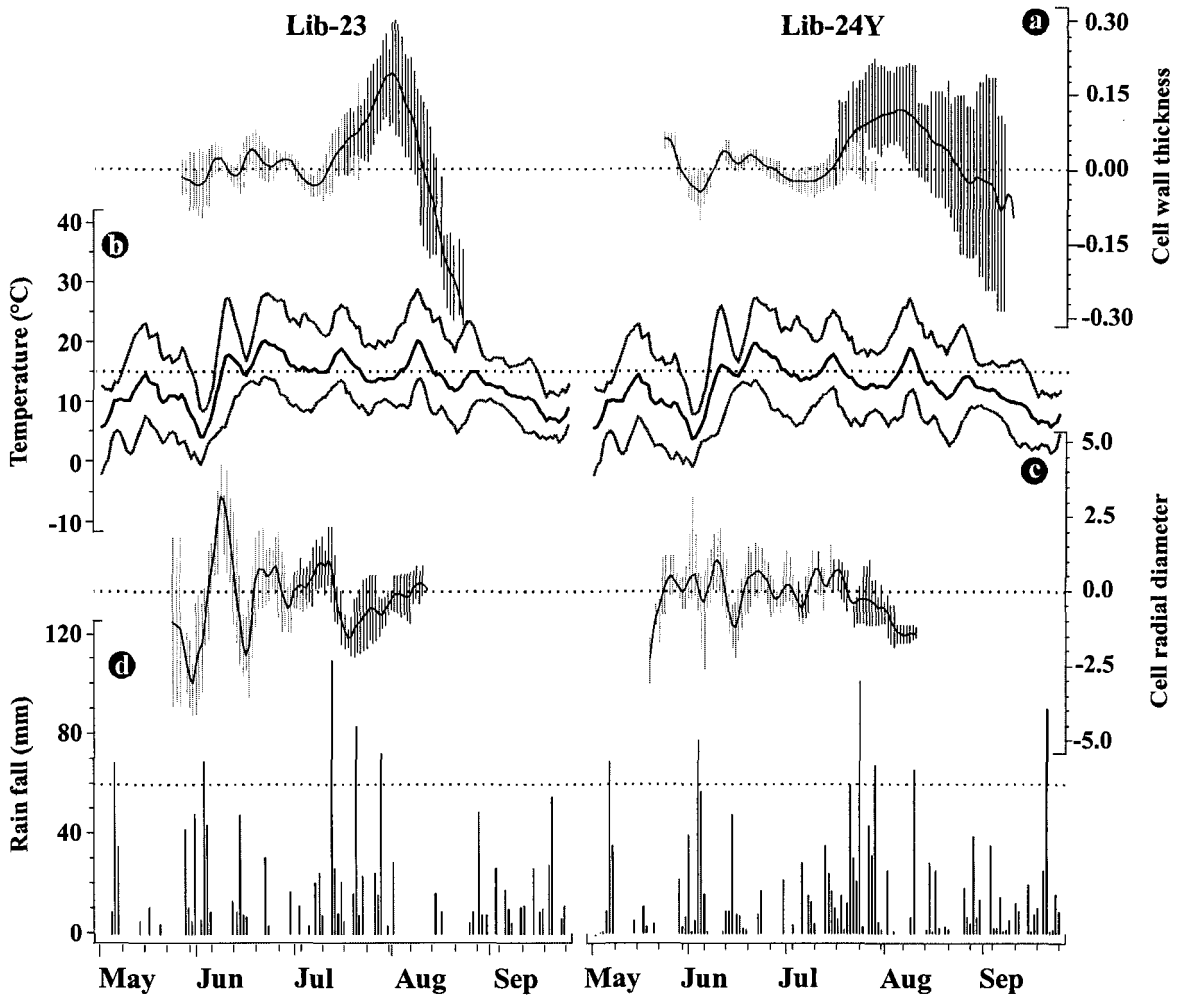

Figure 4.3. Time series of cell dimension variation, temperature and rain fall from May to October at Lib-23 and Lib-24 in 1998. **a** the daily reconstruction of cell wall thickness variation, vertical lines show the standard deviation of earlywood (grey) and latewood (black); **b** daily mean (black), minimum and maxiumum temperature (grey, °C); **c** the daily reconstruction of cell radial diameter variation, vertical lines show the standard deviation of earlywood (grey) and latewood (black); **d** daily total rain fall (mm).

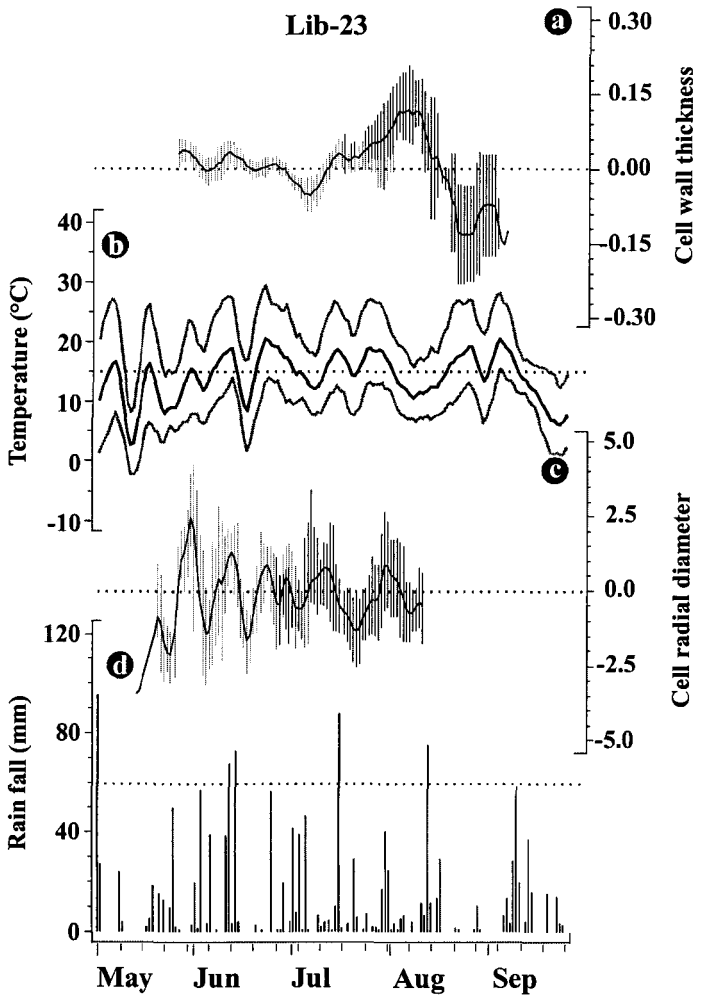

Figure 4.4. Time series of cell dimension variation, temperature and rain fall from May to October at Lib-23 in 1999. **a** the daily reconstruction of cell wall thickness variation, vertical lines show the standard deviation of earlywood (grey) and latewood (black); **b** daily mean (black), minimum and maxiumum temperature (grey, °C); **c** the daily reconstruction of cell radial diameter variation, vertical lines show the standard deviation of earlywood (grey) and latewood (black); **d** daily total rain fall (mm).

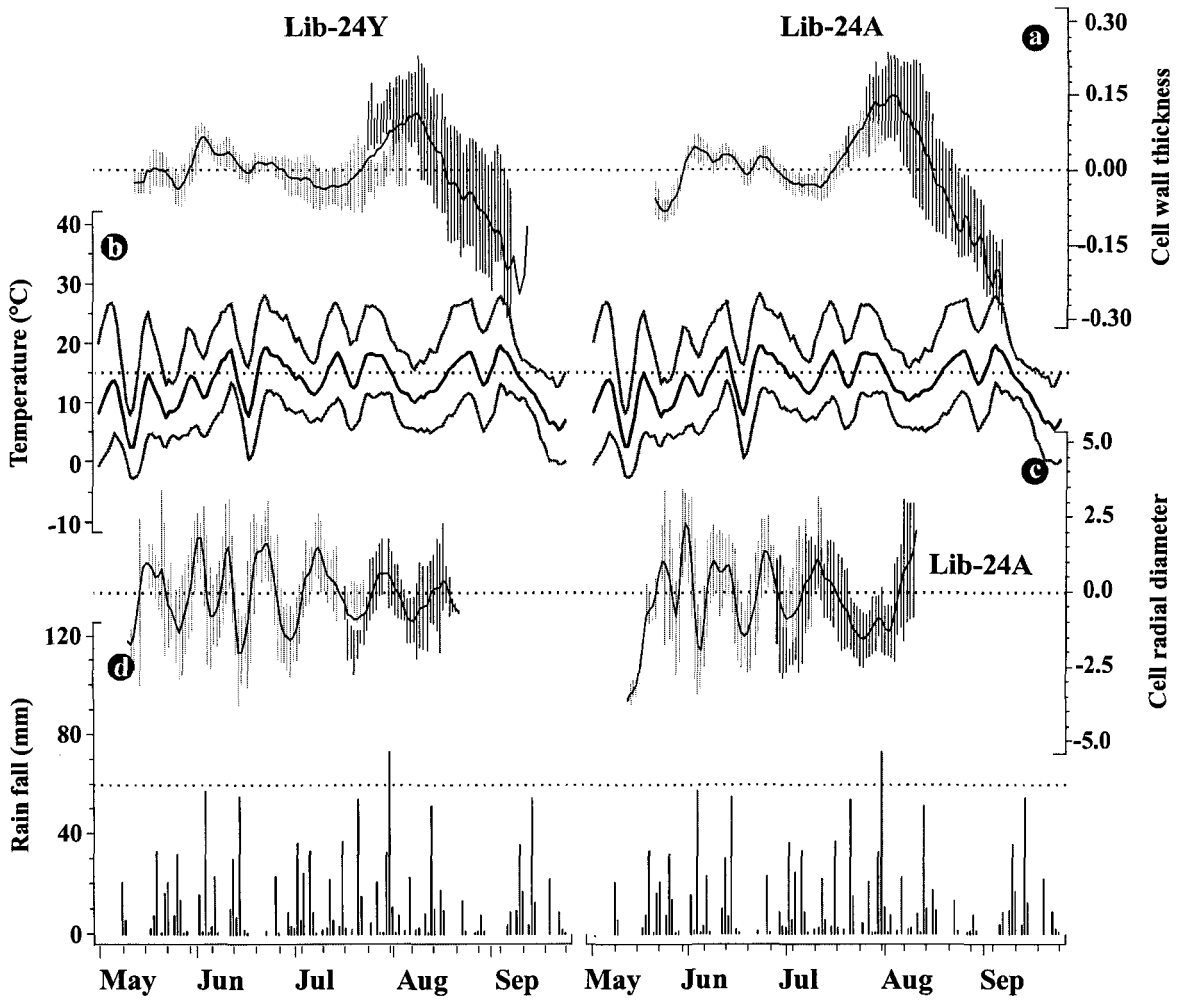

Figure 4.5. Time series of cell dimension variation, temperature and rain fall from May to October at Lib-24 in 1999 for the young and adult trees. **a** the daily reconstruction of cell wall thickness variation, vertical lines show the standard deviation of earlywood (grey) and latewood (black); **b** daily mean (black), minimum and maxiumum temperature (grey, °C); **c** the daily reconstruction of cell radial diameter variation, vertical lines show the standard deviation of earlywood (grey) and latewood (black); **d** daily total rain fall (mm).

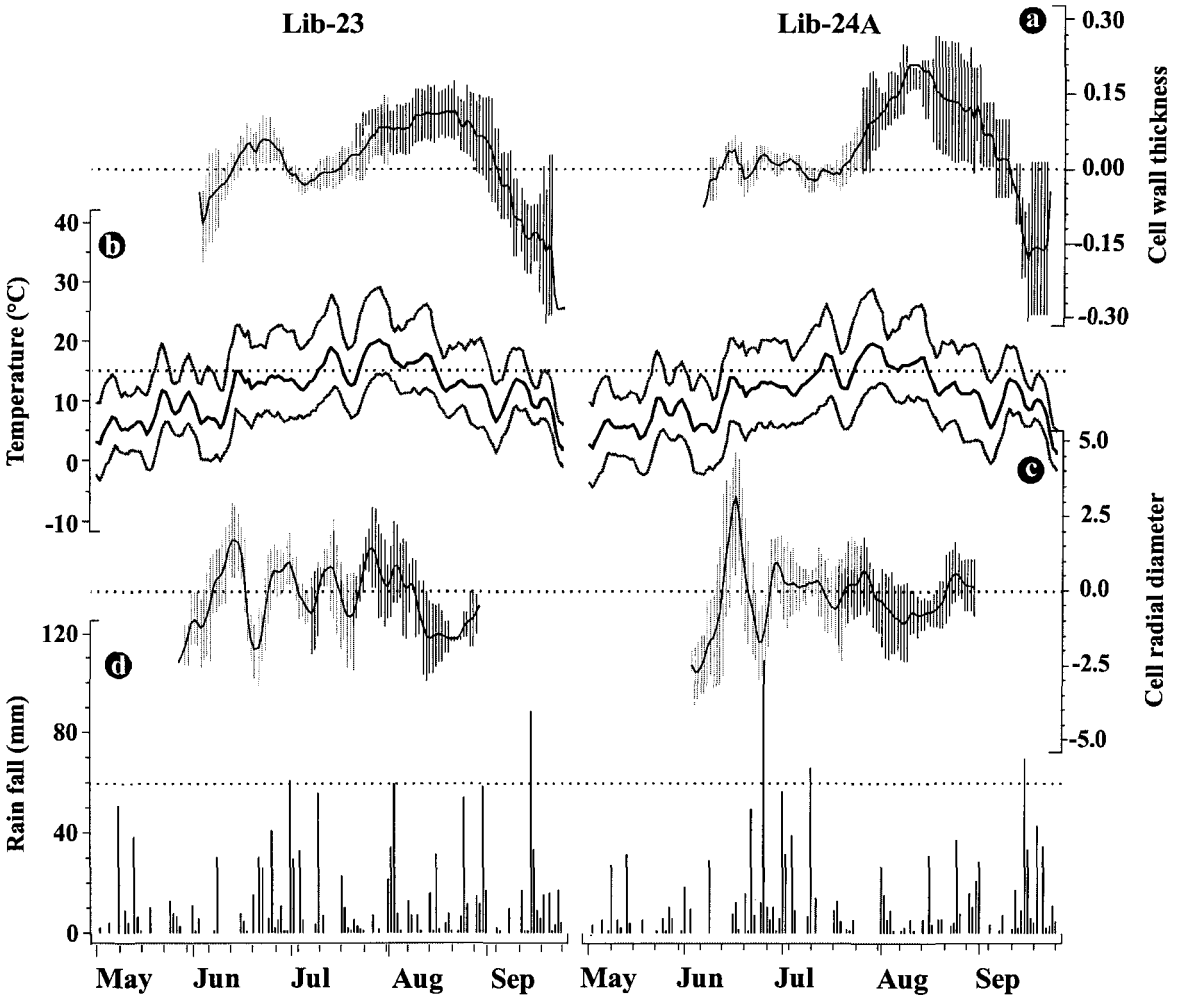

Figure 4.6. Time series of cell dimension variation, temperature and rain fall from May to October at Lib-23 and Lib-24 in 2000. **a** the daily reconstruction of cell wall thickness variation, vertical lines show the standard deviation of earlywood (grey) and latewood (black); **b** daily mean (black), minimum and maxiumum temperature (grey, °C); **c** the daily reconstruction of cell radial diameter variation, vertical lines show the standard deviation of earlywood (grey) and latewood (black); **d** daily total rain fall (mm).

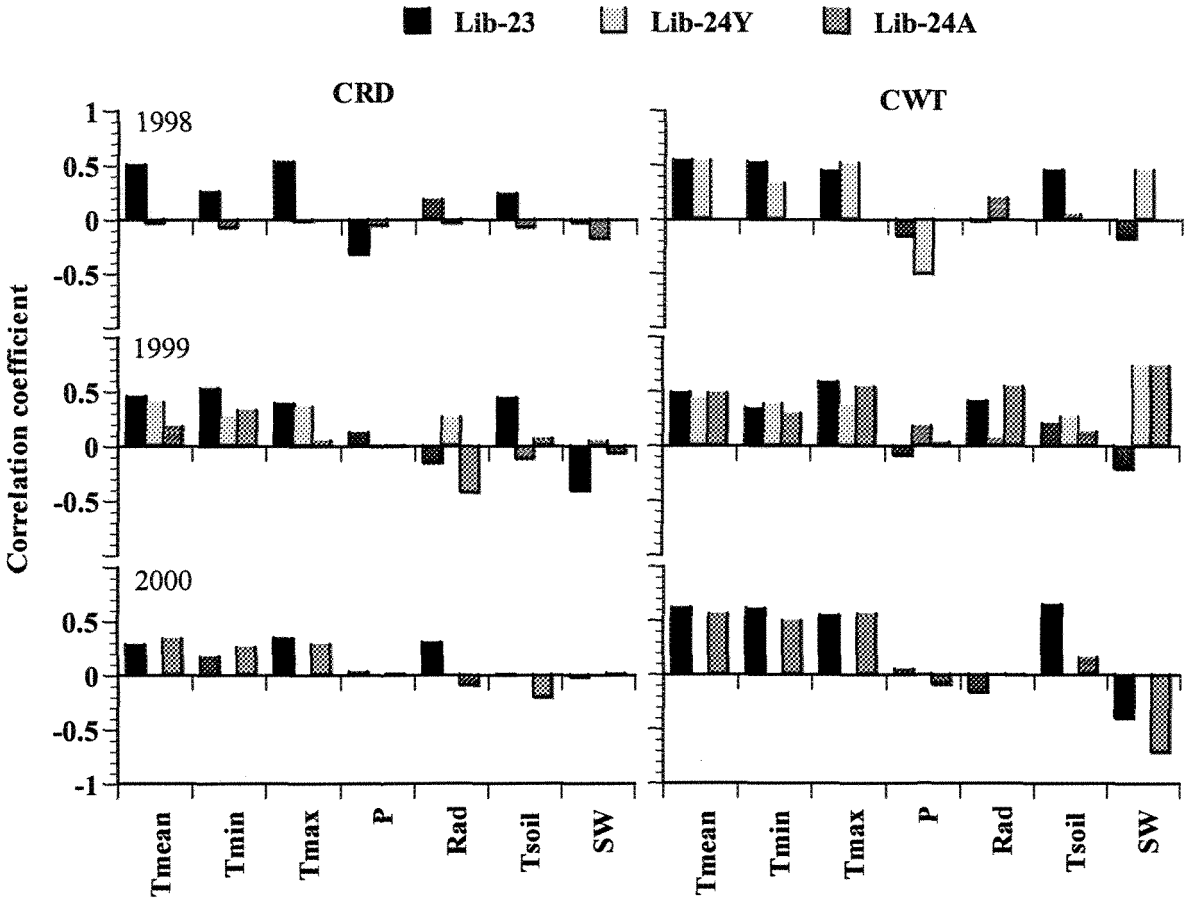

Figure 4.7. Simple correlation coefficient (Pearson $p<0,05$) between the cell radial diameter (CRD), earlywood cell wall thickness (CWT) and the weather series at Lib-23, Lib-24Y (young trees) and Lib-24A (adult trees) from 1998 to 2000. The results shown by the hatched box are not significant. Tmean=mean temperature; Tmin=minimum temperature; Tmax=maximum temperature; P=mean precipitation; Rad=global radiation; Tsoil=humus temperature; SW=soil water content.

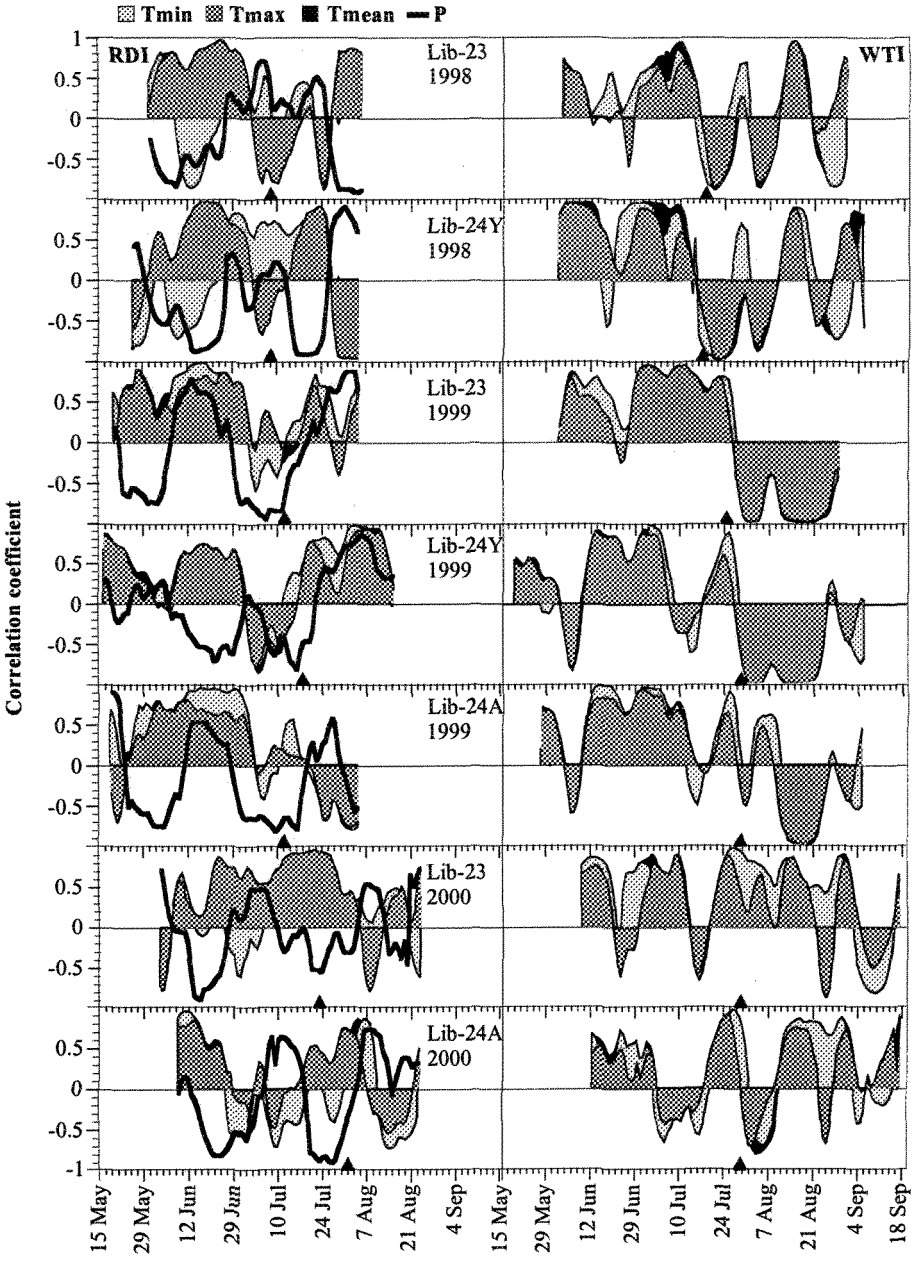

Figure 4.8. Correlation window (15 days) between radial diameter index (RDI, at left), wall thickness index (WTI, at right) and daily temperature (Tmax, Tmin and Tmean) and precipitation (P). The x-axis represents the correlation coefficient against the mid-point of the correlation windows. The correlation is significant (Pearson $p<0.05$) over the correlation coefficient of 0.52. The triangle on the x-axis represents the limit between earlywood and latewood.

CHAPITRE V

CONCLUSION GÉNÉRALE

5.1. Hypothèse et objectifs

La forêt boréale à fait l'objet de nombreuses études concernant sa croissance annuelle et son potentiel forestier. Par contre, l'analyse de la croissance intra-annuelle et la relation avec les facteurs météorologiques des principales espèces commerciales (épinette noire, sapin baumier, pin gris) n'avaient jamais été abordé. Cette thèse présente donc un étude détaillée sur le développement du cerne à l'aide de deux techniques : les analyses cellulaires et les mesures directes de la croissance radiale à l'aide des dendromètres. Ces deux techniques ont permis d'approfondir les connaissances sur le déroulement de la saison de croissance et sur les relations journalières avec les facteurs météorologiques pour le sapin baumier (*Abies balsamea* (L.) Mill.).

5.2. Évaluation du développement du cerne de croissance

Le développement du cerne de croissance a été étudié au chapitre II et III. Chez le sapin baumier en forêt boréale, le développement du cerne de croissance semble bien adapté aux conditions météorologiques qui sont variables d'une année à l'autre. Le début de la saison de croissance est largement dépendant du réchauffement des températures au mois de mai (Tmoy au-dessus de 10-15°C). La croissance débute aussitôt que les conditions de températures deviennent favorables. La saison de croissance débute alors qu'il y a très peu de degrés-jours (supérieur à 5°C) d'accumulés, soit environ un nombre de 100 (figure 5.1). Si ce réchauffement est précoce ou plus tardif, il en sera de même pour le début de l'activité des méristèmes. Le développement du cerne dépend principalement des taux de division (i.e. pente de la courbe logistique, figure 5.1) car le nombre totale de cellules est

sensiblement le même d'année en année et pré-déterminé à 80-90% par les conditions des années précédente (Vaganov 1990). Par exemple, lorsque les saisons de croissance 1998-2000 sont comparées au Lib-23 pratiquement la même quantité de cellules ont été formées avec un taux de croissance élevé sur un courte période ou avec un taux de croissance plus lent sur une plus longue période (figure 5.1). Au chapitre II, un taux de 0.59 cellule/jour pour 62 jours de croissance et correspondant la plus courte saison de croissance a été observé au Lib-23 en 1998. En 1999 et 2000, le nombre de cellule formé par jour était inférieur pour une plus longue saison de croissance. Ces résultats suggèrent donc que la dynamique de formation du cerne varie avec la dynamique des températures saisonnière. Les processus de division et d'élargissement des cellules de bois initial (60-75 % du cerne) se déroulent principalement durant le mois de juin.

L'extraction de l'accroissement journalier mesuré par les dendromètres est une technique plus directe pour suivre l'évolution de l'élargissement du cerne de croissance. Par opposition avec les analyses cellulaires où les cellules sont mesurées lorsqu'elles sont matures et dont les temps de développement doivent être estimés, les analyses effectuées avec les dendromètres fournissent des estimations journalières plus précises. En effet, l'accroissement journalier a été défini comme équivalent à l'élargissement des cellules en développement du xylème et du phloème plus un facteur « d'erreur hydrique ». Ce facteur hydrique, dû aux mouvements de contraction et d'expansion du tronc et de l'écorce (Kozlowski et al. 1991; Zweifel et al. 2000), peut dans certain cas augmenter ou diminuer l'évaluation de l'accroissement journalier. La saison de croissance doit être connue pour

utiliser les dendromètres comme outil d'estimation de l'accroissement journalier. En effet, à mesure que les températures augmentent au printemps et que l'humus dégèle, le tronc et l'écorce se réhydratent produisant un signal en tout point comparable à celui enregistré durant la saison de croissance. Le début de l'extraction doit donc être déterminé à l'aide de l'étude des cellules pour ne pas introduire dans les analyses des accroissements attribuables à la réhydratation des tissus.

Une comparaison entre les deux techniques de mesures journalières a été réalisée au chapitre III. En 1998 et 2001, le cumul de l'accroissement radial mesuré par les dendromètres était équivalent à celui mesuré avec les analyses cellulaires. Par contre en 1999 et 2000, le cumul de l'accroissement était supérieur à celui des analyses cellulaires. En 1999 et 2000, l'erreur hydrique introduite dans les extractions journalière de l'accroissement a été supérieure à celles de 1998 et 2001. Même si la croissance cellulaire a été évaluée dans le détail, il est très difficile de quantifier et d'expliquer cette erreur sans des analyses du flux hydrique au niveau de l'écorce. C'est en fait au niveau du phloème et du cambium que se produisent 90% des mouvements de contraction et d'expansion enregistrés par les dendromètres (Zweifel et al. 2000). Par contre, plus la croissance cellulaire est lente (division et élargissement), plus une fraction importante de l'accroissement peut-être attribuée aux variations hydriques. Le lent et long début de la croissance en 1999 pourrait expliquer les différences observées entre l'extraction de l'accroissement et les mesures cellulaires.

Malgré des taux de croissance différent, les arbres ont réagi de manière synchrone aux événements météorologiques. Par exemple, les accroissements enregistrés par les dendromètres au chapitre III étaient synchrones dans le temps, seule l'amplitude différait entre les arbres. Les amplitudes des accroissements étaient généralement plus élevées chez les arbres formant un plus grand nombre de cellules, démontrant que l'événement météorologique affecte un plus grand nombre de cellules à la fois. Au chapitre IV, les reconstructions journalières de la variation des dimensions cellulaires ont aussi montré un synchronisme dans le développement des trachéides entre les arbres, seules les amplitudes variaient. Par exemple, une élévation de la température de l'air a produit une augmentation du diamètre des cellules. Cette augmentation affectait un plus grand nombre de trachéides chez un arbre ayant une activité cambiale supérieure car plus de cellules se trouvaient alors au stade d'élargissement.

5.3. Effet des variables météorologiques

Les résultats des chapitres III et IV ont montré que le développement du cerne de croissance (élargissement des cellules et formation des parois cellulaires) est affecté par les conditions météorologiques journalières. Les conditions météorologiques auraient donc un effet direct et mesurable sur la dimension des trachéides (figure 5.2). L'effet direct des conditions météorologiques est plus marqué sur le diamètre des cellules qui réagit plus rapidement que l'épaisseur des parois cellulaire. Il aurait été difficile de conclure à un effet direct sans avoir observé des variations synchrones entre les arbres. En effet, une réaction empruntant le chemin indirect (figure 5.2) pourrait plus difficilement produire une réaction

synchrone entre les arbres, ces derniers ayant des taux d'activités métaboliques, de production et d'allocation des ressources différents. Par contre, une réaction directe implique nécessairement que les ressources ne soient pas à un niveau qui pourrait limiter la croissance mesurable.

Au chapitre III les résultats des corrélations et des fonctions de réponse ont démontré que l'accroissement radial journalier mesuré par les dendromètres est relié aux conditions nocturnes de la température maximale, de la précipitation et du déficit de pression de vapeur. Ces conditions influencent surtout l'aspect mécanique de la croissance soit l'élargissement radial des cellules (Ray 1987). Les aspects biochimiques et métaboliques, c'est-à-dire la formation des parois primaires, le contrôle génétique et hormonale, jouant aussi un rôle important dans les processus d'élargissement cellulaire (Savidge 2001), peuvent être influencé différemment. Une compréhension globale de la formation du bois est importante dans l'interprétation de ces résultats car les modèles établis au chapitre III ne mènent pas à une conception complète de l'impact météorologique sur l'activité cambiale.

Au chapitre IV, la formation du cerne de croissance a été reconstruite pour chacune des phases de développement (élargissement des cellules et formation des parois secondaires) sur une base journalière et des corrélations ont été effectuées avec les différentes séries météorologiques. Ces reconstructions représentaient pour une certaine journée, la dimension cellulaire moyenne (diamètre cellulaire ou épaisseur des parois) formée durant cette journée. Les résultats ont montré que la température maximum est le facteur le plus

important influençant le diamètre des cellules pendant la formation du bois initial, soit principalement durant le mois de juin. Pendant la formation du bois final soit durant le mois de juillet et août, les corrélations avec la température sont généralement moins fortes. La température s'est aussi révélée importante pour la variation de l'épaisseur des parois cellulaires. Des corrélations positives ont été observées dans le bois initial de la mi-juin à la mi-juillet. Pour le bois final, les reconstructions journalières présentaient un patron ne permettant pas les analyses.

Au chapitre IV aucune relation significative n'a pu être identifiée entre les précipitations journalières et la dimension radiale des cellules. Par contre, au chapitre III, l'accroissement mesuré par les dendromètres était fortement relié avec les précipitations durant les phases 2-3-4 du cycle diurne. Même si les deux techniques en arrivent à des résultats différents concernant les précipitations elles ne sont pas contradictoires mais bien complémentaires.

En effet, les dendromètres fournissent une mesure de l'accroissement journalier de plusieurs cellules à la fois, c'est-à-dire de celles qui se trouvent dans les zones d'élargissement du xylème (figure 5.3, en B-2) ou du phloème. Un accroissement donné ne correspond pas nécessairement au diamètre d'une cellule mais représente la somme des accroissements simultanés de plusieurs cellules. De plus, la fraction de l'accroissement fournie par chacune des cellules n'est pas la même. L'accroissement des premières cellules situées près de la zone cambiale, est supérieure à celui des cellules situées à la fin de la zone d'élargissement (figure 5.3, en B-1 et B-2). Les résultats au chapitre III ont

permis de connaître et de comprendre les facteurs météorologiques qui affectent les séquences d'élargissement permettant aux cellules d'accomplir cette phase. Par opposition, la reconstruction journalière de la variation du diamètre des cellules a été effectuée à l'aide de la mesure finale des cellules, lorsque ces dernières sont matures (figure 5.3, en B-3). Les séquences d'élargissement qui ont permis à une cellule donnée d'en arriver à son diamètre final ne peuvent donc pas être reconstituées. Les corrélations avec la précipitation sont donc plus difficiles à mettre en évidence parce qu'elles sont importantes dans la phase d'élargissement peut importe le diamètre des trachéides. Par contre, les variations observées dans les diamètres des trachéides du bois initial, semblent reliées aux variations de température.

Les variations rapides et synchrones du diamètre des cellules, reliées principalement avec la température maximale, pourraient démontrer un signal météorologique affectant le taux de développement subséquent des trachéides. Selon Vaganov (1996), ce signal serait enregistré par la nouvelle cellule en développement dans sa transition entre le cambium et la zone d'élargissement (figure 5.3, en B1). La température au début du cycle de différentiation affecterait le taux de croissance métabolique des cellules (Vaganov 1996, Ray 1987). Même si les conditions nocturnes de précipitations, de la température maximum et du déficit de pression de vapeur peuvent tout de même modifier le signal, la température en tout début de phase semblerait déterminante dans la dimension finale de la cellule.

5.4. Implications des résultats

Déroulement de la saison de croissance et relation climat-croissance

Les résultats des chapitres II à IV ont permis de connaître la phénologie du développement du cerne de croissance, nécessaire à l'interprétation de l'effet des variables météorologiques. Désormais dans les régions boréales, les mois d'août et septembre de l'année en cours ne devraient plus être considérés dans les analyses dendroclimatologiques de la largeur du cerne de croissance. Les corrélations trouvées durant ces périodes sont sans signification pour la largeur du cerne. Durant ces mois, seulement quelques cellules de bois final peuvent être formées. Les conditions météorologiques moyennes sur toute la longueur de la saison de croissance (mi-mai à fin juillet) ne devraient plus être considérées car la majorité du cerne est formé tôt et dans des périodes variables selon les années. Seul les conditions météorologiques du mois de juin reflètent mieux le nombre de cellule et la largeur du bois initial.

Même si les degrés-jours sont utilisés pour prédire la croissance des arbres (Ministère des Ressources naturelles 2000) ils ne représentent pas un bon outil de prédiction en forêt boréale. Par exemple, dans sont rapport sur la limite nordique des forêts attribuables, le Ministère des Ressources naturelles (2000) dresse une carte représentant les « degrés-jours de croissance » où la majorité du territoire situé entre le 48^{e}-52^{e} parallèle accumule plus de 640 degrés-jours de croissance, limite fixée par le ministère. Par contre, la formation du cerne, la croissance du sapin baumier au 49^{e} parallèle s'effectue en grande majorité en juin

avec moins de 700 degrés-jours et le nombre de cellules maximum est atteint avec moins de 900 degrés-jours (figure 5.1). À court terme, une accumulation totale supérieure de degrés-jours durant une saison de croissance ne correspond pas non plus à un nombre supérieur de cellules (figure 5.1) car ce dernier est largement pré-déterminé (Vaganov 1990). Des analyses doivent être effectuées dans le but de trouver une relation valable entre le nombre de cellules formées et la température.

Outil de prédiction

Les modèles de fonctions de réponse élaborés au chapitre III pourraient éventuellement servir à une reconstruction de l'accroissement journalier. La reconstruction de l'intervalle de confiance des modèles effectuée à l'aide de la commande « *FILIBR* » (PPPBase, version 9905.1, Guiot and Goeury 1996) est présentée à la figure 5.3 et 5.4 et démontre le potentiel de reconstruction de l'accroissement. Ces figures illustrent la variation de l'accroissement dans le temps (en noir) avec la variation du 5^e et du 95^e percentile du modèle (en gris) et démontrent l'ajustement des modèles générés par les fonctions de réponse. Plus la variation du 5^e et du 95^e percentile suit la variation de l'accroissement, plus le modèle de la fonction de réponse l'explique bien. Selon les figures 5.4 et 5.5, les modèles expliquent mieux l'accroissement lorsque des amplitudes entre 50 et 150 µm sont enregistrées par les dendromètres. Par contre, l'accroissement est moins bien modélisé pour des valeurs inférieures ou supérieures à 50 et 150 µm. Comme les résultats les plus significatifs ont été obtenus avec les variables de précipitation des phases 2-3-4 du cycle diurne (P2-P3-P4), les valeurs de P4 sont illustrées afin de visualiser l'effet de la pluie sur l'accroissement.

Ces résultats démontrent en fait le potentiel des variables météorologiques utilisées dans les fonctions de réponse pour une reconstruction de l'accroissement journalier dans des sites où l'on voudrait connaître l'accroissement des arbres. Par contre, avant de modéliser l'accroissement, plusieurs ajustements aux modèles sont nécessaires. Premièrement, afin d'améliorer l'extraction de l'accroissement, il serait nécessaire de comprendre la part des variations hydriques journalières pour être en mesure de la soustraire des analyses. Cela se traduit par l'étude du flux hydrique au niveau de l'écorce et de son effet sur les phases de contraction et d'expansion ainsi, que la relation entre le flux hydrique et les variables météorologiques.

5.5. Références

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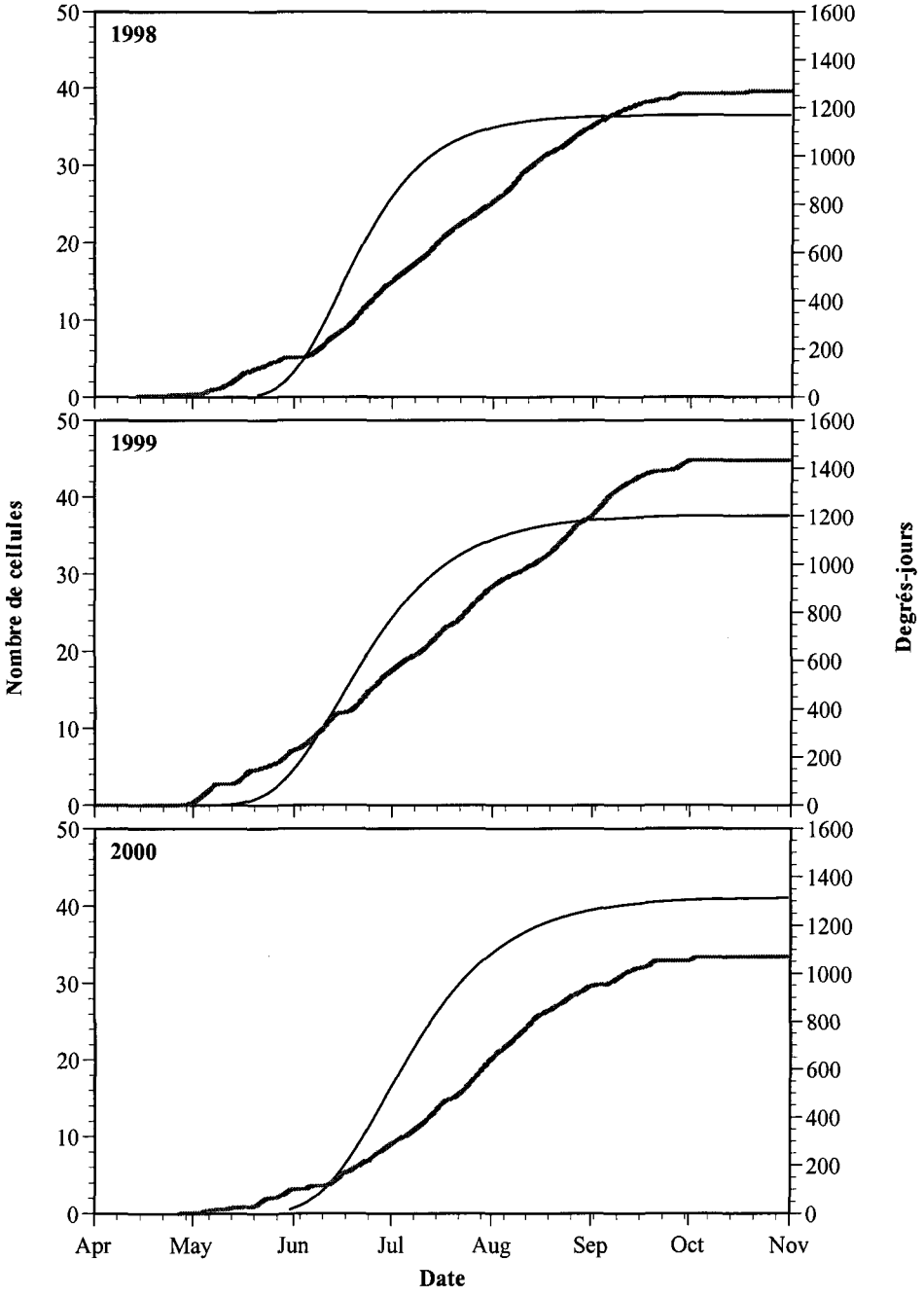

Figure 5.1. Formation du nombre de cellule durant les saisons de croissance 1998 à 2000 (en noir) au site Lib23 et nombre de degrées-jours cumulés (5°C) (en gris).

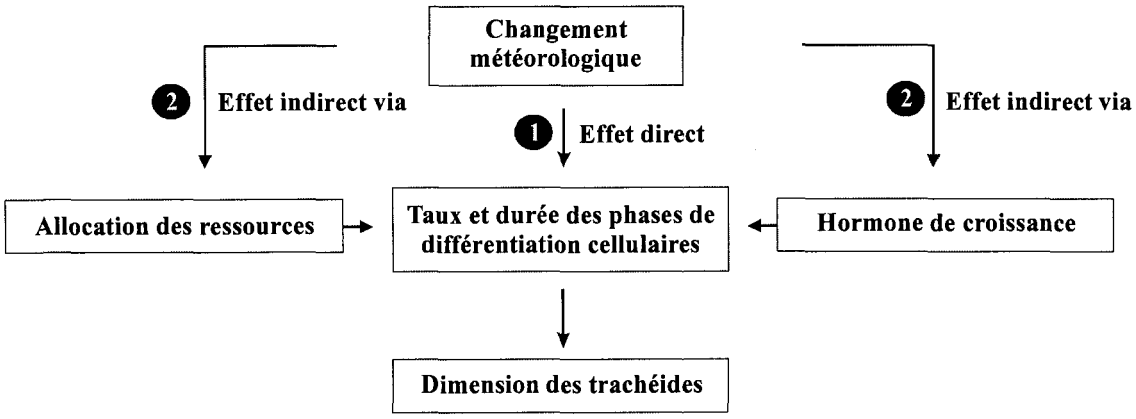

Figure 5.2. Schéma générale simplifié de l'influence d'un changement météorologique quelconque sur la différentiation des cellules du xylème (Vaganov, 1996).

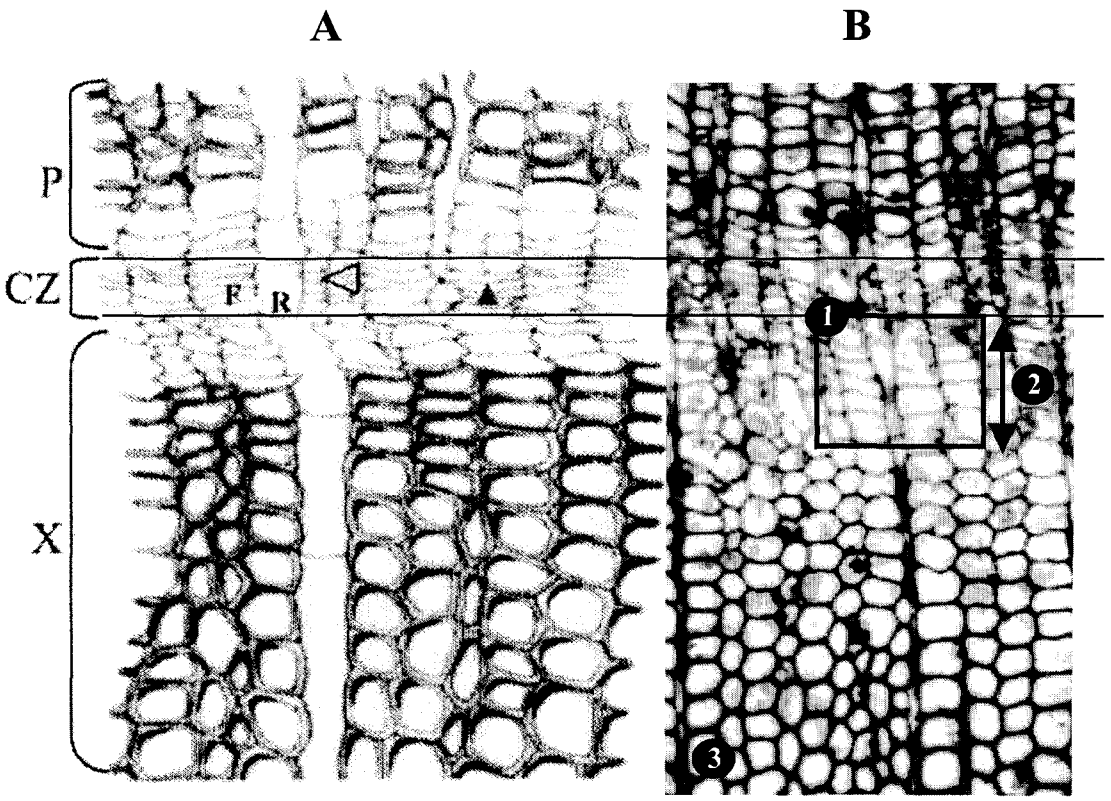

Figure 5.3. Schéma théorique (A, selon Plomion et al. 2001) et observé (B, *Larix decidua*) du cerne de croissance en formation. En A : CZ, zone cambiale ; P, phloème ; X, xylème. En B : 1, transition entre la zone cambiale et la zone de cellules en phase d'élargissement ; 2, zone de cellules en phase d'élargissement ; 3, cellules matures.

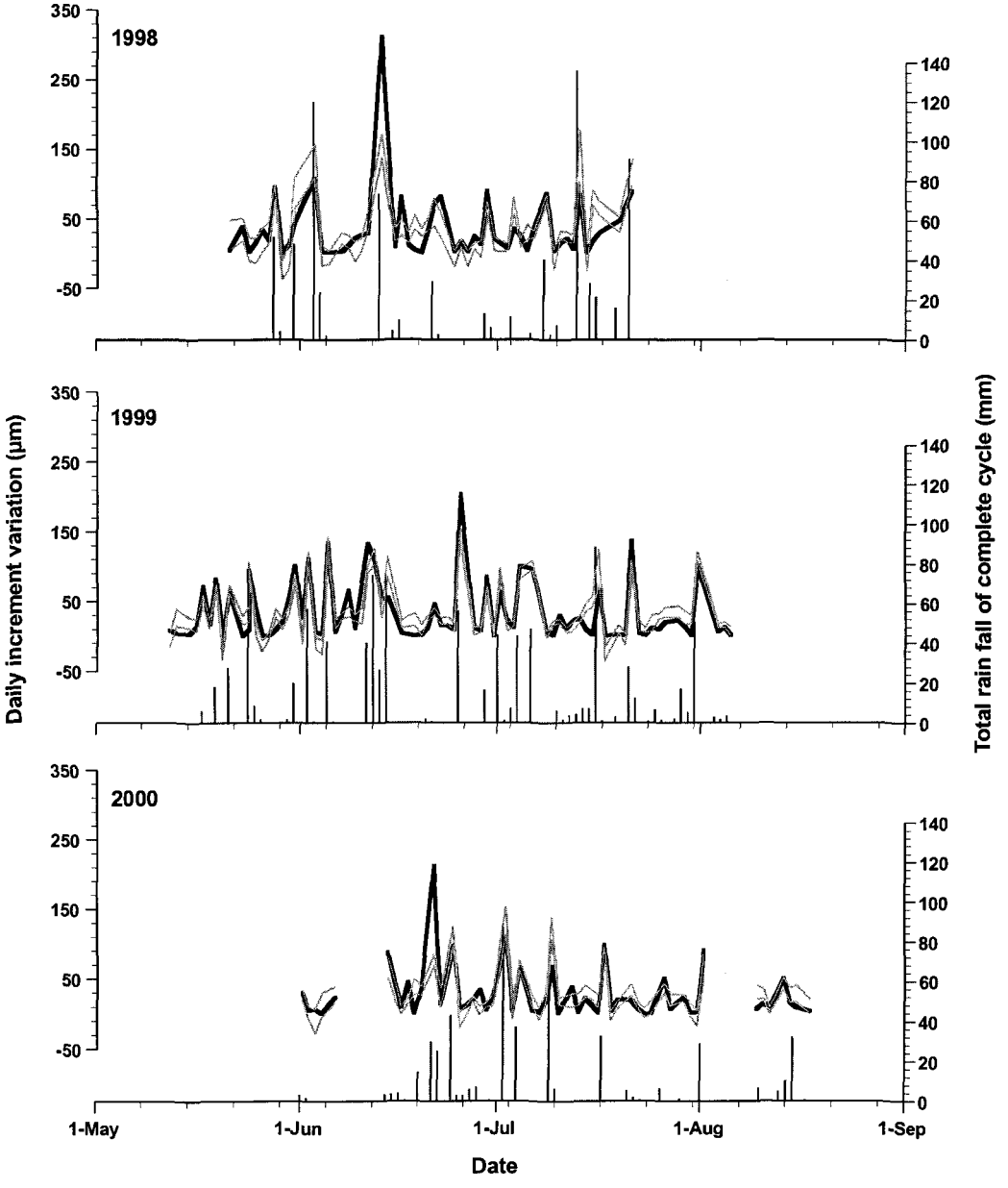

Figure 5.4. Variation de l'accroissement mesuré à l'aide des dendromètres durant la saison (en noir) et reconstruction de l'accroissement (5^{e} et du 95^{e} percentile, en gris), à l'aide des modèles de fonctions de réponse au site Lib-23. La précipitation totale durant le cycle P4 est aussi illustrée.

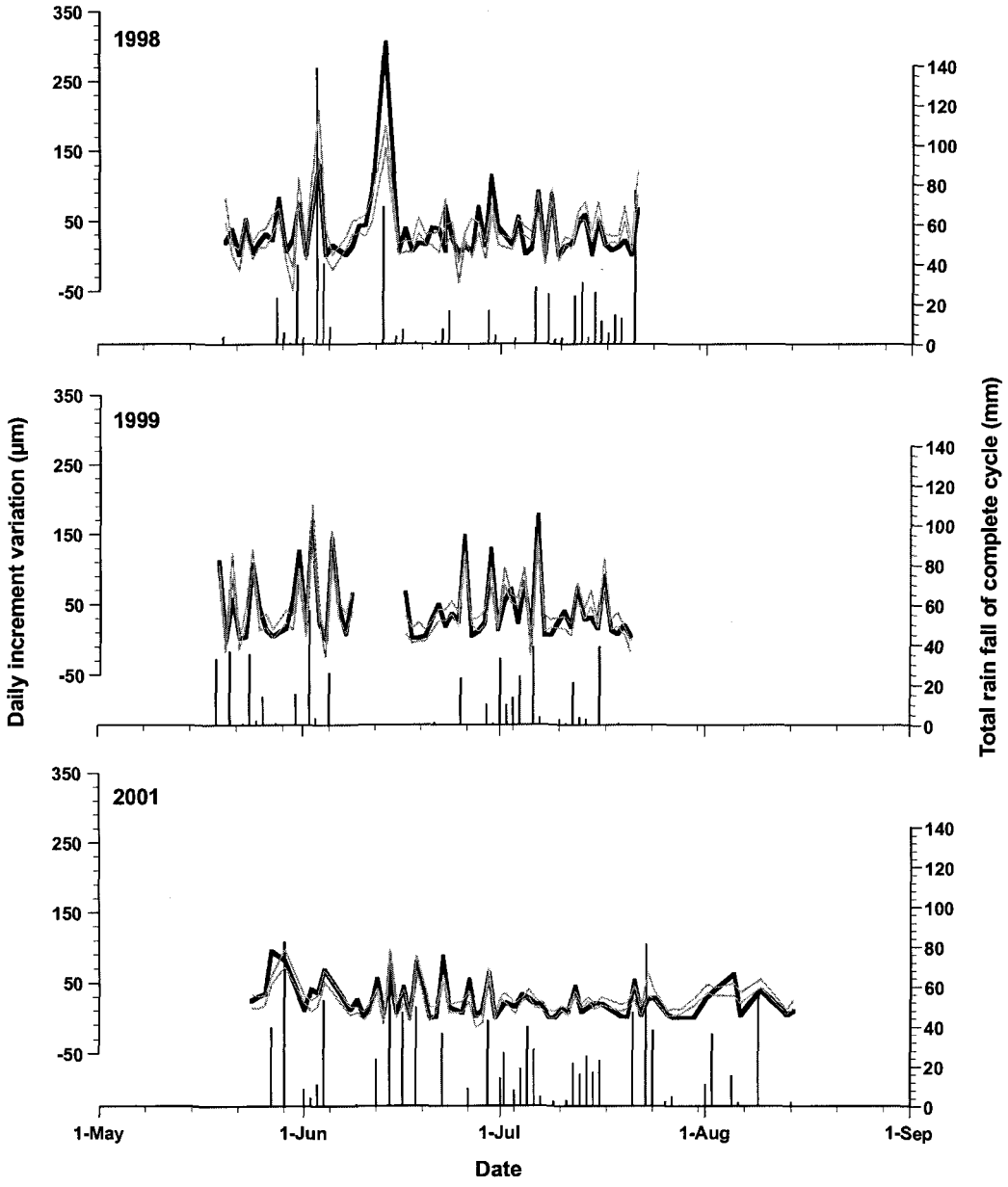

Figure 5.5. Variation de l'accroissement mesuré à l'aide des dendromètres durant la saison (en noir) et reconstruction de l'accroissement (5^{e} et du 95^{e} percentile, en gris), à l'aide des modèles de fonctions de réponse au site Lib-24. La précipitation totale durant le cycle P4 est aussi illustrée.